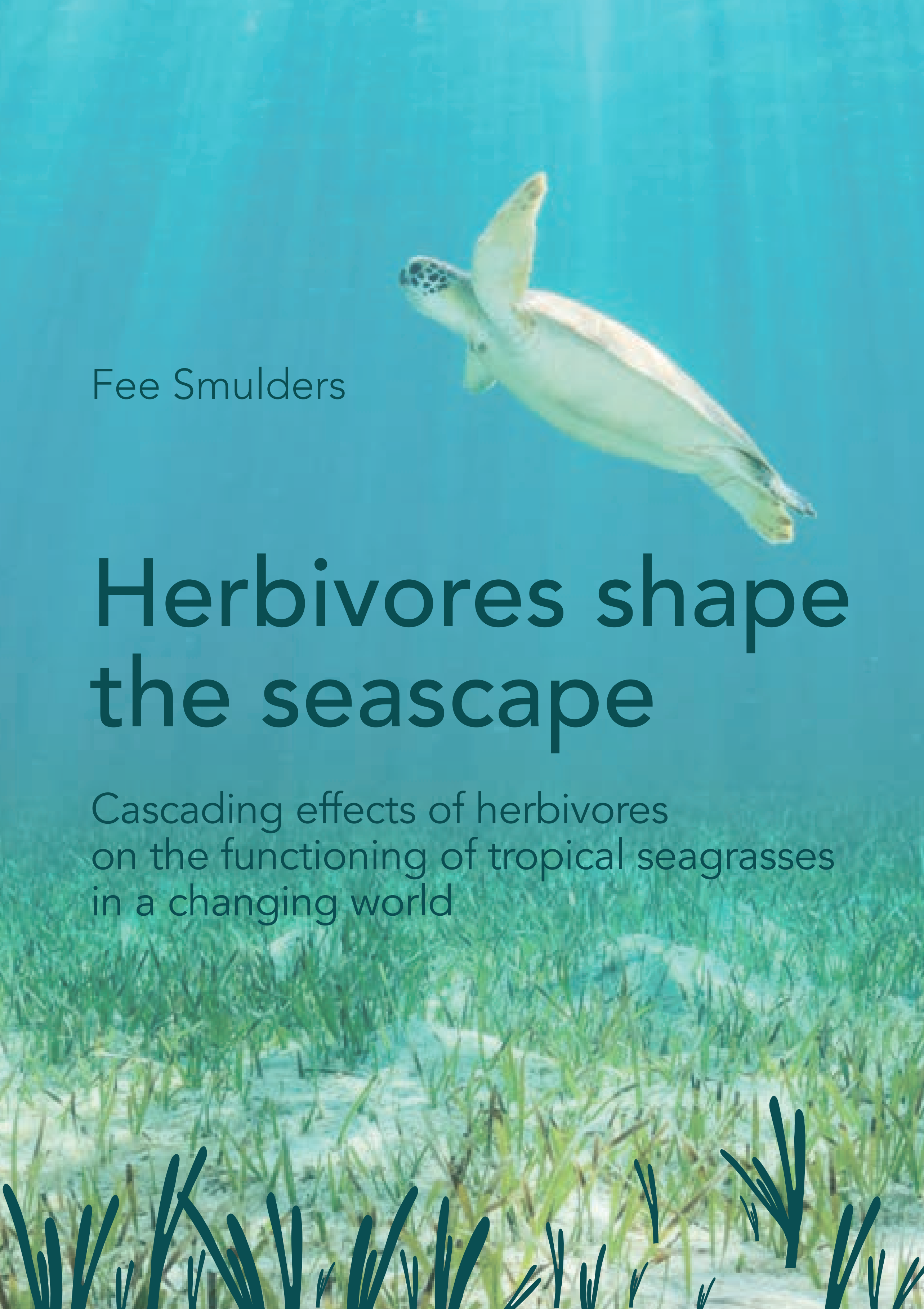

Fee Smulders

Herbivores shape the seascape

Cascading effects of herbivores on the functioning of tropical seagrasses in a changing world

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Voor Lena

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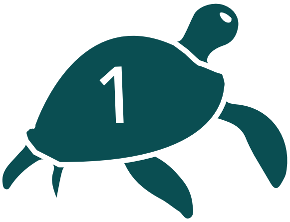
CHAPTER 1



General introduction

1.1 THE SHAPE OF NATURAL LANDSCAPES

Try to visualize the wide array of natural landscapes our world has to offer, such as tropical forests, peatlands, and savannas. What do these landscapes have in common? They are all built by primary producers that convert light energy into green biomass. The species composition and form of these landscapes are initially determined by abiotic factors such as light input, nutrients, temperature and water. Apart from these factors, there is a major role to be played by herbivores. Grazers remove plant biomass thereby shaping the landscape via their grazing preferences and predators can cause variation in grazing pressure by hunting for herbivore prey. In the Anthropocene, mankind has had its own impact in impacting the landscape, both directly and indirectly, for instance through global warming. Knowledge on how herbivores continue to shape these green ecosystems in a changing world is urgently needed, because they may form part of the solution in building resilient ecosystems. Unbeknownst to some, green landscapes in all their complexity also occur beneath the sea level, where incredibly rich ecosystems exist that are made up by marine plants.

1.2 SEAGRASS ECOSYSTEMS

Seagrass ecosystems are among the most productive ecosystems worldwide (Fourqurean et al. 2012). They are built by seagrasses: marine angiosperms with the ability to live and reproduce completely submerged in salt water (Den Hartog 1970). Seagrasses form an ecological group of about 70 species which occur along the temperate and tropical coastlines of the world (Short et al. 2007), and create extensive meadows with aboveground shoots, connected and anchored belowground via rhizomes. Seagrasses are ecosystem engineers that modify their physical and chemical environment, controlling the availability of resources and creating habitats for herbivores, predators and other organisms (Bouma et al., 2009; Gutiérrez et al., 2011; Jones et al., 1994).

Seagrasses provide a range of ecosystem services such as coastal protection, carbon storage and biodiversity (Nordlund et al. 2016). Therefore, advancing knowledge on the impact of various stressors on ecosystem functioning is crucial in maintaining high ecosystem value. The seagrass canopy and rhizomes stabilise the sediment and reduce wave energy and therefore serve as coastal protection (Bouma et al. 2005, Koch et al. 2006, Christianen et al. 2013). The dampening of waves by above- and belowground biomass additionally leads to sediment deposition, and reduced resuspension, resulting in stable sediment with reduced turbidity (Christianen et al. 2013, Potouroglou et al. 2017, Infantes et al. 2022). The presence of seagrass therefore enhances its own growth due to increased light availability (van der Heide et al. 2007, Suykerbuyk et al. 2016). Additionally, although seagrass meadows cover only 0.2% of the ocean floor, they are estimated to store about 10% of the yearly estimated organic carbon buried in the ocean because of their high productivity (Fourqurean et al. 2012). Lastly, a large diversity of adult organisms uses seagrass habitats as a habitat and as a food source (Vonk et al. 2008). Seagrass, together with mangroves, provides a nursery for coral fish and a large variety of other organisms (Nagelkerken et al. 2000, Heck et al. 2003). A substantial part of these organisms are economically valuable for us and therefore seagrasses support fisheries production worldwide (Unsworth et al. 2018). Seagrass is also the primary food source for some (shell)fish species and urchins as well as megaherbivores such as the endangered green turtle (*Chelonia mydas*) and the dugong (*Dugong dugong*) (Bjorndal 1980, Mortimer 1981, Preen 1995, Heck and Valentine 2006). The variation in ecosystem services between and within seagrass species is largely unknown (Nordlund et al. 2017). Currently, there is a need to determine the impact of multiple stressors such as invasive species, defaunation and climate warming on the resilience and ecosystem functioning of valuable seagrass meadows.

Seagrasses, like many other coastal ecosystems, are under increasing pressure from anthropogenic stressors, resulting in a global loss of about 19% of surveyed seagrass area worldwide since 1880 (Dunic et al. 2021, Unsworth et al. 2022b). A recent global overview identified poor water quality and coastal development as the most common drivers of seagrass decline (Dunic et al. 2021). An excess of nutrients in the water due to increased coastal run-off can result in a bloom of opportunistic (epiphytic) algae (Tomasko and Lapointe 1991, Li et al. 2014). These algae block the light for the seagrass, causing them to rely on their rhizomal carbon storage. Eventually, lack of photosynthesis can cause decline and mortality of the seagrass meadow (Sand-Jensen 1977, Tomasko et al. 1996, Gacia et al. 1999, Hughes et al. 2004). Additionally, the increasing frequency and intensity of heatwave events associated with global warming has been reported to damage seagrass meadows (Marbà and Duarte 2010, Serrano et al. 2021). Lastly, herbivore populations that extend their range due to warming oceans can enhance the grazing pressure on poleward seagrass meadows, termed *tropicalization* (Vergés et al. 2014a, Heck et al. 2015). High grazing pressure is generally compensated by high seagrass productivity in the tropics (Hyndes et al. 2016, Vergés et al. 2018). Effects of range-shifting herbivores on subtropical or temperate seagrass meadows, where light limits productivity in winter, is therefore expected to be severe (Fourqurean et al. 2010, Hyndes et al. 2016). Research to date has not yet determined the combined effect of these global-warming related stressors on the resilience of (sub)tropical seagrass meadows. Furthermore, both the arrival of non-native species and increasing populations of large grazers can potentially disrupt the ecological equilibria in seagrass ecosystems (Fig. 1.1).

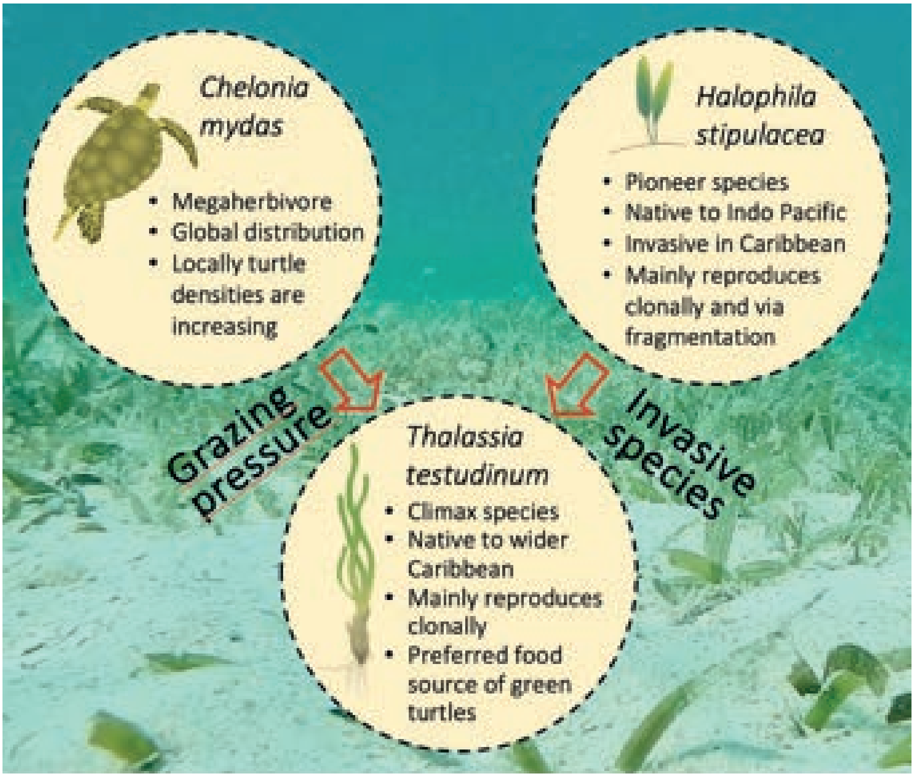


Figure 1.1 Key players in this thesis. Background image: *T. testudinum* meadow cropped by sea turtles and invaded by *H. stipulacea*. Photo by F. Smulders.

1.3 THE RESPONSE OF NATIVE SPECIES TO INVASIVE SEAGRASS EXPANSION

Human activities, such as trade by cross-continental transportation, tourism and aquaculture, can facilitate the invasion of exotic marine species into new habitats where they may impact native species dynamics (Ruiz et al. 2000, Williams 2007, Anderson et al. 2015). The rate at which marine species are invading outside their native range is increasing (Ruiz et al. 2000, Williams 2007). The effects of these species on the native community can vary from a severe decline to an increase in biodiversity and ecosystem value (Rodriguez 2006, Molnar et al. 2008). Exotic species are termed invasive when they have negative ecological or economic impacts. Characteristics of successful macroalgae invaders are: rapid growth, fragment generation and propagation (Williams and Smith 2007). Most of the global seaweed introductions have negatively affected native community structure (Williams and Smith 2007). For seaweeds, herbivores have been shown to sometimes eat invaders, but are unlikely to control them and can sometimes even facilitate invader spread (Williams and Smith 2007). This is in contrast to a meta-analysis on terrestrial and freshwater invasion studies, which showed that large herbivores often provide biotic resistance to plant invasions (Parker et al. 2006, Williams and Smith 2007). Often, invasive species benefit from disturbance events that negatively impact native foundation species (Piazzi and Ceccherelli 2006, Williams and Smith 2007). For example, experimental disturbance by overgrazing of *Posidonia oceanica* leaves increased the establishment and spread of the invasive *Caulerpa racemosa* (Tamburello et al. 2014). Invasive macroalgae are much more abundant and well-studied than invasive seagrass (Williams 2007, Williams and Smith 2007). However, to date, two seagrass species have become abundant outside their native range: *Zostera japonica* and the tropical species *Halophila stipulacea*.

Halophila stipulacea originates from the Red Sea and the western Indian Ocean, settled in the Caribbean in 2002 and has since been termed invasive (Winters et al. 2020). Already around 1850 this species spread from the Indo-Pacific to the Mediterranean Sea due to the opening of the Suez Canal (Lipkin 1975). The success was attributed to rapid vegetative expansion, high salinity tolerance, irradiance and great depths (Lipkin 1975, Cooke et al. 2017). In the Mediterranean, little negative effects have been reported of the introduction of *H. stipulacea* on the native seagrass meadows or its functions

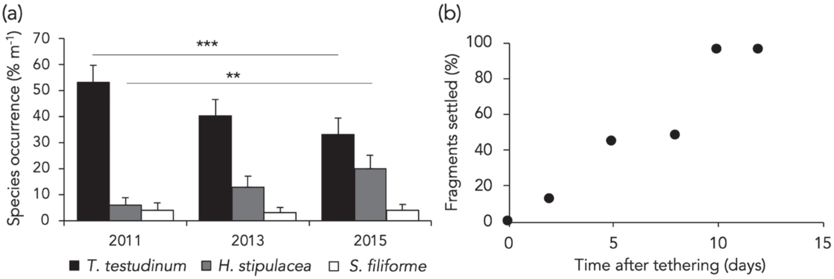
(Winters et al. 2020), and the species was even shown to increase carbon storage in some areas compared to pre-invasion (Wesselmann et al. 2021b). In 2002 a 300m^2 monoculture of *H. stipulacea* was discovered on the Caribbean coast of Grenada, from where it colonised bays in Dominica, Saint Lucia, Bonaire, Guadeloupe and currently is present in at least 19 islands in the Eastern Caribbean (Ruiz and Ballantine 2004, Winters et al. 2020). In a study investigating the reports on reproductive organs, we found that female flowers and seeds are still absent in its Caribbean range (Smulders et al. 2020). Therefore, the species is assumed to spread mainly via fragments created by anchors, grazing and waves, transported by boats and currents (Ruiz and Ballantine 2004, Willette et al. 2014). In previous work we found that these vegetative fragments of *H. stipulacea* remained viable and quickly settled and grew new shoots at a rate of 1.9 shoot per day (Box 1.1, Smulders et al. 2017). The fast expansion thus far and predicted under future global warming scenarios will likely result in further spread of *H. stipulacea* to the Western and Northern Caribbean (Wesselmann et al. 2021a).

The continuous expansion of *H. stipulacea* in the Eastern Caribbean disrupts an equilibrium in which the native *Thalassia testudinum* or *Syringodium filiforme* often dominate the seagrass meadows (Willette et al. 2014). Reports from Dominica show that *H. stipulacea* has been displacing native *S. filiforme* and *Halodule wrightii* seagrass meadows (Willette and Ambrose 2012, Steiner and Willette 2015a, Willette et al. 2020). It is currently unknown whether the invasive species is actively competing with native species for similar resources or if it mainly spreads by benefitting from disturbance and filling up newly available niches. Additionally, because *H. stipulacea* is a fast-growing pioneer species, nutrient enrichment may enhance invasion success. However, direct testing of the nutrient enhancement hypothesis has been limited (Chisholm et al. 1997, Williams and Smith 2007).

The expansion of *H. stipulacea* and the reduction of native seagrass species might modify the value of critical seagrass ecosystem functions (Viana et al. 2019b). In Dominica, *H. stipulacea* supported equal or even higher abundances of different trophic groups compared to the native seagrass (Willette and Ambrose 2012). However, when comparing *T. testudinum* with *H. stipulacea* meadows on Bonaire, the abundance and composition of fish were significantly lower in *H. stipulacea* meadows (Becking et al. 2014). Similarly, fish family diversity was lower in *H. stipulacea* meadows than in native meadows composed of *S. filiforme* and *T. testudinum* on the US Virgin Islands (Olinger et al. 2017). Although *Halophila stipulacea* meadows were found to provide a more nutrient-limited environment compared to *T. testudinum*, significant herbivory was observed (Muthukrishnan et al. 2020).

Box 1.1 Expansion and fragment settlement of the invasive seagrass *Halophila stipulacea*

The non-native seagrass *Halophila stipulacea* has spread throughout the Eastern Caribbean since 2002 and could impact the functioning of local seagrass ecosystems. In an observational study combined with a field experiment, important characteristics for invasiveness such as settlement and expansion rates were studied. Using 49 fixed locations throughout Lac Bay, Bonaire, we found that from 2011 to 2015, the occurrence of *H. stipulacea* increased significantly from 6 to 20 % while the native *T. testudinum* declined from 53 to 33 % (Fig. a). Free-floating fragments of *H. stipulacea* were found to root within 10 days with a 100% success rate (Fig. b), and grow with an average of 0.9 shoots per day.



Given the fast expansion of *H. stipulacea* throughout the bay, likely accelerated by its ability to recruit new areas by fragmentation and subsequent settlement and growth of these fragments, it is important to study the impacts of this invasive species on native species and ecosystem functioning.

Expansion and fragment settlement of the non-native seagrass Halophila stipulacea in a Caribbean bay. F.O.H. Smulders, J.A Vonk, M.S. Engel & M.J.A. Christianen, Marine Biology Research, 2017.

The native Caribbean herbivore community may either provide biotic resistance by consuming *H. stipulacea* or release it from herbivory pressure by consuming only native seagrass. Previously, we provided evidence that the green turtle *Chelonia mydas,* a megaherbivore known to consume substantial parts of seagrass production (Fig. 1.2a), prefers native *T. testudinum*, thereby facilitating the spread of the invasive *H. stipulacea* (Box 1.2, Christianen et al. 2019). The preference of native seagrass species over the invasive *H. stipulacea* has since been confirmed by two other studies (Whitman et al. 2019, Siegwalt et al. 2022). Smaller grazers, such as fish and invertebrates, can also consume a substantial part of the seagrass production (Fig. 1.2b). However, compared to large herbivores, they often have little impact on seagrass density (Kirsch et al. 2002b, Heck and Valentine 2006), with some exceptions reporting large-scale seagrass grazing by mesograzers (Kirsch et al. 2002a). Both herbivore density and herbivore species richness has been shown to be critical factors in understanding the magnitude of herbivore-induced changes in aquatic plants (Wood et al. 2017). Therefore, smaller herbivores should not be left out of experiments and analyses. Very little is currently known whether other native herbivores – apart from the green turtle - may provide biotic resistance by consuming the invasive seagrass, or how other (in)fauna will respond to this invader and if they might have an impact on invasion success.

1.4 THE ROLE OF LARGE GRAZERS IN SHAPING SEAGRASS ECOSYSTEMS

Herbivory in both freshwater and marine ecosystems has long been regarded as almost negligible (Bakker et al. 2016b). Since the 1990s, substantial primary research has been done providing evidence that herbivores not only consume a substantial amount of biomass in aquatic systems (40-48% compared to 4-8% in terrestrial systems) but also are critical drivers of benthic ecosystems (Turcotte et al. 2014, Bakker et al. 2016b, Wood et al. 2017). Submerged aquatic plants generally have a higher nitrogen content and are therefore more palatable than emergent and terrestrial plants, because they need fewer structural components (Bakker et al. 2016b). The scientific evidence on herbivory in aquatic systems is increasing, and it is widely accepted that herbivores can induce significant changes in plant dynamics with (in)direct effects on ecosystem functioning (Bakker et al. 2016b, Valentine and Heck 2021).

Large seagrass herbivores have been abundant throughout most of the evolutionary history of seagrasses (Heck and Valentine 2006). Especially in the tropics, green turtles and marine mammals depended on a considerable amount of seagrass production for their daily nutrition (Domning 2001, Heck and Valentine 2006, Esteban et al. 2020). These megaherbivores prevented climax species from dominating seagrass ecosystems,

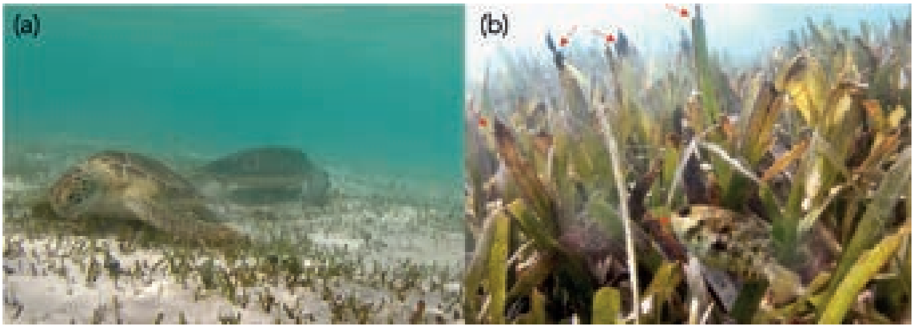


Figure 1.2 Differential impact of mega and mesoherbivores. (A) The green turtle, a megaherbivore, can crop the seagrass short and maintain grazing patches. (B) Mesoherbivores, such as the parrotfish *Sparisoma radians* in the photo, generally leave crescent shaped bite marks in tall-canopy seagrass leaves. Photos by F. Smulders

and promoted diversity (Domning 2001). A stable apex-predator community likely controlled their prey population (Heithaus et al. 2008a). Because of this grazing pressure, seagrasses developed many traits comparable to terrestrial grass that are considered grazer-derived adaptations, such as clonal reproduction, fast regeneration and branching rhizomes (Valentine and Heck 1999). However, over the last hundreds of years, humans have significantly reduced the amount and diversity of herbivores and their predators in coastal waters when industrial fishing took off (Raup et al. 1982, Domning 2001, McCauley et al. 2015). Large animals such as megaherbivores and apex predators have been the first to go functionally extinct (Jackson et al. 2001, Estes et al. 2011). Therefore, the role of grazing became relatively small compared to historical conditions, and the energy pathway became predominantly detritus-based (Domning 2001, Jackson et al. 2001).

In the last decades, the tide has turned as we witness an increase in green turtle populations in several regions due to successful conservation measures (Chaloupka et al. 2008, Lal et al. 2010, Weber et al. 2014). Therefore, some seagrass meadows are being transformed to their natural grazed state (Christianen 2021). Green turtles and dugongs often maintain grazing plots of seagrass, as they prefer to consume young, nutritious leaves (Preen 1995, Hernández and Van Tussenbroek 2014, Gulick et al. 2021). Moderate turtle grazing has been found to have both an ecophysiological effect by increasing leaf productivity and nutrient content, and a morphological effect by decreasing leaf length, width and overall canopy structure (Moran and Bjorndal

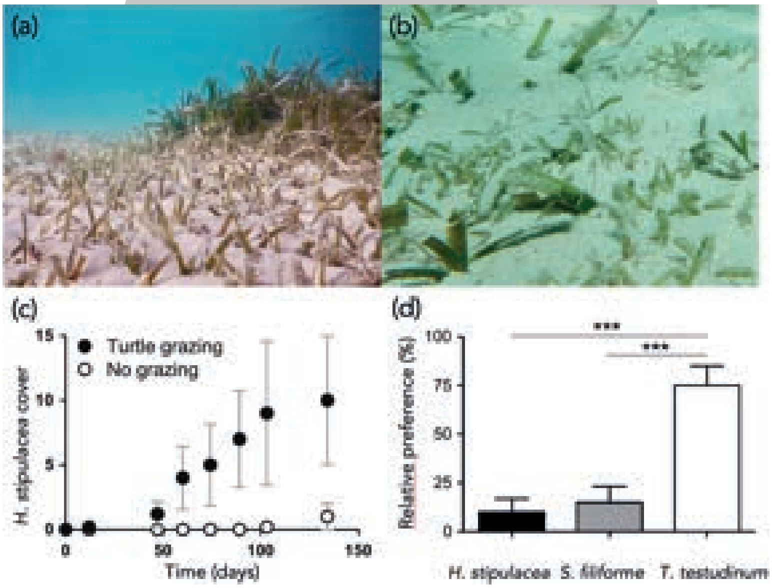
2005, 2007, Gulick et al. 2020). Turtle grazing can additionally impact seagrass species composition (Box 1.2, Christianen et al. 2019), whereby intensive grazing has been reported to cause a shift from climax species to pioneer species (Kelkar et al. 2013, López et al. 2019). Although there is an increase in research on the grazing behavior and impact of green turtles on seagrass at the small scale, there is still uncertainty about the factors that determine their spatial and temporal behavioral strategies within their foraging habitat and how this is impacted by human activity or the presence of predators.

Recent increases in turtle populations have led to localized overgrazing of seagrass meadows (Fourqurean et al. 2019, Rodriguez and Heck 2021). Intensive grazing in combination with other human-induced stressors can risk the collapse of seagrass meadows (Christianen et al. 2014, Gangal et al. 2021). In addition, the large-scale absence of turtle predators, likely resulted in a loss of non-consumptive fear effects, which caused a relative increase in herbivory pressure on the seagrass ecosystem (Heithaus et al., 2014). Predator presence can create landscapes of fear still visible in e.g. Western Australia, where dugongs prefer to forage in lower-quality meadows with low predation risk from tiger sharks (Wirsing et al. 2007c, Burkepile 2013). However, due to large-scale absence of predators, the impact of such a marine landscape of fear on megaherbivore (grazing) behavior and ecosystem functioning remains unknown. The presence or absence of both predators and herbivores in a system is expected to have a great impact on ecosystem functioning and the services the seagrass meadows provide (Bakker et al. 2016a, Scott et al. 2018). Often ecosystem services are measured separately; For example, intensively grazed meadows were shown to harbour lower invertebrate (Johnson et al. 2020b) and fish (Inoue et al. 2021) abundance and have a lower coastal protection function (James et al. 2020) compared to ungrazed meadows. As green turtle populations are rising, there is an urgent need to study the impact of megaherbivore grazing is on ecosystem functioning as a whole, by combining the assessment of multiple ecosystem services within one system.

Box 1.2 Green sea turtles facilitate the expansion of invasive seagrass

Herbivores may contribute to the expansion success of invasive plant species by their grazing behavior. To investigate the role of green sea turtles in the expansion of the invasive seagrass *Halophila stipulacea*, we looked at sea turtle grazing preference, movement patterns and grazing impact within an invaded seagrass bay on Bonaire.

We found that sea turtles prefer native seagrass: since the arrival of the invasive species, the turtles initiated new grazing patches in previously ungrazed native *T. testudinum* seagrass areas (Fig. a), and the locations of GPS transmitters fitted on sea turtles confirmed high site fidelity to these newly cropped patches. Additionally, a turtle exclosure experiment showed that the invasive seagrass had higher expansion rates with turtle grazing present (Fig. d), compared to inside the exclosures (Fig. c). The preference of sea turtles for native seagrass was confirmed in food choice experiments (Fig. d).



Green turtles likely modify the rate and spatial extent of the invasive seagrass expansion, by preferring native seagrass and thereby increasing the settlement space for *H. stipulacea* in between cropped shoots (Fig. b). Large herbivores can therefore play an important role in plant invasions of aquatic ecosystems.

Megaherbivores may impact expansion of invasive seagrass in the Caribbean.
M.J.A. Christianen, F.O.H. Smulders, M.S. Engel, M.I. Nava, S. Willis, A.O. Debrot, P.J. Palsbøll, J.A. Vonk, L.E. Becking, Journal of Ecology, 2019.

1.5 OBJECTIVES AND AIM OF THIS THESIS

In this thesis, I investigate the impact of fish herbivores and of green sea turtles – marine megaherbivores with increasing populations – on the resilience and ecosystem services of (invaded) tropical seagrass meadows (Fig. 1.3). This will increase our understanding how valuable Caribbean seagrass meadows, dominated by the climax species *Thalassia testudinum*, respond to changing ecological dynamics within their ecosystem. It is currently unknown how the arrival of an exotic seagrass species and the increase in both green sea turtle populations and human-induced stressors will change the form and functioning of these seagrass meadows.

Specifically, I describe how the invasion of an exotic seagrass impacts the native seagrass ecosystem community (**Chapter 2, 3**), and how megaherbivores can shape the seascape and determine ecosystem multifunctionality (**Chapter 4, 5, 6**). Lastly, I explore the resilience of native seagrass species to future global-warming related drivers (**Chapter 7**), and discuss the findings of this thesis, formulating new knowledge gaps (**Chapter 8**).

I expect that native herbivores may either provide biotic resistance or facilitate the invasive plant by avoiding it as a food source, while other infauna that disturb the native ecosystem may benefit fast-growing invasive species. Rising numbers of megaherbivores will likely negatively impact seagrass ecosystem multifunctionality, while natural or anthropogenic top-down actors such as tourists or predators may have an impact in shaping seagrass meadows through cascading grazing effects. Lastly, I expect that tropical seagrass resilience is mainly driven by light and nutrient availability, and that herbivory may limit seagrass resilience.

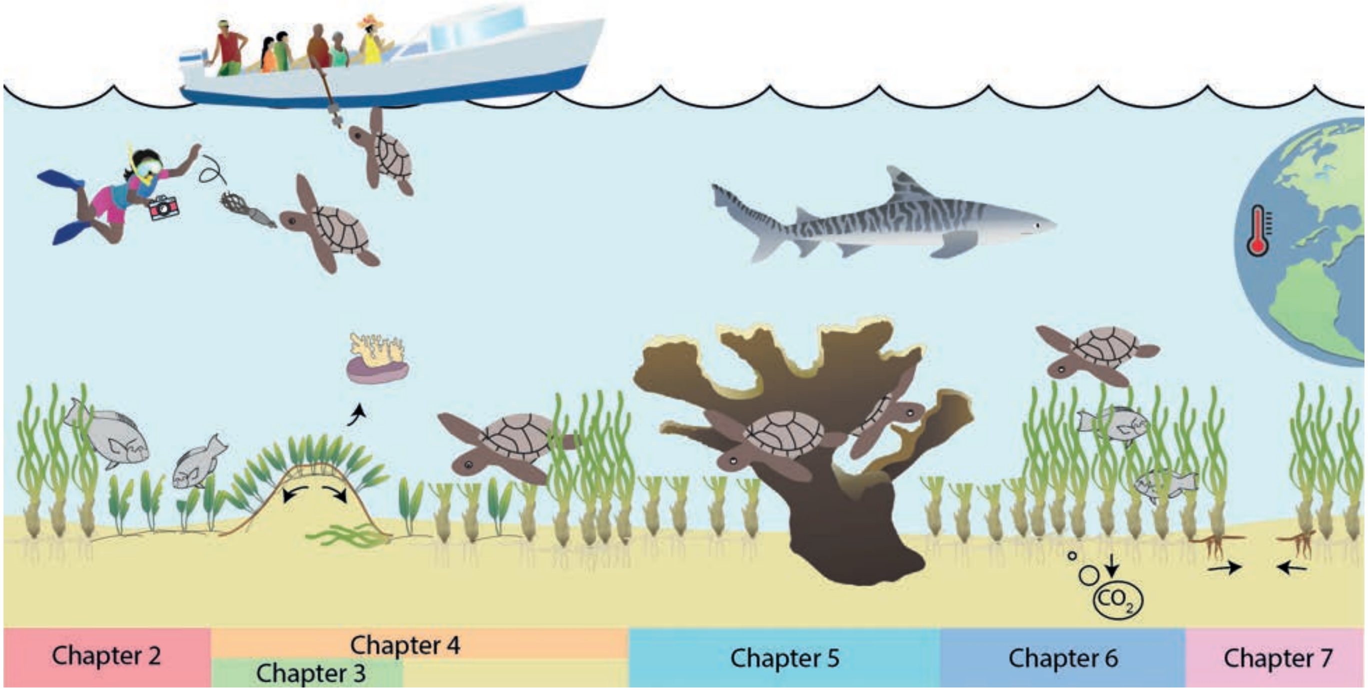


Figure 1.3 Visualization of the chapters of this thesis. Seagrass shoots with oval-shaped leaves represent the invasive seagrass H. stipulacea and strap-shaped shoots represent the native T. testudinum.

CHAPTER 2

Fish grazing enhanced by nutrient enrichment may limit invasive seagrass expansion

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ABSTRACT

The success of invasive macrophytes can depend on local nutrient availability and consumer pressure, which may interact. We therefore experimentally investigated the interacting effects of nutrient (nitrogen and phosphorus) addition, the exclusion of large herbivorous fishes and mimicked grazing on the expansion rates of the invasive seagrass *Halophila stipulacea*. The experiments were established on Bonaire and Aruba, two islands in the southern Caribbean, which differ in fish community structure. We observed that multiple Caribbean fish species feed on *H. stipulacea*. At both study sites, nutrient enrichment decreased invasive leaf carbon:nitrogen ratios. However only on Bonaire, where herbivore fish abundance was 7 times higher and diversity was 4.5 times higher, did nutrient enrichment result in a significant reduction of *H. stipulacea* expansion into native *Thalassia testudinum* meadows. This effect was likely due to increased herbivory on nutrient enriched seagrass leaves, as we found that excluding large herbivorous fish (e.g. parrotfish) doubled invasive expansion rates in bare patches on Bonaire. On Aruba, *H. stipulacea* expansion rates were higher overall, which coincided with lower abundances and diversity of native fishes, and were limited by mimicked fish grazing. We suggest that top-down control by the native fish community may counteract eutrophication effects by increased grazing pressure on nutrient-rich invasive seagrass leaves. We conclude that diverse and abundant herbivore communities likely play an important role in limiting invasion success and their conservation and restoration may serve as a tool to slow down seagrass invasions.

2.1 INTRODUCTION

Coastal ecosystems around the world are experiencing a rapid increase in the number of non-native species that often negatively impact ecosystem functioning (Molnar et al. 2008, Gallardo et al. 2016, Papacostas et al. 2017). The success of invasive macropyhtes may depend on local conditions such as nutrient availability and native biodiversity (Havel et al. 2015, Chapman 2017). High nutrient availability may make a habitat more vulnerable to invasion (Wersal and Madsen 2011, Gennaro et al. 2015), while high species richness and functional group diversity of the native plant and herbivore community may enhance the resilience of an ecosystem via mechanisms of niche complementarity, competition and strong top-down control, thereby providing biotic resistance to invasions (Elton 1958, Polunin et al. 1993, Gray et al. 2016, Blowes et al. 2020).

Consumer pressure is suggested to be the most important factor in limiting invasion success in both freshwater and marine ecosystems (Alofs and Jackson 2014, Papacostas et al. 2017). Preference of native herbivores for invasive macrophytes can be site and species specific (Tomas et al. 2010, Morrison and Hay 2011). Specialized herbivores preferring native plants can lead to invasive plants escaping top-down control (Davis et al. 2005, Gollan and Wright 2006, Vermeij et al. 2009b, Christianen et al. 2019), following the 'enemy release hypothesis' (Keane and Crawley 2002). However, since most marine herbivores are considered generalists (Parker and Hay 2005, Fleming and Dibble 2014), there are various examples of native generalist herbivores reducing invasive macrophyte success (Ribas et al. 2017, Tomas et al. 2011).

The impact of herbivores on invasion success can be altered by bottom-up forcings (Bakker et al. 2016b, Gallardo et al. 2016, Wang et al. 2019). Local nutrient enrichment can increase survival and growth rates of fast-growing (invasive) plant species (Davis et al. 2000, Vermeij et al. 2009a, Wersal and Madsen 2011), thus stimulating invasion. Invasive macrophytes that are adapted to quickly take up nutrients and invest their energy in expansion can therefore outcompete slow-growing native species under nutrient enriched conditions (Ceccherelli and Cinelli 1997, Gennaro et al. 2015, Teixeira et al. 2017, Uddin and Robinson 2018). However, fertilization may also alter the nutritional quality and chemical defenses of plants, potentially increasing the grazing pressure of (generalist) herbivores on nutrient-enriched leaves and their epiphytes (Chase and Knight 2006, Bakker and Nolet 2014, Jiménez-Ramos et al. 2017, Campbell et al. 2018, Liu et al. 2021), thus reducing invasion success. Depending on herbivore preference and invasive plant growth strategy, nutrient enrichment may favor either native plants or invasive plants. Thus, overall invasion success is likely dependent upon various site idiosyncrasies (Blumenthal 2006)

Seagrass meadows form complex ecosystems harboring multiple seagrass species and associated herbivores (Heck and Valentine 2006). Native tropical climax seagrass species are often adapted to oligotrophic conditions and high grazing pressure, by having (1) a complex root structure to access belowground nutrient pools, and (2) high levels of carbohydrate storage in the rhizomes (van Tussenbroek et al. 2006). Currently, seagrass meadows are prone to eutrophication, overfishing and invasion by exotic fast growing macrophytes (Williams 2007, Waycott et al. 2009). The introduction of the invasive seagrass *Halophila stipulacea* to the Caribbean in 2002 led to reports of apparent competition and replacement of the native species *Thalassia testudinum* and *Syringodium filiforme* across multiple islands in the Caribbean (Winters et al. 2020). *H. stipulacea* has been reported to invade both native seagrass habitat or previously unvegetated habitat (Willette and Ambrose 2012, Steiner and Willette 2015b, Smulders et al. 2017, Willette et al. 2020). It is currently unknown whether native herbivore species graze on *H. stipulacea,* and what effects fish grazing and nutrient enrichment have on *H. stipulacea* expansion (Winters et al. 2020).

Understanding the relative importance of top-down and bottom-up effects on the expansion capacity of invasive seagrass is vital for the conservation of native seagrass meadows that are currently facing multiple threats. Here, we address the following questions: (1) Does nutrient enrichment impact *H. stipulacea* leaf nutrient content and expansion rates? (2) Does fish grazing affect the expansion rate of *H. stipulacea*? (3) How do nutrient enrichment and (mimicked) fish grazing interact to impact the expansion rates of invasive *H. stipulacea*? To answer these questions, we set up experiments at two islands in the southern Caribbean that likely differed in their top-down strength due to contrasting protection status: a protected seagrass meadow on Bonaire and an unprotected meadow on Aruba. Fertilization, mimicked fish grazing and exclosure treatments were used to assess the separate and combined impact of fish grazing pressure and nutrient availability on the expansion of *H. stipulacea*. We hypothesize that (1) nutrient enrichment will increase the leaf nutrient content at both sites but will only lead to an increase in expansion rates of invasive *H. stipulacea* on Aruba with lower fish densities compared to Bonaire, (2) fish grazing reduces the expansion rates of the invasive seagrass *H. stipulacea*; excluding herbivorous fish will increase invasive seagrass expansion rate on Bonaire where herbivorous fish density and diversity is high, while mimicked grazing will decrease invasive seagrass expansion rate on Aruba, where herbivore fish density and diversity is low, and (3) that nutrient enrichment will strengthen the top-down control of herbivore fish on invasive seagrass when herbivore fish density and diversity is high (e.g. on Bonaire, but not on Aruba).

2.2 MATERIALS AND METHODS

2.2.1 Study species

In this study, we measured the responses of two seagrass species to bottom-up and top-down impacts. The native seagrass species *Thalassia testudinum* is a slow-growing climax species that is adapted to oligotrophic conditions (van Tussenbroek et al. 2006). A dense rhizome and root complex with stored carbohydrates ensures the ability of *T. testudinum* to withstand periods of intensive grazing (van Tussenbroek et al. 2006, Christianen et al. 2019). *T. testudinum* generally shows year-round productivity in tropical areas, mainly expanding through clonal growth with limited new recruitment through seed dispersal (Tussenbroek et al. 2014). The seagrass species *Halophila stipulacea* is native to Red Sea, Persian Gulf and Indian Ocean, and spread consecutively to the Mediterranean Sea (first reported in 1894) and Caribbean Sea (first reported in 2002) (Ruiz and Ballantine 2004, Winters et al. 2020). *Halophila stipulacea* is a fast-growing pioneer species capable of growing in high nutrient environments (Beca-Carretero et al. 2020, Winters et al. 2020, Helber et al. 2021). The species has wide phenotypic plasticity, potentially contributing to its invasive success (Winters et al. 2020). The roots of *H. stipulacea* are thin and expand quickly in the upper layer of the sediment (Smulders et al. 2017), which likely results in lower resistance to periods of intensive grazing. As of yet, there are no reports of sexual reproduction of *H. stipulacea* in the Caribbean Sea, and the species is assumed to use clonal growth as main reproductive strategy (Smulders et al. 2020). In native habitat with seasonal differences, *H. stipulacea* growth rates have been found to change across seasons (Wahbeh 1984, Beca-Carretero et al. 2020). In invaded habitats without seasonal differences (as Bonaire and Aruba), *H. stipulacea* cover and growth rates appear consistent throughout the year (pers. obs. F.O.H. Smulders, S.T. Becker).

2.2.2 Study site

The experiments were set-up in two islands in the Southern Dutch Caribbean at the same latitude (12°N, no seasonality in sea temperature and sun hours, Appendix 2.A), with contrasting protection status. On Bonaire, the experiments were conducted in

Lac Bay (12.103261 °N, 68.2390056 °W) from October 2018 - December 2018 and October 2019 - November 2019. Lac Bay, located on the southeastern side of the island, is part of the Bonaire National Marine Park and the oldest marine reserve in the world (established in 1979) as well as a protected Ramsar site (Debrot et al. 2012). On Aruba, the experiments were conducted near the southwestern shore of the island in Barcadera (12.4802380 °N, 69.9921950 °W) from April 2018 - June 2018. The coastal zones of Aruba have historically been unprotected, with an increase in number of small scale fisheries over the past decades (Sadovy 2005).

Lac Bay on Bonaire is an oligotrophic bay with extensive seagrass meadows (~ 7 km^2) fringed by a coral reef. The invasive seagrass *H. stipulacea* has spread throughout the center of this bay since 2010 (Christianen et al. 2019). Grazing pressure is high within the bay, both by mega- and mesoherbivores. Megaherbivore green turtle (*Chelonia mydas*) densities are highest at the northeastern side and center of the bay resulting in either monospecific *H. stipulacea* meadows or mixed meadows with low-canopy native *T. testudinum* (Christianen et al. 2019). Mesoherbivore fish densities are highest in the shallow parts of the bay (e.g. the mangrove fringe) where absence of turtle grazing leads to monospecific *T. testudinum* meadows with a high canopy which provide food and shelter to a high diversity of fish (Debrot et al. 2012), which is constant throughout the year (unpublished results). Grazing pressure by epifaunal crustacean and invertebrate grazers is limited in this bay (unpublished results). Experimental plots were established near the mangrove fringe in monospecific meadows of the two seagrass species, where turtle grazing was absent (pers. obs. F.O.H. Smulders).

On Aruba, *H. stipulacea* was first reported in 2013 (Willette et al. 2014) and in 2020 has spread to almost the entire leeward coast (pers.obs. S.T. Becker). The study site Barcadera is protected from wave action by narrow mangrove-reef islands and a sandbar. Turtle grazing is absent at this site and fish densities are low. The seagrass meadows consist of both mixed and monospecific meadows of *H. stipulacea* and *T. testudinum.* Experimental plots were established nearshore in monospecific meadows of the two seagrass species, with the *H. stipulacea* plots situated closer to the mangrove-reef islands relative to the *T. testudinum* plots. For the experimental plots, we chose shallow seagrass meadows on Bonaire and Aruba that were similar in density and depth (Appendix 2.B).

2.2.3 The impact of nutrient enrichment on invasive seagrass expansion into native seagrass

To investigate bottom-up control on expansion of invasive seagrass into native seagrass patches, reciprocal transplantation experiments with nutrient treatments were conducted on Aruba and Bonaire. An experimental duration of 10 weeks was chosen to be able to measure the responses of the fast-growing *H. stipulacea* and the slow-growing *T. testudinum* to nutrient enrichment. At each site, ten 0.25 m^2 plots were set up in an invasive species meadow and ten 0.25 m^2 plots were set up in a native seagrass meadow with at least 2 m distance between plots. Half of the plots were subjected to nutrient enrichment (n = 5, randomly assigned), using slow-release fertilizer enclosed in fiberglass mesh bags and suspended in the water column at the center of the plot (300 g Osmocote, NPK 14:14:14, following Campbell et al. 2018). The other plots did not receive any fertilizer (ambient conditions). In each plot, we transplanted circular seagrass sods with a diameter of 15.3 cm and 15 cm depth of the native species to the invasive plots and vice versa. At each site, three replicate procedural control plots (0.25 m^2) were established in which native and invasive seagrass sods (diameter 15.3 cm) were transplanted into its own habitat, to assess the impact of transplantation on shoot survival.

The expansion of the invasive seagrass was determined by counting the number of shoots that expanded through clonal expansion outside of its transplant (outward expansion) or into the native transplant (inward expansion) after 10 weeks. To compare expansion of *H. stipulacea* in native habitat to expansion in bare substrate, expansion of *H. stipulacea* shoots within a 0.25 x 0.25 m quadrant surrounding the invasive transplant (Fig. 2.1a) or within the 15.3 diameter area of the native transplant (Fig. 2.1b) was converted to gram dry weight m^{-2} day^{-1} by first multiplying the shoot count with the average biomass shoot^{-1} of newly grown shoots per location, then dividing by area (either within 15.3 diameter sods or within the plot minus the sod surface) and by experimental days. The impact of the treatments on native seagrass was measured by measuring existing shoot densities of the native seagrass in all plots at the start of the experiment and again after 10 weeks, expressing this difference as percentage of shoots (((# shoots end - # shoots start)/# shoots start) * 100). Additionally, we tested if there was an impact of native shoot density on the expansion rates of invasive seagrass by testing the strength of the relationship between the number of native seagrass shoots at the start of the experiment and the number of invasive seagrass shoots that had expanded outward and inwards after 10 weeks.

2.2.4 The impact of nutrient enrichment and fish grazing pressure on the expansion of invasive seagrass into bare substrate

To determine the combined impact of nutrient enrichment and fish grazing pressure on invasive seagrass expansion in bare substrate, we set-up two experiments with a crossed design. For this experiment, a duration of 4 weeks was chosen to measure the response of the fast-growing *H. stipulacea* to the treatments. On Aruba, a total of twenty 0.25 m^2 plots were created in a seagrass meadow invaded by *H. stipulacea* with at least 2 m between the plots. In each plot, a sediment core of 15.3 cm diameter and 15 cm depth was taken at the start of the experiment, creating a gap in the plot of the same dimensions. The bare gap was filled with clean sediment from that site until the sediment level was equal to the surroundings. Four treatments were set up (n = 5 each, randomly assigned); nutrient enrichment, mimicked grazing pressure, a combination of nutrient enrichment and mimicked grazing or ambient conditions. The nutrient treatments followed the same methods as described above. Mimicked grazing treatments were created by bi-weekly clipping of all leaves at 2 cm above the sediment surface using scissors (Short and Coles 2001, Kirsch et al. 2002). Initial grazing pressure surveys at both study sites indicated a minimal number of fish bites on *T. testudinum* leaves on Aruba (0.4 bites leaf^{-1}) compared to Bonaire (2.4 bites leaf^{-1}). Additionally, nutrient enrichment only caused an increase in bite marks on Bonaire (Appendix 2.C). Because of the high natural fish grazing pressure on Bonaire, an extra treatment with fish exclosures was added to the experimental design to exclude all herbivores >1.5 cm. Exclosures were made from plastic extruded mesh (mesh size 1.5 cm, height 50 cm) that was cleaned weekly.

After 4 weeks, the number of *H. stipulacea* shoots that had regrown into the bare area was counted. Expansion of *H. stipulacea* shoots was converted to gram dry weight m^{-2} day^{-1} by first multiplying the shoot count with the average biomass shoot^{-1} of newly grown shoots per location, then dividing by area (within the 15.3 diameter gap) and by number of experimental days. In two plots at each site, a bioturbator had settled within the bare patch, disturbing the sediment and seagrass growth. Therefore, these plots were removed from analysis, reducing the number of replicates for these treatments from five to four. After 10 weeks of treatment, a subsample of seagrass leaves was extracted for plant nutrient content. Seagrass was dried at 60 °C, ground with mortar and pestle and analyzed on a C/N elemental analyzer (FlashEA 1112; Thermo Fisher Scientific, USA).

2.2.5 Fish community structure

The local fish community at each study site was determined using visual underwater surveys. A benthic area of 5 m x 2 m (10 m^2, 1 m height, n = 10 per site) was monitored while snorkeling. First, the observer waited for 5 minutes to minimize fish disturbance. Then for 10 minutes, the observer counted and identified all fish species in the array along a transect line. The last 5 minutes were used to move through the array and count fish hiding in the seagrass canopy. The observed number of fish and number of herbivore fish were calculated to individuals * 100 m^{-2} (Polunin et al. 1993)

Secondly, video analysis was used to observe which fish species include *H. stipulacea* in their diet, and measure differences in fish density between plots with nutrient and exclosure treatments. A GoPro (Hero 3) with battery pack was attached to a PVC pole and positioned next to plots of the experiment assessing invasive seagrass expansion in bare areas, so all fish within the 0.5 m x 0.5 m plot were visible. 1-minute video fragments were sampled from a video of 3 hours per treatment, with at least 30 minutes between each fragment to ensure independent replicates. During these 1-minute fragments, fish species and abundance were recorded following the MaxN method, to give a conservative estimate of relative density (Mallet and Pelletier 2014). All fish species that were observed directly grazing on *H. stipulacea* were noted. At both study sites, fish density was compared between ambient and nutrient enriched plots. On Bonaire, fish density was additionally quantified in the exclosure treatments with or without nutrient enrichment.

2.2.6 Data analysis

All data was first checked for normality and homogeneity of variances (Shapiro Wilk test, Levene test, $P > 0.05$). Differences in native and invasive seagrass expansion with or without nutrient enrichment in the transplantation experiments were analyzed with an independent samples T-test, or Wilcoxon signed rank test as non-parametric alternative. A Pearson correlation coefficient was computed to assess the relationship between number of native shoots and number of invaded shoots. The expansion of invasive seagrass into bare patches and leaf C:N ratios were analyzed with a two-way ANOVA with mimicked grazing and nutrient enrichment as separate factors with each two levels on Aruba. For the Bonaire dataset, a similar procedure was followed using a three-way ANOVA with caging as a third factor with two levels. The factors were analyzed both separately as well as their interaction term. Differences in fish abundance between treatments were analyzed with a two-way ANOVA with caging and nutrient enrichment as separate factors with each two levels on Bonaire, and with a Wilcoxon signed rank test comparing ambient and nutrient enriched plots on Aruba. Statistics were performed in R (R Core Team 2019) using the packages "dplyr", "car", "ggplot" and "ggpubr". Average (*Avg*) values are presented together with standard errors (*SE*).

2.3 RESULTS

2.3.1 The impact of nutrient enrichment on invasive seagrass expansion into native seagrass

Halophila stipulacea expanded both from the transplanted sods into the surrounding native meadows (outward expansion) and from the surrounding meadows into the transplanted native *Thalassia testudinum* sods (inward expansion) (Fig. 2.1). On Bonaire, nutrient enrichment caused a 2-fold reduction in outward expansion of *H. stipulacea* (T test, t(8) = 2.5341, $P < 0.05$, Fig. 2.1a) and a 4-fold reduction of the inward expansion of *H. stipulacea* into *T. testudinum* transplants (Wilcoxon test, W = 24, $P < 0.05$, Fig. 2.1b). On Aruba, the nutrient addition did not influence the outward or inward expansion of *H. stipulacea* ($P > 0.05$, Fig. 2.1). The seagrass shoots in the procedural controls showed on average ≥ 80% survival for both species after 10 weeks: on Aruba for *H. stipulacea* 80 ± 18 % and for *T. testudinum* 83 ± 8 %, and on Bonaire for *H. stipulacea* 82 ± 3 % and for *T. testudinum* 90 ± 5 %.

There was no correlation between native shoot density at the start of the experiment and invasive seagrass expansion of both sites grouped together, both in the ambient plots (r(17) = .30, $P > 0.05$) and nutrient enriched plots (r(17) = .21, $P > 0.05$). The *T. testudinum* transplants did not expand but survived, at slightly lower densities on Aruba (87 ± 8 % and 86 ± 4% ambient and enriched) compared to Bonaire (114 ± 16 % and 110 ± 6 % ambient and enriched), without significant differences between treatments ($P > 0.05$, Appendix 2.D). Native *T. testudinum* shoot number surrounding the *H. stipulacea* transplant did not show differences between nutrient enriched and ambient treatments in Bonaire and Aruba ($P > 0.05$, Appendix 2.D).

2.3.2 Expansion of invasive seagrass into bare substrate

Inward *H. stipulacea* expansion into bare patches within their meadow was observed in all treatments within 4 weeks after clearing (Fig. 2.2). On Bonaire, excluding large fish (> 1.5cm) doubled *H. stipulacea* expansion rates from 0.09 ± 0.02 to 0.18 ± 0.02 g dry wt m^{-2} day^{-1} (Three-way ANOVA, F(1,30) = 7.065, $P <0.05$, Fig. 2.2a, Table 2.1). Highest average

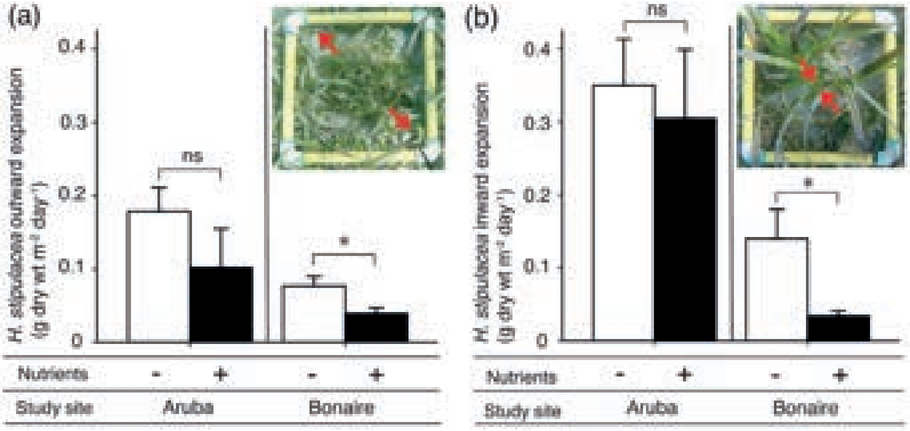


Figure 2.1 Effects of nutrient enrichment on the expansion of invasive *Halophila stipulacea* in native seagrass habitat on Aruba compared to Bonaire (n=5). Bars represent expansion rates (g dry wt m^{-2}day^{-1}; *Avg* ± *SE*) of *H. stipulacea* (a) outwards of its transplantation sod into the surrounding native *T. testudinum* patch, and (b) into a transplantation sod of native *T. testudinum*. The arrows on the inset images depict the direction of *H. stipulacea* shoot expansion of the two separate transplantation experiments. Significant effects are indicated with an asterisk (*$*P <$ 0.05*, **$P < 0.01$, ***$P < 0.001$).

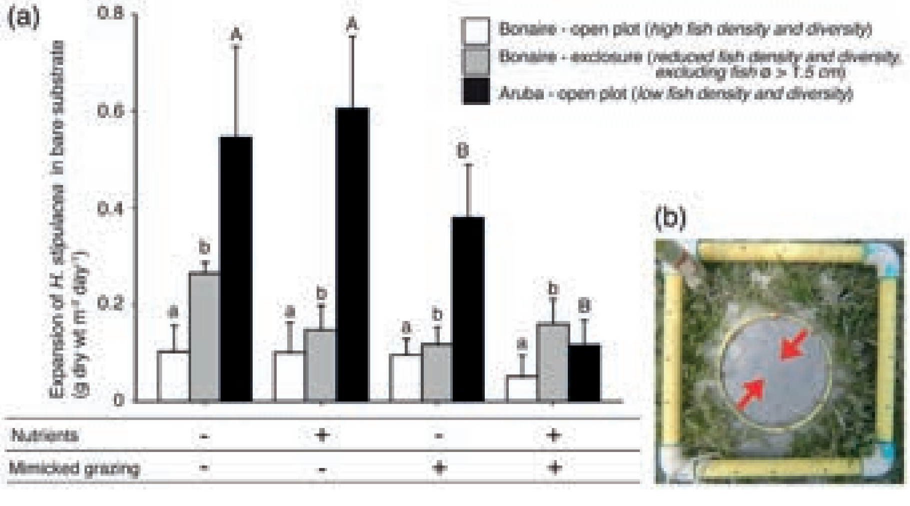


Figure 2.2 (a) Effects of nutrient enrichment and mimicked grazing on expansion of invasive *Halophila stipulacea* into bare substrate on Bonaire with natural grazing (white), on Bonaire with fish exclosures (mesh size excluded fish with a diameter > 1.5 cm, grey), and on Aruba (black). Bars represent expansion rates in g dry wt m^{-2}day^{-1} (*Avg* ± *SE* n = 5). Statistical analysis was performed separately for Bonaire and Aruba. Significant differences between nutrient and (mimicked) grazing treatments are indicated with distinct lower-case letters for Bonaire, and distinct upper-case letters for Aruba ($P < 0.05$). (b) Arrows show the direction of expanded shoot biomass into bare substrate.

expansion rates were measured in exclosure plots without nutrients and clipping treatment (0.26 ± 0.02 g dry wt m^{-2} day^{-1}). There was no significant effect of mimicked grazing or nutrient enrichment ($P > 0.05$) on expansion of *H. stipulacea* after 4 weeks.

On Aruba, mimicked grazing reduced *H. stipulacea* expansion rates compared to ambient grazing (0.25 ± 0.07 and 0.58 ± 0.11 g dry wt m^{-2} day^{-1} respectively, Two-way ANOVA, F(1,14) = 5.743, $P < 0.05$, Fig. 2.2a, Table 2.1). There was no significant effect of nutrient enrichment or interaction effect ($P > 0.05$) on *H. stipulacea* expansion.
Nutrient enrichment reduced C:N ratios in the aboveground biomass of *H. stipulacea* compared to ambient conditions, both on Bonaire (19.2 ± 0.7 to 16.3 ± 0.9, Three-way ANOVA, F(1,20) = 17.34, $P < 0.001$) and Aruba (19.3 ± 0.7 to 16.6 ± 1.0, F(1,13) = 9.449, Two-way ANOVA, $P < 0.01$, Appendix 2.E).

Table 2.1 Treatment effects on invasive seagrass expansion rates as analyzed with a threefactor ANOVA with the factors nutrient enrichment (N), caging (C) and mimicked grazing (G) on Bonaire and the two-factor ANOVA with the factors nutrient enrichment and mimicked grazing on Aruba. All factors had two levels. Shown are the df, Mean Square, F-values and Pvalues. Significant values are indicated in bold together with an asterisk (*P < 0.05, **P <0.01, ***P < 0.001).

Site	Variable	df	MS	F	P value
Bonaire	Nutrients (N)	1	0.01115	1.065	0.3103
	Caging (C)	1	0.07396	7.065	**0.0125***
	Mimicked grazing (G)	1	0.02058	1.966	0.1712
	N x C	1	0.00121	0.115	0.7366
	N x G	1	0.00642	0.614	0.4396
	C x G	1	0.00368	0.352	0.5575
Aruba	N x G x C	1	0.02388	2.281	0.1414
	Nutrients (N)	1	0.0642	0.777	0.3931
	Mimicked grazing (G)	1	0.4749	5.743	**0.0311***
	N x G	1	0.1150	1.391	0.2579

2.3.3 Fish community structure and grazing pressure

Underwater visual census revealed similar total fish densities between Aruba and Bonaire (472 ± 95 individuals 100 m^{-2} and 566 ± 113 individuals 100 m^{-2} respectively). However, herbivorous fish density was about 7 times higher on Bonaire (221 ± 51 individuals 100 m^{-2}) compared to Aruba (31 ± 12 individuals 100 m^{-2}). Total fish species richness was 28 on Bonaire and 14 on Aruba. On Bonaire, nine different herbivorous fish were encountered of which two were the only herbivorous fish species observed on Aruba (Table 2.2).

Table 2.2 List of seagrass herbivores observed on Bonaire and on Aruba during the visual and video surveys. Species with asterisk (*) were seen grazing on invasive *Halophila stipulacea* on video (Appendix 2.F).

Herbivore fish scientific name	Herbivore fish common name	Bonaire	Aruba	Literature supporting classification as seagrass herbivore
Acanthurus chirurgus	Doctor fish	X		(Greenway 1976)
Acanthurus coeruleus	Blue tang	X		(Ogden 1976)
Cryptotomus roseus	Bluelip parrotfish	X		(Dromard et al. 2017)
Nicholsina usta	Emerald parrotfish*	X	X	(Prado and Heck 2011)
Scarus iserti	Striped parrotfish	X		(Dromard et al. 2017)
Sparisoma aurofrenatum	Redband parrotfish*	X	X	(Tribble 1981)
Sparisoma chrysopterum	Redtail parrotfish*	X		(Lewis 1985)
Sparisoma radians	Bucktooth parrotfish*	X		(Holzer et al. 2013)
Sparisoma rubripinne	Yellowtail parrotfish*	X		(Hay 1981)

In the video surveys the number of herbivorous fish observed on Bonaire was higher in the nutrient enriched plots compared to ambient plots (ambient: 0.5 ± 0.2, enriched: 1.5 ± 0.6 fish min^{-1}, Two way ANOVA, F(1,16)=5.714, $P < 0.05$). On Aruba, there was no significant effect of nutrient enrichment on observed fish densities (ambient: 0.0, enriched: 0.4 ± 0.2 fish min^{-1}, Wilcoxon test, $P = 0.2$). Fewer fish were observed inside exclosures (0.4 ± 0.2 fish min^{-1}) compared to outside exclosures on Bonaire (1.6, ± 0.4 fish min^{-1}, Two-way ANOVA, F(1.16)=8.229, $P < 0.05$). All fish that were observed inside the exclosures were < 1.5 cm such as juvenile redband (*Sparisoma aurofrenatum*) and bucktooth (*Sparisoma radians*) parrotfish. The number of juvenile fish that still entered the cages was 0.2 ± 0.2 fish min^{-1} in ambient exclosure plots and 0.6 ± 0.4 fish min^{-1} in enriched exclosure plots. Several species were recorded to be grazing on *H. stipulacea* during video analysis (Table 2.2, Appendix 2.F).

2.4 DISCUSSION

We document that the expansion of the invasive seagrass *Halophila stipulacea* in the Caribbean Sea may be limited by top-down control associated with herbivorous fishes. Bottom-up forcing through nutrient enrichment was found to enhance this top-down control in a habitat with a diverse and abundant fish community. This is further supported by our contrasting observations in a habitat with relatively low herbivore densities where *H. stipulacea* invasion rates were higher in general and only impacted by mimicked grazing. In both habitats, native *Thalassia testudinum* shoot density did not change with or without nutrient enrichment and native shoot density did not impact invasive expansion success, indicating that competitive interactions did not drive this effect. Our results provide novel insights into the relative and combined effect of bottom-up and top-down processes in invaded seagrass meadows.

2.4.1 Effects of nutrient enrichment

Nutrient enrichment can increase plant productivity and biomass, favoring fast-growing invasive macrophyte species over native species (Gennaro and Piazzi 2011, Wersal and Madsen 2011, Teixeira et al. 2017). In this study, we measured a reduction in *H. stipulacea* leaf C:N ratios within the nutrient enriched plots on Bonaire and Aruba, indicating increased nutrient uptake. However, instead of a corresponding increase in biomass production rates, we found a decrease on Bonaire and no effect of nutrient enrichment on Aruba. On Bonaire, this resulted in a 50% reduction in outward and 79% reduction in inward expansion rate under enriched compared to ambient conditions.

This is in contrast to previous research where nutrient enriched conditions corresponded to high invasion success of fast growing macrophytes (Ceccherelli and Cinelli 1997, Gennaro and Piazzi 2011, Teixeira et al. 2017, Wang et al. 2019), including *H. stipulacea* (van Tussenbroek et al. 2016). A likely explanation for the changes in expansion of *H. stipulacea* under enriched conditions on Bonaire, is that the diverse and abundant fish community responded to nutrient enrichment by increasing grazing pressure while on Aruba the low-diverse community did not cause this effect. The same mechanism of increased grazing pressure after nutrient enrichment was found in our initial grazing surveys on Bonaire (Appendix 2.C). Nutrient toxicity is a less likely explanation for this reduced expansion as pilot studies in the lab showed that *H. stipulacea* could withstand high nutrient concentrations in uptake experiments (unpublished results). In the short-term experiment assessing *H. stipulacea* expansion rates into bare substrate, no significant impact of nutrient enrichment was observed on Bonaire. However, in our video analysis, we did measure significantly higher fish abundance in the nutrient enriched plots, which may have been attracted to the enriched seagrass leaves and their epiphytes (McSkimming et al. 2015, Mutchler and Hoffman 2017, Campbell et al. 2018). Nutrient enrichment increased the leaf nutrient content in our study, which has been found to enhance the plant palatability to herbivores, increasing grazing pressure and potentially reducing expansion rates (Boyer et al. 2004, Prado and Heck 2011, Jiménez-Ramos et al. 2017, Campbell et al. 2018, Ravaglioli et al. 2018). Although more research is needed into the long-term effects of nutrient enrichment on both native and invasive seagrass, we conclude that in systems with an intact generalist herbivore community, the interaction between local nutrient enrichment and biotic control may have an opposite impact on invasive seagrass success compared to systems with depleted herbivore communities.

2.4.2 Effects of fish grazing

Apart from nutrient-induced grazing effects, we confirmed our hypothesis that direct grazing had a significant negative impact on invasive plant expansion, both as natural fish grazing on Bonaire as well as mimicked grazing on Aruba. We showed that invasive seagrass expansion rates could be doubled by locally excluding fish > 1.5 cm on Bonaire and reduced by > 50% with mimicked grazing on Aruba. Mimicked grazing did not significantly impact expansion on Bonaire, likely because of background grazing pressure both in and outside of exclosure plots reducing the impact of this treatment, while on Aruba limited ambient grazing pressure caused a large treatment effect. Our results indicate that invasive seagrass expansion rates were higher on Aruba compared to Bonaire, while the herbivore community was 4.5 times as diverse and seven times more abundant on Bonaire compared to Aruba. Together with our experimental results, our study suggests that a diverse and abundant fish community may provide biotic resistance to invasive macrophyte species. Studies about grazing impacts of herbivores on invasive macrophyte expansion are limited, but can provide new insights into biotic resistance theory, since most aquatic herbivores are generalist feeders (Bakker et al. 2016b, Petruzzella et al. 2017), and have been shown to select their food source based on plant traits instead of novelty (Grutters et al. 2017). Based on our study, nutrient-induced and direct grazing effects by an abundant herbivore community may even be more important in determining the competitive outcome than direct impacts of nutrients on plant physiology. Top-down control could therefore reduce the competitive advantage fast-growing invasive species might have in nutrient-rich conditions. In future experiments assessing fish grazing pressure using exclosures, it should be taken into account that herbivore fish < 1.5 cm can still have significant grazing impacts. Feeding trials are needed to reveal the preference of the various seagrass herbivores for native and invasive macrophytes, to further predict the potential of biotic resistance in invaded seagrass meadows (Parker et al. 2006).

2.4.3 Herbivore community

High grazer abundance and diversity may have contrasting effects on the expansion of invasive species depending on food preferences of the species (Gollan and Wright 2006, Tomas et al. 2011b, Engelen et al. 2011). Based on our results, the dense *T. testudinum* border close to the mangroves within the invaded area of Bonaire is likely more resistant to seagrass invasion compared to the center. High-canopy seagrass harbors greater fish abundance and diversity because of shelter and spillover from the mangroves (Debrot et al. 2012). Besides known generalist seagrass herbivores such as the bucktooth (*Sparisoma radians)* and redband (*Sparisoma aurofrenatum)* parrotfish (Weinstein and Heck 1979, Kirsch et al. 2002), the emerald parrotfish *(Nicholsina usta*) was often seen grazing on *H. stipulacea* on Bonaire. This species is increasing in number in the Gulf of Mexico due to tropicalization (Fodrie et al. 2010), was found to consume five to 36 times more native seagrass than other grazers in an earlier study (Prado and Heck 2011), and may therefore be an important ecological component in biotic resistance in seagrass meadows. High herbivore fish density and diversity together with our experimental results help to understand the current absence of *H. stipulacea* in high-canopy *T. testudinum* habitat (Christianen et al. 2019). In contrast, green sea turtles have been shown to prefer native seagrass and crop it short thereby facilitating invasive seagrass expansion in certain areas within the same bay (Christianen et al. 2019). This explains that even within a protected area with high biodiversity, invasive seagrass densities can become high. A dynamic grazing regime of green turtles resulting in variation in *T. testudinum* canopy height (Christianen 2021) may sustain areas with high herbivore fish densities and therefore locally limit *H. stipulacea* expansion. Similarly, in Mediterranean seagrass habitats it has been previously suggested while some herbivore fish species may limit the expansion rate of invasive *Caulerpa racemosa*, the protection of marine habitat can also lead to returning herbivorous fish grazing on native seagrass leaves, therefore promoting the invasion of the alga (Caronni et al. 2015). The degree of biotic resistance to invasion is therefore species and context dependent (Caselle et al. 2018).

2.4.4 Protection status

A more diverse herbivore community likely has the potential to exert top-down control over the invasive seagrass species *H. stipulacea* and therefore decrease the success of these invaders. High (juvenile) herbivorous fish diversity and density may be related to the protection status of the habitat (Polunin et al. 1993, Alonso Aller et al. 2017, Alonso Aller 2018). Even though the role of parrotfish in increasing the resilience of other marine ecosystems like coral reefs inside protected areas is being questioned due to lack of field data (Bruno et al. 2019), our results provide first evidence that high levels of parrotfish grazing pressure within the selected protected area most likely decreases the expansion rates of invasive seagrass. Apparent higher general expansion rates of the invasive seagrass on Aruba compared to Bonaire could be the result of low fish grazing pressure, however other factors related to protection status could also be important drivers. Concentrations of nitrogen in *H. stipulacea* and *T. testudinum* leaves were similar at both study sites (Appendix 2.B), suggesting nutrient loading to be comparable in both habitats. However, in the unprotected area on Aruba, the impact of local anthropogenic disturbances (e.g. a drink- and wastewater processing facility), was reflected by a high algal cover (predominantly *Acanthophora spicifera*) and abundance of detritivores. This high algal cover on Aruba may shift feeding preferences of fishes to algae (Duarte 1995, Littler et al. 2006), and because the algal layer is situated on top of the seagrass it can also physically prevent fish from foraging on the seagrass (Heck and Valentine 2006). In future studies it would be valuable to include measurements of water quality and the response of algae, including epiphytes, to nutrient enrichment. Invasion success can be driven by a combination of different trophic effects, resilience of the native plant community, water quality, anthropogenic disturbance and many other mechanisms that should be considered when managing an area. Our study provides a starting point to investigate the relationship between marine protection status and biotic resistance to invasive seagrass species in seagrass ecosystems.

2.4.5 Conclusion

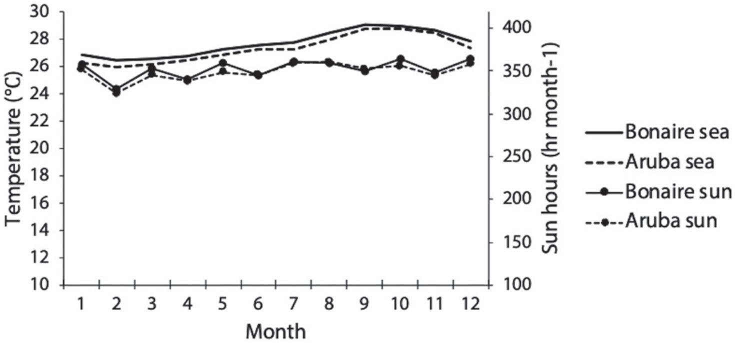
As demonstrated by the fast expansion and settlement of *H. stipulacea* to various islands in the Caribbean since 2002, the arrival and subsequent expansion of *H. stipulacea* to new habitats is often unavoidable (Smulders et al. 2017, Willette et al. 2020, Winters et al. 2020). Plant invasion can have unforeseen impacts on ecological interactions and ecosystem services in seagrass meadows (Williams 2007, James et al. 2020). Therefore, it is important to maintain or even enhance seagrass resistance to invasion. A key role for limiting expansion of invasive plant species may be provided by the community of generalist herbivores, including fish species. Management strategies to maintain or restore these generalist herbivore communities and their habitats can therefore be important to mitigate potential negative effects of invasive plants after their establishment in new seagrass habitats.

ACKNOWLEDGMENTS

For help during the experimental work on Bonaire we thank Irene Kranendonk, Julia van Duijnhoven, Olivier Kramer, Dave Willemsz, Wout Hendriks and Sabine Engel. For laboratory support we thank Nico Helmsing. Logistic support was provided by the Biology and Chemistry department at Colegio Arubano, Aruba and STINAPA, Bonaire. This study was carried out as part of the project 'Global defaunation and plant invasion: cascading effects on seagrass ecosystem services' appointed to MJAC (NWO 016. Veni.181.002). The authors do not have a conflict of interest to declare.

APPENDIX 2.A

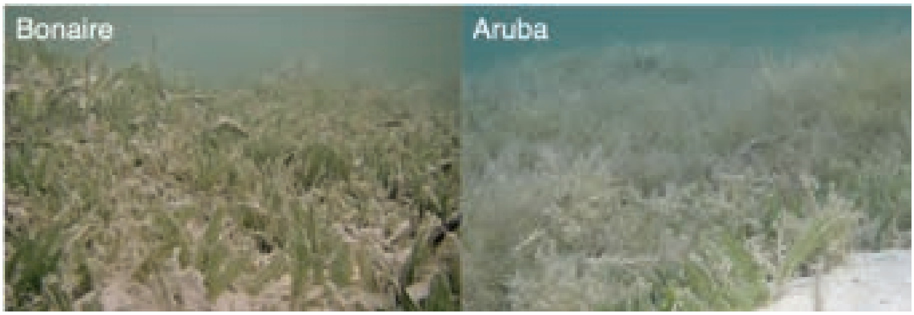
Historical averages of surface sea water temperature (https://seatemperature.info/) and sun hours (https://www.worldweatheronline.com/) per month on Bonaire and Aruba.



APPENDIX 2.B

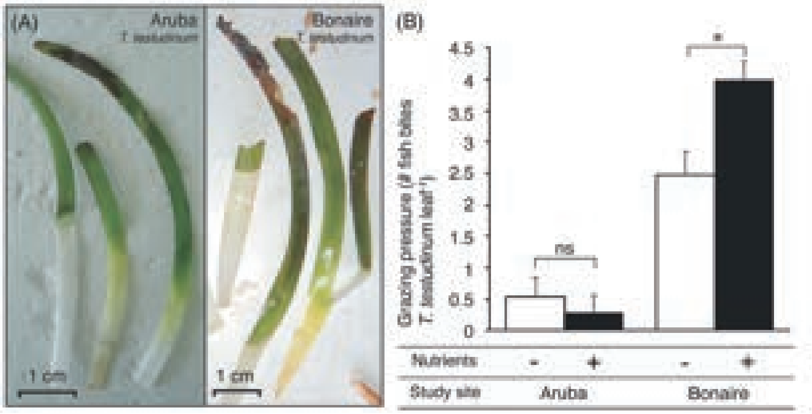
Characteristics of the study sites on Bonaire and on Aruba as found in this study, with underwater pictures of the *H. stipulacea* meadows.

	Bonaire	Aruba
Protection status	Protected	Unprotected
T. testudinum shoot density (shoots/m^2 ± SE)	304.6 ± 0.5	399.8 ± 0.6
H. stipulacea shoot density (shoots/m^2 ± SE)	4939 ± 979	5898 ± 395
Depth (m)	1.5	0.7
Algae cover	Low	High
% DW N in *H. stipulacea* leaves	1.4 ± 0.09	1.4 ± 0.05
% DW N in *T. testudinum* leaves*	2.0 ± 0.13	1.8 ± 0.25
Nearby industrial human activities	Low	High
* Methods correspond to described methods of the determination of %N in *H. stipulacea* leaves		



APPENDIX 2.C

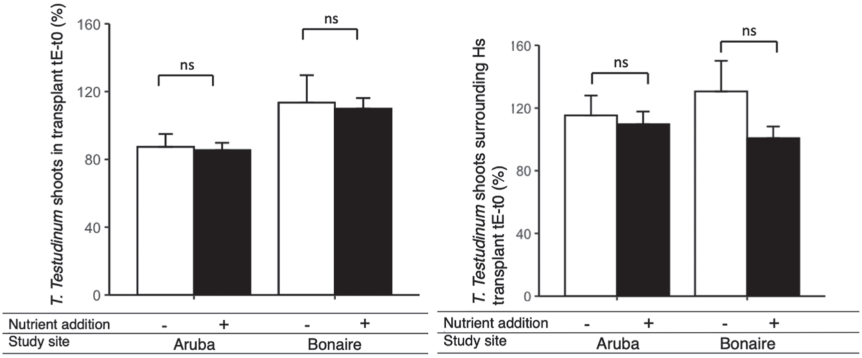
Figures indicating low grazing pressure on Aruba compared to Bonaire (A) Pictures of *T. testudinum* leaves sampled on Bonaire and Aruba. (B) Comparison of grazing pressure on native seagrass leaves on Aruba and Bonaire with and without nutrient enrichment. Bars represent # fish bites per *Thalassia testudinum* leaf (*Avg* ± *SE*) based on 10 shoots per replicate (n = 5). Significant effects are indicated with an asterisk (Two-sample T test, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).



APPENDIX 2.D

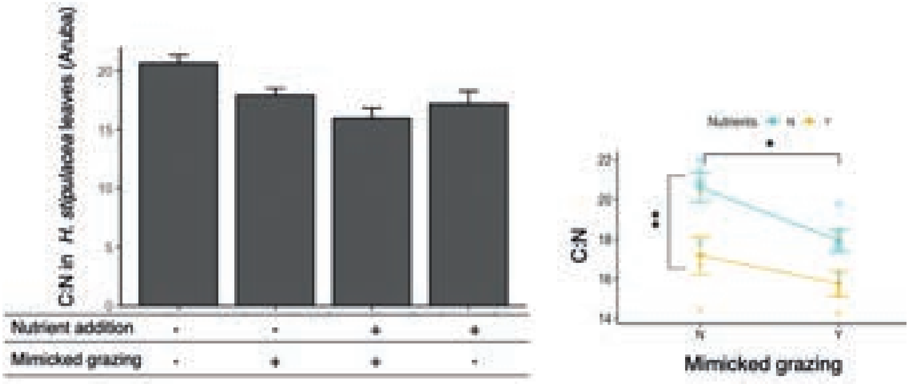
Appendix 2.D

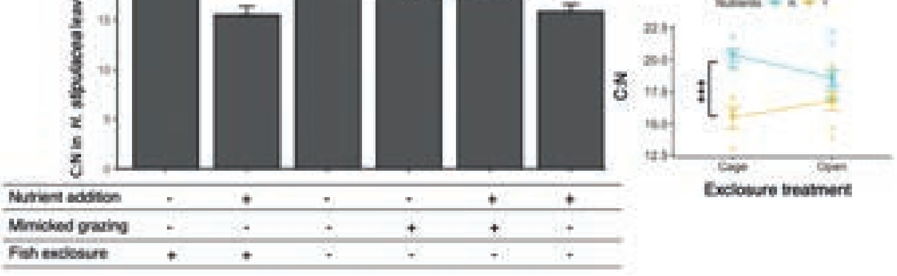
Relative changes in *T. testudinum* density (%) over the course of the *H. stipulacea* expansion experiments (Avg ± *SE*) for the transplanted *T. testudinum* sods (left panel) and the *T. testudinum* plots surrounding the *H. stipulacea* sods (right panel) in both ambient (white bars) and nutrient (black bars) treatments. Only small changes in *T. testudinum* were observed, while nutrient enrichment did not induce significant effects



APPENDIX 2.E

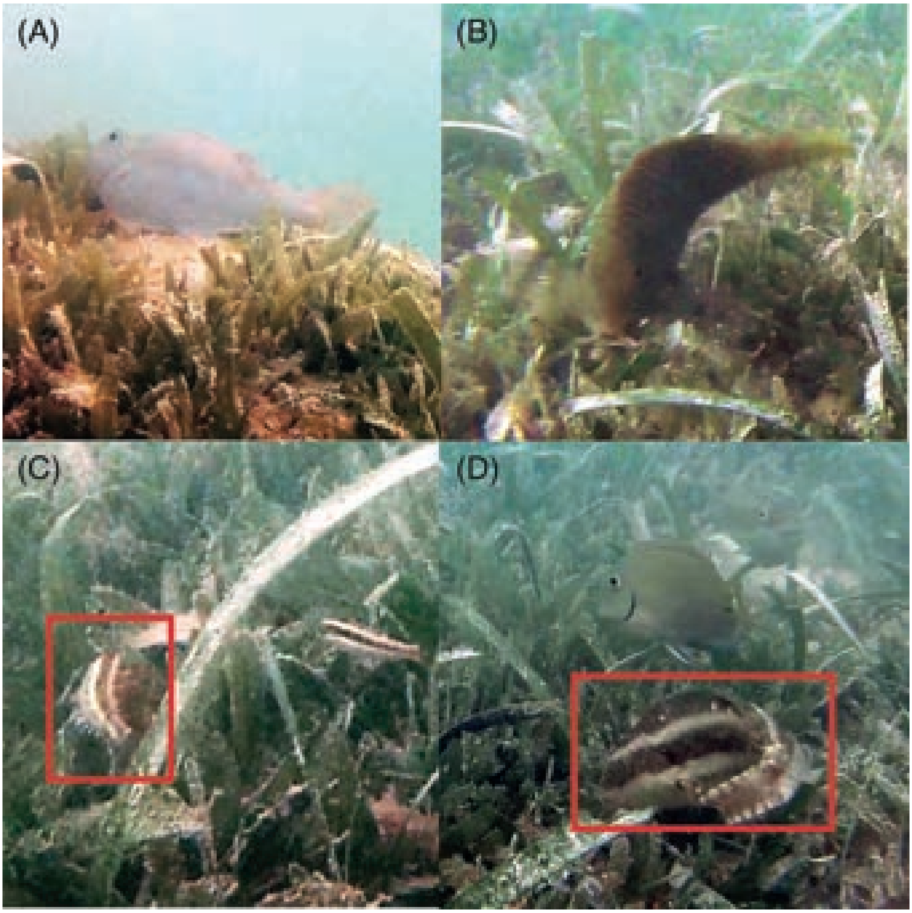
Effects of nutrient enrichment and mimicked grazing on C:N ratios of *Halophila stipulacea* leaves regrown into bare substrate on Aruba (n=5). Left panel: bars represent C:N ratios (*Avg* ± *SE*). Right panel: Two-way interaction plot indicates significant differences between nutrient and mimicked grazing treatments (**P < 0.05*, ***P* < 0.01, ****P* < 0.001). Effects of nutrient enrichment, mimicked grazing and fish exclosures on C:N ratios of *Halophila stipulacea* leaves regrown into bare substrate on Bonaire (n = 5). Left panel: bars represent C:N ratios (*Avg* ± *SE*). Right panel: Two-way interaction plot indicates significant differences between nutrient and exclosure treatments (**P < 0.05*, ***P* < 0.01, ****P* < 0.001).





APPENDIX 2.F

Pictures A to D: Screenshots from videos showing evidence of fish taking bites of *Halophila stipulacea* leaves on Bonaire. (A) emerald parrotfish (*Nicholsina usta*). (B) yellowtail parrotfish (*Sparisoma rubripinne*). (C) bucktooth parrotfish (*Sparisoma radians*) (D) redband parrotfish (*Sparisoma aurofrenatum*).



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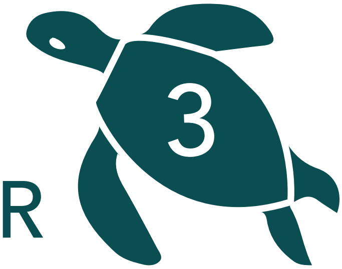
CHAPTER 3



Battle for the mounds: niche competition between upside-down jellyfish and invasive seagrass

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Marjolijn J.A. Christianen, J. Arie Vonk

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In tropical ecosystems, autotroph organisms are continuously competing for space, with some plant species benefiting from disturbances such as fire, grazing, or bioturbation that clear habitat (Pulsford et al. 2016). These disturbances can open up layers of vegetation, thereby promoting colonization of opportunistic species that would have been competitively inferior without disturbance (Castorani et al. 2018). Opportunistic fast-growing species also include often invasive species that are therefore also likely to increase in dominance after disturbance (Altman and Whitlatch 2007). In seagrass meadows in the southern Caribbean, we observed that the marine invasive plant *Halophila stipulacea* uses bioturbation mounds, created by burrowing infauna such as sea cucumbers and shrimp (see (Suchanek 1983), to colonize new habitats (Fig. 3.1a, b). On Bonaire and Curaçao, in habitats with ~100% native *Thalassia testudinum* cover, invasive *H. stipulacea* often at first only occurred on bioturbation mounds that smothered native *T. testudinum* seagrass, likely due to fragmentation and subsequent settlement (Smulders et al. 2017). These observations suggest that bioturbation mounds serve as starting points for further invasion (Fig. 3.1c).

These bioturbation mounds add a different kind of disturbance as a mechanism to free up space to settle and expand from than previously described for invasive marine plants (Christianen et al. 2019, Hernández-Delgado et al. 2020). This interaction between invasive marine plants and burrowing organisms could disrupt the natural balance between opportunists and climax species within the ecosystem. Invasive species may compete with native weak competitors in newly created niches after disturbance (Peltzer et al. 2009). This can lead to co-existence or declines of native species when these are weak competitors and are being pushed out by the invasive species (Altman and Whitlatch 2007, Hobbs et al. 2009). In this paper, we report evidence of a novel ecological interaction in a tropical seagrass ecosystem, between two autotroph species, the invasive seagrass *H. stipulacea* and the native upside-down jellyfish *Cassiopea* spp. We discuss the ecological implications and suggest future directions for research.

After our first observation, our curiosity increased as we saw that, on Curaçao, the bioturbation mounds often became occupied by a combination of upside-down jellyfish and shoots of *H. stipulacea* (Fig. 3.1d) that seem to occupy the same niche. Upside-down jellyfish belonging to the genus *Cassiopea* (hereafter referred to as *Cassiopea*) have photosynthesizing dinoflagellates as symbionts and have a benthic lifestyle associated with Caribbean mangrove, seagrass, and coral ecosystems (Niggl and Wild 2010). To quantify the preference of invasive seagrass and *Cassiopea* for bioturbation

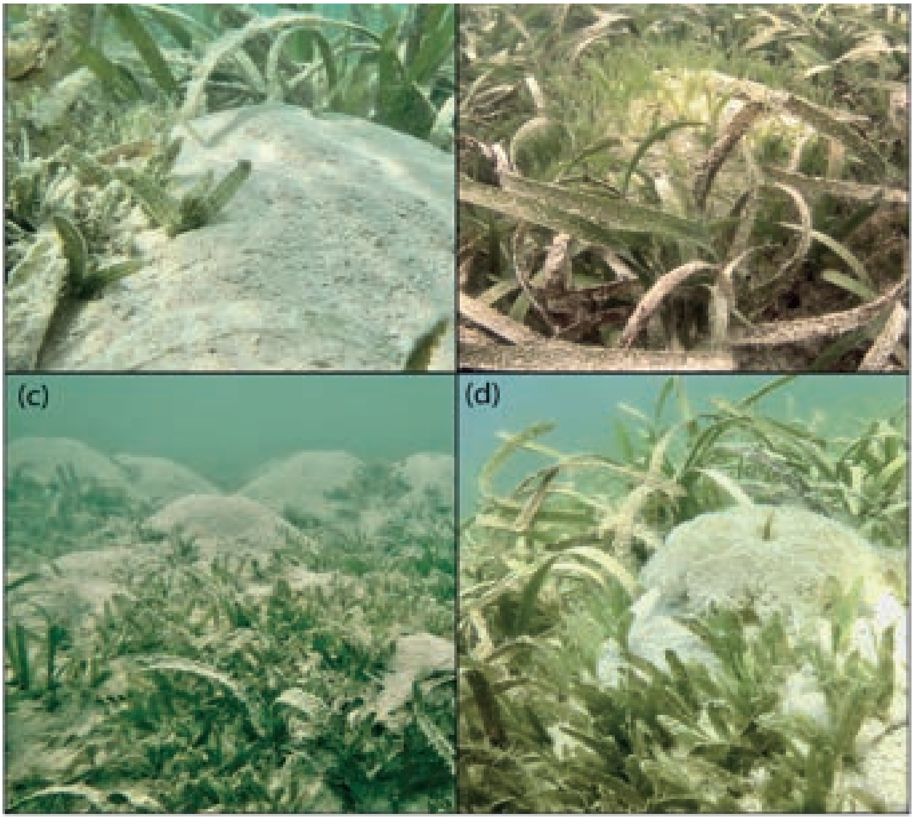

Figure 3.1 Bioturbation activity in native Thalassia testudinum seagrass meadows creates an opportunity for the colonization and expansion of invasive seagrass Halophila stipulacea as observed on (a) Bonaire and on (b) Curaçao. (C) Seagrass meadows on Bonaire that have been invaded for more than a decade have higher densities of both H. stipulacea and bioturbation mounds compared to Curaçao (pers. obs. F.O.H. Smulders & N. Slikboer). (D) On Curaçao, both invasive seagrass and upside-down jellyfish Cassiopea spp. were observed occupying bioturbation mounds. Picture (a) and (c) taken by F.O.H. Smulders in Lac Bay, Bonaire on 19th November 2021, pictures (b) and (d) taken by N. Slikboer in Spanish Water Bay, Curaçao on 15th of November and 27th of December 2020 respectively.

mounds in seagrass meadows and to study potential niche competition we conducted a pilot experiment on Curaçao. We monitored ten natural bioturbation mounds, five artificial bioturbation mounds, and five vegetated plots without bioturbation every three days for 45 days. All treatments were situated between 1 and 2.3 m depth and randomized over space with at least 2 m in between plots, which resembled the average natural mound density in the larger area. The artificial bioturbation mounds were made of sediment collected nearby the study site and mimicked the average dimensions of the natural bioturbation mounds (diameter 40 cm; maximum height 20 cm). For each treatment, plots of 0.5 x 0.5 m were marked with PVC poles. Within each plot, a circle (40 cm diameter) was marked with six bamboo skewers, and all seagrass shoots (*T. testudinum* and *H. stipulacea*) and *Cassiopea* individuals within this circle were counted at each sampling moment. The plots were all situated in a mixed seagrass meadow dominated by *T. testudinum* with a sparse *H. stipulacea* understory.

The results from our pilot experiment suggest that *H. stipulacea* and *Cassiopea* both prefer niches where most bare sediment is available. *H. stipulacea* shoot development was 1.9 ± 0.3 shoots day^{-1} on artificial mounds compared to 1.6 ± 0.5 shoots day^{-1} on natural bioturbation mounds and 1.0 ± 0.4 shoots day^{-1} on vegetated plots (One-way ANOVA, F(2,17) = 0.624, p = 0.55). For *Cassiopea*, we found an average occurrence of 9.5 ± 5.0 individuals on natural bioturbation mounds, followed by 5.6 ± 1.6 individuals on artificial mounds and 1.4 ± 3.3 individuals in vegetated plots (Kruskal-Wallis, H(2) = 4.118, p = 0.13). Additionally, we observed that *Cassiopea* individuals spent less time in vegetated seagrass habitat (~1 day), and stayed longer on bare (artificial) bioturbation mounds (> 10 days), suggesting that the individuals are mostly passing through habitats with high seagrass cover selecting open spaces to settle (corresponding to findings of Niggl and Wild 2010). Average (± SE) *Thalassia testudinum* shoot growth was low in each treatment (0.04 ± 0.02 shoots day^{-1}). Therefore, the data from this pilot experiment confirmed our observations that both *Cassiopea* and *H. stipulacea* prefer open habitats created by bioturbation activity and are in niche competition. Both the photosynthetic invertebrate and invasive seagrass are likely competing because of their similar requirements for light and space. Our next question was which species will win this competition, or is co-existence possible?

To explore the relationship between the presence of *Cassiopea*. and *H. stipulacea* and their potential competitive exclusion or co-existence, we pooled the artificial and natural bioturbation plots and visualized the average number of *H. stipulacea* and *Cassiopea* individuals over time (Fig. 3.2a). Densities of *H. stipulacea* steadily increased over time, while *Cassiopea* showed a peak halfway and decreasing densities towards the end of the experiment. To further visualize the differences in dynamics between plots, we compared the species composition at the end of the experiment (based on the ratio of *H. stipulacea* shoots:*Cassiopea* individuals) (Fig. 3.2b). After 45 days, *H. stipulacea* was dominant in 80% (= 12 out of 15) of the plots. In the remaining 20% of the plots, no shoots of *H. stipulacea* were observed during the whole experimental period and only *Cassiopea* was present at the end of the experiment. Therefore, in all plots where at least one *H. stipulacea* shoot started growing, the invasive seagrass became dominant relative to *Cassiopea* within 1.5 months. This is a different outcome of seagrass-*Cassiopea* interaction as was suggested by (Stoner et al. 2014), who discussed that high densities of *Cassiopea* may negatively impact seagrass cover through shading or other processes. Additionally, 27% of the plots were exclusively covered with *H. stipulacea* at the end of the experiment, while all plots had *Cassiopea* individuals present at some point during the experiment. This corresponded with our observations in the field: when the bioturbation mounds gradually became invaded by invasive seagrass, the *Cassiopea* individuals were seen leaving the plots with the last individuals remaining positioned themselves vertically between the leaves (Fig. 3.2c).

We report a novel interaction between an invertebrate with photosynthetic symbionts and an invasive plant after natural disturbance through bioturbation activity. We hypothesize that the arrival of the invasive *H. stipulacea* likely shifts patch dynamics in the seagrass ecosystem and thereby niche competition between seagrasses and *Cassiopea*. Within the native seagrass community dominated by *T. testudinum*, bioturbators are limited by strong root-rhizome networks (Bernard et al. 2019). These open habitats are thus created at a low frequency but remain stable for considerable time because *T. testudinum* does not quickly recover after disturbance (O'Brien et al. 2018). Native *Cassiopea* can therefore stay for a long period of time in the open habitat created by bioturbators. After introduction of the invasive seagrass, bioturbation mounds are quickly covered by invasive shoots. In time, as the cover of invasive seagrass increases, we predict that the bioturbation frequency will go up (Fig. 3.1c). Biannual seagrass monitoring in Lac Bay, Bonaire since seagrass invasion started (2011), provides the opportunity to explore this relationship.

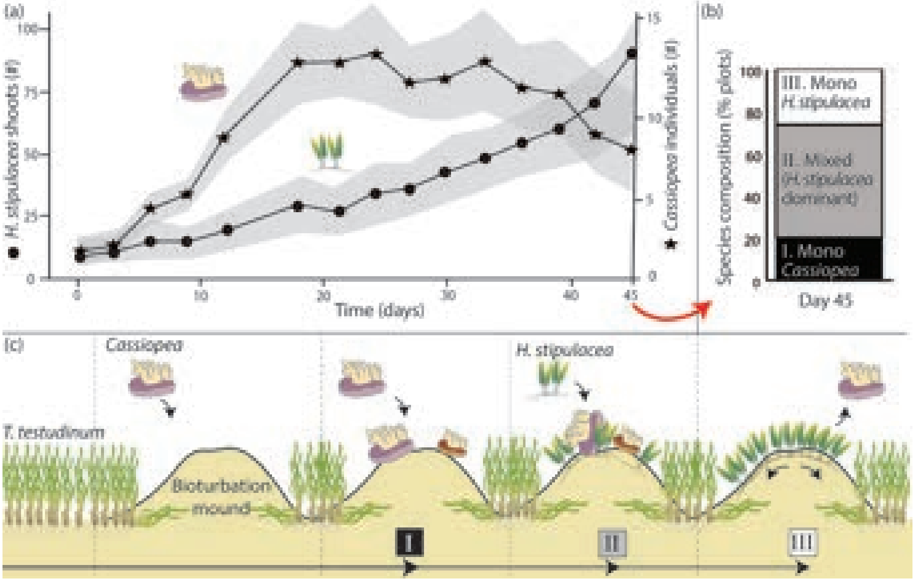

Figure 3.2 Interactions between presence of *H. stipulacea* and *Cassiopea*. (A) Time series of the average number ± SE of H. stipulacea shoots and *Cassiopea* individuals on artificial and natural bioturbation mounds pooled together (N = 15). (B) The percentage of plots with a certain species composition as measured at the end of the experiment (day 45). We calculated the ratio of *H. stipulacea:Cassiopea*, plots with a ratio >1 were defined as *H. stipulacea* dominated, while plots below 1 were defined as *Cassiopea* dominated. At the end point, there were no mixed plots with Cassiopea dominance. Plots where only *Cassiopea* was present (mono *Cassiopea*) are labelled stadium I, mixed plots with *H. stipulacea* dominance are labelled stadium II, and plots where only *H. stipulacea* was present (mono *H. stipulacea*) are labelled stadium III. (C) Diagram based on our observations and pilot data of the development of species composition over time on newly created bioturbation mounds. Without *H. stipulacea* presence, the mound can stay in stadium I, providing habitat for *Cassiopea*. However, when *H. stipulacea* shoots start growing (stadium II) it is likely that *Cassiopea* gets pushed out of its habitat and decreases in number while *H. stipulacea* steadily increases (stadium III).

Previously we have shown that cross-sections of this bay reflect a gradient of invasion history through time (Smulders et al. 2017, Christianen et al. 2019). Based on this monitoring data, we compared the number of invasive *H. stipulacea* shoots and bioturbation mounds in habitats that have been recently invaded to habitats that have been invaded for a longer time within 12 transects along the invasion gradient on Bonaire. Each transect consisted of 4 to 6 monitoring points (1 m^2), which were at least 20 m apart, and each point along the transect was situated either in a long-term or recently invaded habitat. Seagrass and bioturbation data were collected in February and March 2022, first averaged per habitat per transect and then compared between habitats (N = 12). We found that there was a significantly higher number of bioturbation mounds (paired t-test, t(11) = 2.983, p = 0.012) as well as *H. stipulacea* shoots (paired Wilcoxon rank-sum test, V = 64, p = 0.007) in areas that had been invaded for a longer time (2.8 ± 0.2 mounds m^{-2}, 767.0 ± 245.6 shoots m^{-2}) compared to recently invaded areas (1.6 ± 0.2 mounds m^{-2}, 140.6 ± 55.1 shoots m^{-2}). We hypothesize that this trend can be explained by the fact that plant species with colonizing traits such as *H. stipulacea* have a shallow and low biomass root system. This provides a more favorable habitat for burrowing animals, just like has been found for squirrel mounds that show a higher density in areas with more invasive cheatgrass which is structurally less complex (Blank et al. 2013). Therefore, there will likely be a more frequent creation of bare habitats, but these habitats do not persist as the invasive seagrass *H. stipulacea* can quickly cover the bioturbation mounds. *Cassiopea* will thus have to increase its moving frequency between these mounds, which alters its metabolic costs and may potentially impact its survival.

Our preliminary data suggests that there is competition between the native opportunist species, the photosynthesizing *Cassiopea* spp., and the fast-growing invasive seagrass *H. stipulacea* within niches created by bioturbation activity. A suggestion for future work would be to monitor the bioturbation frequency and reproductive success of *Cassiopea* over time in invaded ecosystems. It is recommended to test if invasive seagrass generally wins this competition as our preliminary data suggests, or under which conditions co-existence may be possible (Valladares et al. 2015). Overall, the detected pattern involving invasive seagrass, native jellyfish, and bioturbating ecosystem engineers has the potential to drive patch dynamics within these vegetated marine ecosystems.

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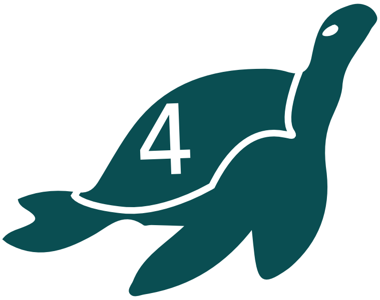

CHAPTER

Animal-borne video reveals atypical behaviour in provisioned green turtles: a global perspective of a widespread tourist activity

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ABSTRACT

Feeding wildlife as a tourist activity is a growing industry around the world. However, providing alternative food sources can affect wildlife ecology and behaviour. In this study, we combined animal-borne cameras on five sub-adult green turtles (*Chelonia mydas*) from the Bahamas with a global review to directly assess impacts of provisioning on the behaviour of an endangered marine species for the first time. Descriptive evidence from video footage, with videos included in the manuscript, showed that the tagged turtles spent 86% of their time in shallow water (< 1.5 m) at a provisioning site. All individuals observed, both tagged and untagged, actively approached people and boats, with up to 10 turtles recorded feeding on squid offered by tourists at one time. During these feeding events, multiple accounts of atypical aggressive behaviour such as biting and ramming conspecifics were recorded. Furthermore, a review of online sources revealed the widespread significance of turtle feeding as a tourist activity in at least 20 locations within the global range of green sea turtles, as well as five locations with regular provisioning of loggerhead (*Caretta Caretta*) and hawksbill (*Eretmochelys imbracata*) turtles. At the majority of the locations, turtles were fed animal matter such as fish scraps and squid. Although sample size limited quantitative analyses, we found indications of relatively high growth rates of two tagged turtles and low seagrass intake rates of all five tagged turtles. Therefore, our results emphasize the need to further investigate the impacts of turtle provisioning on natural foraging behaviour, ecosystem functioning as well as turtle growth rates and health implications. Supplemental feeding may increase habituation and dependency of turtles on humans with risks for turtle conservation. The innovative use of animal-borne camera technology may provide novel insights to behavioural consequences of human-wildlife interactions that can aid in the management and conservation of rare or endangered species.

Link to videos

4.1 INTRODUCTION

Globally, wildlife tourism is a rapidly growing industry centred around observation and interaction with wild animals. One such method employed to predictably experience wildlife, is the use of bait to attract and feed the animals, referred to hereafter as 'provisioning'. This tourist activity started in terrestrial ecosystems as reported for wild monkeys and bears (Knight 2010, Kojola and Heikkinen 2012), and is now widely reported in marine systems, such as provisioning of sharks, dolphins, stingrays, teleost fish and other species (Shackley 1998, Maljković and Côté 2011, Feitosa et al. 2012, Foroughirad and Mann 2013). Provisioning can lead to positive impacts on wildlife conservation through increased awareness and connecting people with nature, which, in some cases has been demonstrated to have little to no negative effect to marine animal behaviour and functioning (Maljković and Côté 2011, Hammerschlag et al. 2017). However, provisioning wildlife can also have both short and long-term negative effects, such as reduced health of the animals, dependency on the food provided by humans and inter or intraspecific aggressive behaviour (Orams 2002, Dubois and Fraser 2013, Murray et al. 2016). Eventually, this could impact the breeding success of entire populations (Orams 2002, Higginbottom 2004). For example, southern stingrays (*Hypanus americanus*) that were fed by tourists in the Caribbean, were more likely to contain ecto-dermal parasites and more likely to be injured by boats or predators than non-fed stingrays (Semeniuk and Rothley 2008). Furthermore, provisioning bottlenose dolphins (*Tursiops aduncus/truncatus*) has resulted in both agonistic behaviour towards tourists and conspecifics as well as decreased female reproductive success compared to non-provisioned females (Orams et al. 1996, Senigaglia et al. 2019). Given the global increase in wildlife tourism, it is critical to develop research tools to closely monitor these interactions in order to mitigate potential impacts to wildlife.

Green turtles (*Chelonia mydas*) are considered herbivorous during most of their juvenile to adult life stages but have been reported as omnivorous in some locations (Bjorndal 1980, Mortimer 1981, Seminoff et al. 2002, Nagaoka et al. 2012). Further, they have been demonstrated to prefer a food source that is high in protein, such as fish, when presented with the opportunity (Stewart et al. 2016, Monzón-Argüello et al. 2018). Therefore, green turtles are reliable candidates for tour operators to attract using fish as bait. Green turtles are internationally protected by law preventing global trade (CITES 1973), after (sub) populations were historically decimated due to decades of exploitation (Jackson et al. 2001). National laws have incorporated further protection of sea turtles. For example, in The Bahamas, turtles have been fully protected since

2009, prohibiting the harvesting, possession, purchase and sale of all species and their eggs (Bjorndal and Bolten 2010). However, in many nations, legislation does not extend to touching, handling or feeding turtles. This is of concern, as turtles can be exploited in novel ways due to global demand for wildlife tourism and provisioning activities may be having unknown impacts on turtle behaviour as well as their habitats throughout their range. Furthermore, insight into the global scale at which provisioning activities currently occurs and how those activities impact the behaviour of green turtles is urgently required to improve management and future conservation of this endangered species.

Here, we used camera tag technology as a novel method to investigate how turtle provisioning may affect the behaviour of sub-adult green turtles at an established tourism site from The Bahamas. In addition, we collated online sources in the assessment of a global review of turtle provisioning from similar tourism operations, and through our own study, propose important considerations for future research efforts.

4.2 MATERIALS AND METHODS

This study was conducted at Bottom Harbour, north Eleuthera, The Bahamas (25°.465294, -76°.634903) in November 2019. Bottom Harbour is a shallow water inlet of the western Atlantic Ocean with a mean depth of approximately 3.5 meters and dominated by vast, continuous *Thalassia testudinum* seagrass meadows, interspersed with soft sediments and low-profile coral reef (Figures in Appendix 4.A). The site was selected because of the high volume of green turtles historically encountered there, and subsequent tourist provisioning operations that have since been established. Provisioning of turtles at this site started in August 2017, and both guided tour and private boat visits have increased since then up to a current rate of about 10 boats day^{-1} in low season (April to November) and 30 to 40 boats day^{-1} in high season (November to April) (O'Shea. Pers. Obs.).

Activity of green turtles was recorded using animal-borne camera tags. Turtles were captured by hand in the morning at a location where feeding regularly takes place (1 m deep, Appendix 4.A). Metrics of size were recorded (curved carapace length *CCL* (cm), curved carapace width *CCW* (cm) and weight (kg)) before camera tags were attached. Tag packages consisted of an action camera in a housing (Drift Ghost X), depth and temperature datalogger (Sensus Ultra), a GPS tracker for retrieval (Spy Spot investigations, GL300-W) attached to a foam float (30 g of ethylene-vinyl acetate copolymer, 120 kg m^{-1}). The design of the camera package allowed its dry weight to be offset whilst submerged, so to minimize positive buoyancy that may influence turtle behaviour (dry weight: 407 g, wet weight: 420 g, 89 g upward buoyancy). The camera tags were attached via corrodible pop-up links to the carapace of the turtle with cool-setting epoxy (after Thomson and Heithaus 2014). Turtles were subsequently released over one km from the position of capture at the opposite side of the bay, to a shallow (2 m) high-canopy seagrass meadow (Appendix 4.A). Cameras recorded turtle behaviour for a maximum of five hours or until darkness. The camera tag was released from the turtle ~5-9 hours after deployment and retrieved through real-time GPS tracking.

To investigate behaviour and habitat use, all videos were viewed in their entirety by one observer and the behaviour of the tagged turtles was classified every second into the main behaviour types: swimming, resting, natural grazing and provisioning. All turtles resumed typical behaviours (feeding, resting) within 30 minutes of deployment; therefore, the first 30 minutes were removed from video and depth data analyses. Additionally, untagged turtles recorded on camera were identified by morphological irregularities (such as irregular carapace scutes and scars) in combination with identification of unique facial scute patterns (Reisser et al. 2008). Turtles that could be identified this way were separately labelled (Appendix 4.C). The number of feeding events during provisioning of both untagged and tagged turtles was counted. Aggressive encounters, which were defined by turtles specifically targeting other turtles (both tagged and non-tagged) by either biting, ramming, high-speed chasing and stealing bait were recorded, and treated as separate observations. Daily seagrass intake rates were extrapolated using camera observations and seagrass field measurements. Growth rates of recaptured individuals were calculated (see Appendix 4.F for methods).

To analyse the global significance of provisioning of sea turtles by tourists, we compiled a database with locations where feeding activity has been reported multiple times in the last five years. This was done by searching on various social media and repository websites, such as Web of Science, Youtube, Instagram, Twitter and TripAdvisor for keywords “feeding” or “fed” and “turtle(s)” or “sea turtle(s)”. Only locations where photographs or videos provided direct evidence of feeding activity were included.

4.3 RESULTS AND DISCUSSION

4.3.1 Behavioural observations from camera tags

In total, we analysed 1088 minutes (~ 18 hours) of video footage from cameras retrieved from five individual turtles and we were able to identify and observe the behaviour of a further 12 individuals through filmed encounters. One turtle was tagged on a day when tourist boats were absent. Six videos show compilations of observed atypical turtle behaviour and encounters with conspecifics and humans (all videos accessible through digital version of the paper).

All tagged turtles showed habituation to regular provisioning activity by spending on average 406 ± 66 minutes (86% ± 6) of their time resting, swimming and feeding in the shallows (<1.5 m) in immediate proximity to the primary provisioning site (Appendix 4.B), resting in groups of up to 12 individuals (Fig. 4.1A, Video 4.1). Turtles were shown to return to the provisioning site (17 ± 4 minutes) after release. Resting in very shallow habitats is uncommon for this species, as shallow, higher-energy zones are known to exacerbate buoyancy regulation in turtles (as seen in Video 4.1) (Hays et al. 2004, Seminoff et al. 2006). This suggests that the camera tags were not negatively influencing the buoyancy in these individuals. Lastly, observing these turtles resting in loose aggregations as observed here, particularly during diurnal periods, is further confounding from what we know for this species (Bjorndal 1980, Ogden et al. 1983, Fujisaki et al. 2016).

Adaptive behaviour of solitary animals gathering in anticipation of provisioning activity was also seen in bull sharks (*Carcharhinus leucas*) and multiple ray species (as summarized by Burgin and Hardiman 2015). All turtles in this study were resting at the provisioning site at sunset, thus, corroborating behavioural responses of other known provisioned sub-populations, for example, whitetip reef sharks (*Triaenodon obesus*), southern stingrays and long-tailed macaques (*Macaca fascicularis*) (Fitzpatrick et al. 2011, Corcoran et al. 2013, Ilham et al. 2018). Therefore, these turtles may have optimized their diurnal spatial movements in order to benefit most from the provisioning activity.

One tagged turtle and at least nine untagged individual turtles recorded on camera were offered squid and all were observed to consume the squid during multiple provisioning events from multiple operators (Fig. 4.1C, D, Video 4.2, 4.3, 4.4). The tagged turtle consumed 35 portions of squid supplemented by at least five separate tourist boat tours within a period of one hour. Although videos of the other four

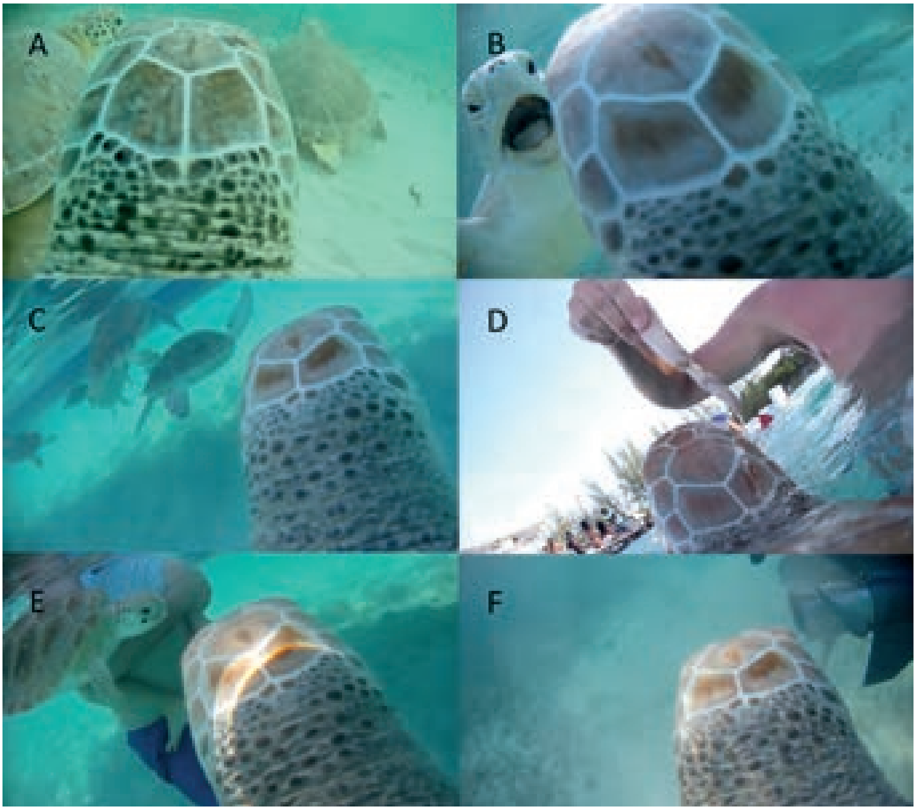

Figure 4.1 Video stills A-F link directly to Videos 4.1-4.6 of atypical behaviour associated with the provisioning on green sea turtles (*Chelonia mydas*) behaviour. **A)** Turtles resting in groups near the provisioning site (Video 4.1). **B)** Turtles displaying aggressive behaviour during provisioning (Video 4.2). **C)** Provisioning of a group of turtles by multiple tourist boats (Video 4.3). **D)** Turtles being hand-fed by tourists (Video 4.4). **E)** Turtles approaching and biting tourists in the water (Video 4.5). **F)** Turtles approaching jetties, boats and engine propellers (Video 4.6). Link to videos: https://doi.org/10.4121/86ec78aa-288a-44c7-b71e-a34ddec913bf

tagged turtles did not record provisioning activity, their behaviour suggested they are regularly fed squid, including their capture by hand, at the provisioning site for the present study. This was further evidenced by individuals being identified and observed feeding at the provisioning site on different days prior to and after their camera tag was released (Appendix 4.E).

Provisioning resulted in an increase of behaviours considered atypical, both among turtles as well as between turtles and people feeding them. The provisioned turtle that was fitted with a camera tag was involved in 15 separate events of intraspecific aggressive behaviour, while five untagged turtles were recorded displaying aggressive behaviour towards conspecifics, all during provisioning (Fig. 4.1B, Video 4.2). A single southern stingray and various teleost species were observed during provisioning events competing for squid and resulting in direct competition with the turtles (Fig. 4.1B,C, Video 4.2, 4.3). Aggression during foraging is not considered natural behaviour for green turtles from this region (Bjorndal 1980); however, aggressive behaviour linked to provisioning was earlier reported in tourist-fed loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea (Comis et al. 2015), and many other marine animals, such as various stingray and dolphin species (Orams et al. 1996, Semeniuk and Rothley 2008), with potential impacts on social behaviour and structure of the fed animals (Orams 2002).

Furthermore, turtles were observed to actively approach and bite tourists with and without the provision of squid (Fig. 4.1E, Video 4.5). This behaviour is becoming increasingly frequent near the provisioning site and has seemingly been exacerbated by the sudden decrease in tourism and associated provisioning activity in 2020 due to COVID-19 restrictions (pers. comms. with local residents). Increases in agonistic behaviour towards people or biting incidents as a consequence of wildlife provisioning has been reported for a large range of animals such as sharks, bears, dolphins and groupers (Perrine 1989, Orams et al. 1996, Hammerschlag et al. 2012, Kojola and Heikkinen 2012), potentially leading to counter-productive perceptions of wildlife by tourists, subsequently harming conservation efforts for endangered species (Hobday 2012).

4.3.2 Global scale and prospective regulation of sea turtle provisioning activity

Across their global range, green turtles are regularly being fed from at least 20 locations in 15 countries in-situ to their natural habitat (Fig. 4.2, Appendix 4.D, 4.E), which may be having unreported deleterious effects on this species. At 13 of these locations (65%), the main food type offered to the turtles consisted of animal matter such as fish scraps, squid or conch. At seven other locations, plant matter such as fruit, lettuce or macroalgae was fed to the turtles. This global concept is not only restricted to green turtles, as we found evidence of loggerhead turtles being fed at four locations in two countries in the Mediterranean Sea, and hawksbill turtles at one location in the Pacific

Ocean (Fig. 4.2). Habituation of turtles to humans and provisioning activity – such as groups of gathered turtles and tourists handling turtles above water - is clearly visible on the images provided by tour operators and their customers worldwide and in line with results from our camera study (Video 4.3, 4.5, Appendix 4.E). Manipulating site fidelity and habituation to people may exacerbate poaching activity, which, despite local and regional laws, does still occur in various locations throughout these turtle's range, such as in Malaysia and in the Gulf of Venezuela (Joseph et al. 2019, Barrios-Garrido et al. 2020). The anticipated increased risk of poaching became reality for this research site in The Bahamas. Within a year after completing the fieldwork, a local tour operator illegally removed eight turtles from this provisioning site to presumably sell within a nearby island community (this was witnessed and relayed to the authors on the condition of anonymity).

Provisioned turtles may also be at greater risk of boat strike incidents, as postulated earlier by Stewart et al. (2016) and Monzón-Argüello et al. (2018). In our study, turtles were observed to actively approach jetties and boats - likely due to a conditioning of engine noise - and seemed unperturbed by propellers until they were in very close proximity (Fig. 4.1F, Video 6). Consequences of similar behaviour were reported for tourist-fed southern stingrays, where 85% of the individuals had injuries such as propeller cuts, related to feeding activity in Grand Cayman (Semeniuk and Rothley 2008).

Figure 4.2 Locations where regular provisioning of green sea turtles (*Chelonia mydas*, circles), loggerhead turtles (*Caretta caretta*, triangles) and hawksbill turtles (*Eretmochelys imbricata*, rectangles) as a tourist activity has been reported. Arrow points to the location of this study. In green: main habitat range of green sea turtles (adjusted from Seminoff 2004).

Another potential threat is that apex predators such as sharks are attracted to sites where tourists are provisioning their prey, increasing the risk of incidental attacks (Brena et al. 2015) and disrupting natural predator-prey behaviour with impacts on the wider ecosystem (Kiszka et al. 2015). Turtle provisioning most likely increases the dependency on humans for food, causing behavioural anomalies and under-nourishment when tourist activity fluctuates or is suddenly terminated, such as seen globally during the decreasing tourist numbers following the COVID-19 pandemic (Higginbottom 2004, Nicola et al. 2020).

Wildlife interactions that reduce harm or impact to the target species can be encouraged by local education, regulation and management. Education about the potential impacts of wildlife provisioning has shown to be important in the development of sustainable tourist-wildlife activities (Murray et al. 2016). Tour operators can be informed by local nature management agencies about the potential consequences of feeding, such as shifts in aggression towards people. Local governments or conservation agencies may consider enforcing bans on the feeding of sea turtles, as has been done for bears, dolphins and monkeys (Orams 2002). With global increases in wildlife provisioning, attention is required to monitor and mitigate impacts associated with wildlife tourism and to develop sustainable tourist-wildlife activities.

4.3.3 Priority questions to motivate future research

Our results emphasize the need to study impacts of provisioning on seagrass intake rates, turtle health and ecosystem dynamics. Future studies should address increases in sample size and a direct comparison to non-provisioned turtles to investigate whether provisioning is causing the behavioural observations observed here (biased site fidelity, altered diet, aggressive behaviour), and validated though the wider assessments presented here. Additionally, a potential shift in diet may impact natural grazing behaviour and seagrass dynamics. The videos show that turtles would still eat seagrass outside of provisioning activity (Video 4.6). We calculated that the tagged turtles had a low average projected daily seagrass intake (6.4 g DW/day/turtle, Appendix 4.B) when tourists were present, but that the turtle tagged on the day when tourists were absent, had a higher daily seagrass intake (34.3 g DW/day), which falls within the reported range of 30-220 g DW needed per sub-adult turtle per day (Bjorndal 1982, Thayer et al. 1982, Williams 1988). Therefore, turtles may either increase their seagrass uptake rate in absence of provisioning or have adjusted their seagrass intake as a direct result of provisioning, with potentially unknown impacts on wider ecosystem functioning.

Lastly, two of our studied turtles had been previously tagged and measured revealing rudimentary growth rates. One turtle, which was initially tagged in 2017, just after provisioning charters started, revealed values exceeding previous reported Bahamian turtle growth rates (Bjorndal and Bolten 1988), with an increase in Body Condition Index (BCI) from 1.17 (2017) to 1.27 (2019), 5.49 cm CCL and 6.8 kg year^{-1}. Increases in weight, length and BCI as well as the well-fed appearance of other provisioned turtles in Video 4.3 and 4.4 suggest that provisioning may compensate for the recorded low seagrass intake rates in terms of growth. The global study revealed that mostly animal matter is fed to the turtles, which is a food source outside their usual trophic level and can increase growth rates and impact green turtle health (Bjorndal 1985, Stewart et al. 2016). Therefore, it is worthwhile to study the impacts of potential atypical growth rates of provisioned turtles on turtle health and reproductive success.

4.3.4 Conclusion

Here, we demonstrated for the first time, behavioural impacts associated with tourist driven provisioning of wild marine turtles using a novel animal-borne tag package and applications of such technology. Further, addressing these types of manipulated wildlife interactions at a global scale, highlights the potential broader implications for animal welfare, conservation and wider ecosystem function. Animal-borne camera tags were found to be highly practical and efficient for data collection and this study serves as a pioneering proof of concept to observe interactions between wildlife and humans. Together with additional long-term and comparative studies with increased sample sizes these camera data will underpin more effective methods in assessing the impact that feeding has on wild animal behaviour, growth and reproductive success. Increased education, monitoring and regulation with regards to the feeding of sea turtles and other wildlife may ensure sustainable tourist-wildlife relationships in the future.

ACKNOWLEDGMENTS

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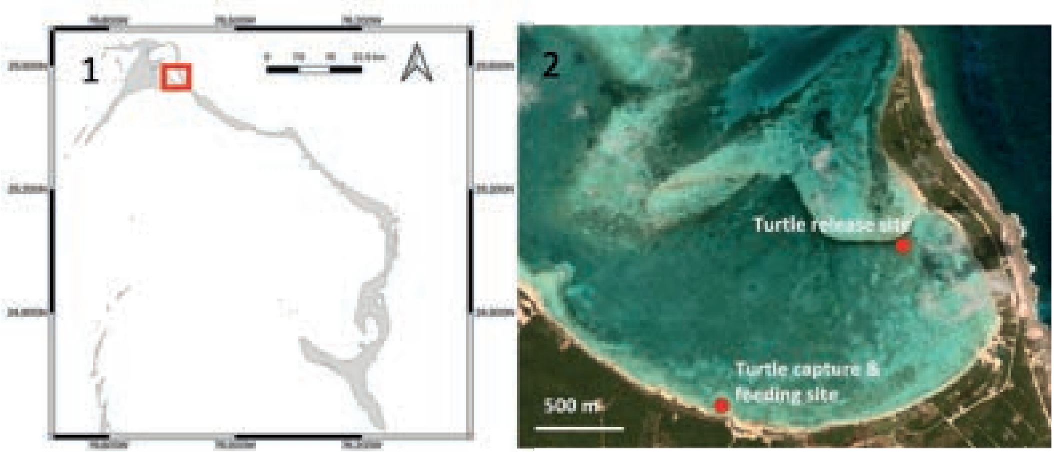
APPENDIX 4.A

Study site



APPENDIX 4.B

B1. Metrics of size of individual green turtles and camera tag recordings (BCI: Body Condition Index). B2. Activity budget and seagrass intake quantity of the studied green turtles

Turtle ID	Date	Provisioning activity observed on date of tagging	Weight (kg)	BCI	Duration depth data (min, first 30 min removed)	Duration video data (min, first 30 min removed)	Average depth (meters +/- SD)
CM1*	8 Nov '19	Yes	13.5	1.25	553	250	0.82 +/- 0.3
CM2	8 Nov '19	Yes	16.5	1.44	325	199	0.63 +/- 0.3
CM3*	9 Nov '19	No	27.5	1.27	418	220	0.69 +/- 0.3
CM4	10 Nov '19	Yes	9.5	1.12	----	264	----------------
CM5	10 Nov '19	Yes	19.5	1.19	568	155	0.72 +/- 0.2

* turtle from tag-recapture study

Turtle ID	% Resting (% of analysed video data)	% Swimming (% of analysed video data)	% Grazing seagrass+ macroalgae (% of analysed video data)	% Feeding of tourists (% of analysed video data)	Total intake Seagrass (g DW for analysed video data)	Projected intake seagrass (g DW day^{-1})
CM1*	63	37	0	0	0	0
CM2	3	70	11	16	2.1	7.6
CM3*	16	47	37	0	10.5	34.3
CM4	15	73	13	0	1.9	5.1
CM5	57	33	10	0	0	0

* turtle from tag-recapture study

APPENDIX 4.C

Raw data on feeding and aggressive events of tagged turtle CM2 and untagged turtles (labelled “Turtle #”) on November 8, 2019.

				Agresive behaviour					Provisioning activity		
Video	Time	Turtle ID	Tagged/ Untagged	Biting	Stealing	Ramming	Chasing	Receiving Turtle	Squid by stick	Squid in water	Squid by hand
VID00014	19:47	CM2	Tagged				1	Turtle #7			
VID00014	19:48	Turtle #7	Untagged							1	
VID00014	19:56	CM2	Tagged	1				Turtle #8			
VID00014	20:15	Turtle #9	Untagged	1				CM2			
VID00014	23:20	CM2	Tagged	1				Turtle #9			
VID00014	24:13:00	Turtle #10	Untagged	1				CM2			
VID00014	24:56:00	Turtle #11	Untagged	1				CM2			
VID00014	28:49:00	Turtle #1	Untagged						1		
VID00014	28:52:00	Turtle #9	Untagged			1		CM2			
VID00014	28:45-29:51	CM2	Tagged						9		
VID00014	29:30:00	Turtle #4	Untagged						1		
VID00015	00:19	CM2	Tagged							1	
VID00015	01:07	CM2	Tagged						1		
VID00015	01:14	CM2	Tagged						1		
VID00015	01:35	Turtle #7	Untagged						1		
VID00015	01:39	CM2	Tagged						2		
VID00015	01:47	Turtle #3	Untagged						1		
VID00015	03:35	CM2	Tagged								
VID00015	06:45	CM2	Tagged							1	
VID00015	06:52	CM2	Tagged							1	
VID00015	10:11	Turtle #6	Untagged						1		
VID00015	10:19	CM2	Tagged							1	
VID00015	16:40	CM2	Tagged	1				Turtle #3			
VID00015	18:15	Turtle #3	Untagged							1	
VID00015	19:36	CM2	Tagged								
VID00016	03:51	CM2	Tagged								1
VID00016	04:00	CM2	Tagged								1
VID00016	04:14	CM2	Tagged								1
VID00016	04:35	CM2	Tagged								1
VID00016	05:15	Turtle #9	Untagged								1
VID00016	05:20	Turtle #9	Untagged		1			CM2			

VID00016	05:21	CM2	Tagged						1
VID00016	05:30	CM2	Tagged						1
VID00016	05:37	Turtle #12	Untagged						1
VID00016	05:45	CM2	Tagged		1		Turtle #12		
VID00016	05:50	CM2	Tagged						1
VID00016	05:51	Turtle #12	Untagged	1			CM2		
VID00016	05:55	CM2	Tagged						1
VID00016	06:05	CM2	Tagged						1
VID00016	06:18	Turtle #12	Untagged						1
VID00016	06:48	CM2	Tagged						1
VID00016	06:51	Turtle #12	Untagged						1
VID00016	06:54	CM2	Tagged						1
VID00016	07:01	CM2	Tagged						1
VID00016	07:07	Turtle #12	Untagged						1
VID00016	07:05	Turtle 2	Untagged						1
VID00016	07:13	CM2	Tagged						1
VID00016	07:18	CM2	Tagged					1	
VID00016	07:30	CM2	Tagged					1	
VID00016	07:47	CM2	Tagged						1
VID00016	07:52	Turtle #12	Untagged						1
VID00016	07:57	CM2	Tagged						1
VID00016	08:05	CM2	Tagged						1
VID00016	08:16	Turtle #12	Untagged						1
VID00016	11:46	Turtle #3	Untagged						
VID00016	11:57	Turtle #3	Untagged						
VID00016	11:58	Turtle #10	Untagged						
VID00016	12:01	Turtle #3	Untagged		1		CM2		
VID00016	12:12	CM2	Tagged		1		Turtle #3		
VID00016	12:15	CM2	Tagged						1
VID00016	12:32	CM2	Tagged						
VID00016	13:00	CM2	Tagged	1			Turtle #11		
VID00017	06:00	CM2	Tagged			1			

APPENDIX 4.D

Global review of locations where provisioning activity was reported multiple times in the last five years. The most extensive source is given, when needed followed by a second source to support the evidence. Sources that are preceded by bold letters in brackets correspond to the images in Appendix 4.E.

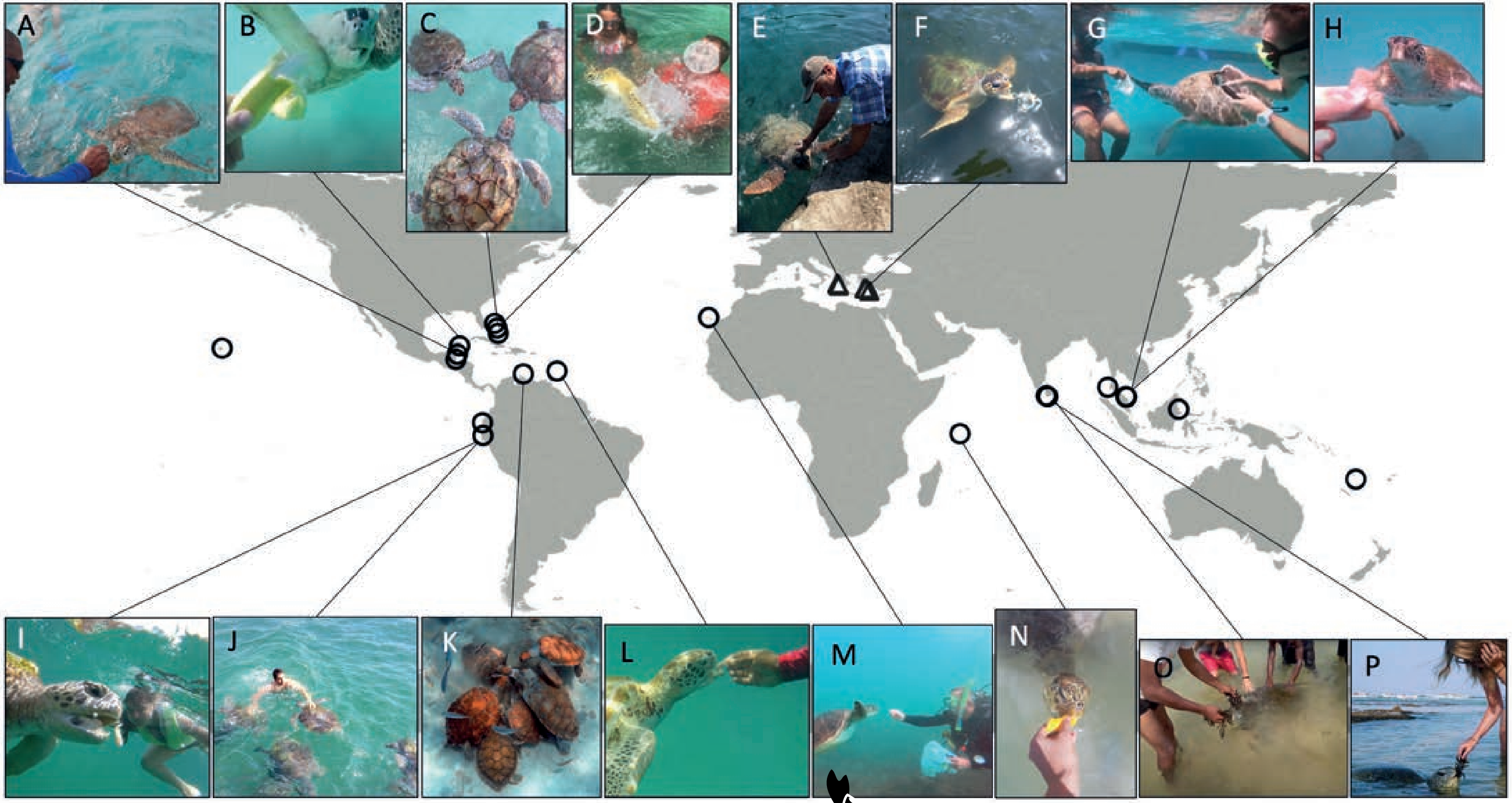
Location	Species	Type food	Feeding interaction	Source
Argostoli, Greece	C. *Caretta*	Fish, scraps	Fishermen and tourists from	https://www.tripadvisor.com/Attraction_Review-g780715-d11742463-Reviews-or5-Argostoli_Harbour-Argostolion_Cephalonia_Ionian_Islands.html#REVIEWS
	C. *Caretta*	Fruit	dock or from boats	https://www.researchgate.net/publication/281149662_Feeding_loggerhead_sea_turtles_increased_their_social_antagonistic_interactions_in_Kefalonia_Greece
Zakynthos,Greece	C. *Caretta*	Fruit	Tourists	https://www.archelon.gr/eng/ourdeltia.php?row=row10&nid=933
Kastellorizo, Greece	C. *Caretta*	Scraps	Fishermen from dock	**(e)** https://www.tripadvisor.com/Restaurant_Review-g189441-d1897678-Reviews-Athena_Fish_Tavern-Kastellorizo_Dodecanese_South_Aegean.html
Dalyan, Turkey	C. *Caretta*	Crab	Tourist boat tours	https://www.tripadvisor.com/Attraction_Review-g311315-d2513280-Reviews-or10-Iztuzu_Beach-Dalyan_Mugla_Province_Turkish_Aegean_Coast.html#REVIEWS
	C. *Caretta*	Crab		**(f)** https://www.tripadvisor.com/Attraction_Review-g298033-d552749-Reviews-Dalyan_Nehri-Marmaris_Marmaris_District_Mugla_Province_Turkish_Aegean_Coast.html
Tenerife	C. *Mydas*	Fish, scraps	Tourist boat tours	https://doi.org/10.1016/j.scitotenv.2017.10.126
	C. *Mydas*	Fish, scraps		**(m)** https://www.tripadvisor.com/Attraction_Review-g315919-d3187102-Reviews-Paradise_Divers-Adeje_Tenerife_Canary_Islands.html#REVIEWS
Mirissa/Weligama, Sri Lanka	C. *Mydas*	Macroalgae	Tourist boat tours	https://www.tripadvisor.com/Attraction_Review-g612380-d15814049-Reviews-Turtle_Bay_Activities-Weligama_Matara_Southern_Province.html
	C. *Mydas*	Macroalgae		https://thrillingtravel.in/turtles-snorkeling-in-mirissa-sri-lanka.html
Hickaduwa, Sri Lanka	C. *Mydas*	Macroalgae	Tourist tours at the beach	**(n)** https://www.youtube.com/watch?v=_VUxQLJz2YI
	C. *Mydas*	Macroalgae		https://www.tripadvisor.co.nz/Attraction_Review-g304134-d7034305-Reviews-Hikkaduwa_Beach-Hikkaduwa_Galle_District_Southern_Province.html#REVIEWS

Similan islands, Thailand	*C. Mydas*	Fish, scraps	Tourist boat tours	https://sanookscuba.com/mooring-rocks/
	C. Mydas	Fruit		https://www.youtube.com/watch?v=gvl-bn9agEA
Pulau Redang,Malaysia	*C. Mydas*	Shrimp	Tourists	(g,h) https://www.youtube.com/watch?v=PuBzSQ0Nczg
Perhentian, Malaysia	*C. Mydas*	Squid	Tourist tours	https://www.tripadvisor.com/Attraction_Review-g304003-d4893824-Reviews-Turtle_Sanctuary_Beach-Pulau_Perhentian_Besar_Perhentian_Islands_Terengganu.html,
Pulau Derawan, Indonesia	*C. Mydas*	Banana leaves	Tourist tours at the beach	https://www.youtube.com/watch?v=uZWktNt9RFQ
Efate, Vanuatu	*C. Mydas*	Fruit	Tourist tours, semi-	(p) https://www.tripadvisor.com/Attraction_Review-g294144-d10086076-Reviews-John_s_Authentic_Island_Tours-Port_Vila_Efate.html
	C. Mydas	Fruit	enclosed bay	https://www.tripadvisor.com/Attraction_Review-g294144-d1469457-Reviews-Off_Road_Adventures-Port_Vila_Efate.html
Great barrier reef, Australia	*C. mydas*	Macroalgae	Divers	https://rumble.com/v4npal-feeding-a-turtle-in-the-great-barrier-reef.html and https://www.youtube.com/watch?v=SOjRhbUvK7Q&ab_channel=StephenStefiuk
Kimbe bay, Papua New Guinea	*E. imbricata*	Sponges	Divers	(o) https://www.youtube.com/watch?v=v6n0-eZ3AiQ&ab_channel=RumbleViral and https://www.sciencephoto.com/media/247863/view/feeding-a-hawksbill-turtle
Hawaii	*C. Mydas*	Fish, scraps	Tourist boat tours	https://www.tripadvisor.com/Attraction_Review-g60583-d3629089-Reviews-Kamaaina_Custom_Tours-Hilo_Island_of_Hawaii_Hawaii.html
	C. Mydas	unknown		https://twitter.com/DanChew68/status/468130767436922880
Placencia, Belize	*C. Mydas*	Lobster, conch	Tourist boat tours	http://www.ecomarbelize.org/wildlife-interactions.html
	C. Mydas	Conch		https://www.tripadvisor.co.uk/ShowUserReviews-g291977-d1739026-r132741009-Placencia_Eagle_Ray_Tours-Placencia_Stann_Creek.html
Ambergris Caye, Belize	*C. Mydas*	Conch	Tourist boat tour	(a) https://www.tripadvisor.com/Attraction_Review-g291962-d4242476-Reviews-Belize_Master_Tours-San_Pedro_Ambergris_Caye_Belize_Cayes.html#REVIEWS
Puerto aventuras, Mexico	*C. Mydas*	Fruit	Tourists	(b) https://www.youtube.com/watch?v=bw62PwtGA2c
	C. Mydas	Fruit		https://www.tripadvisor.co.nz/ShowUserReviews-g153510-d673129-r628847150-Barcelo_Maya_Palace-Puerto_Aventuras_Yucatan_Peninsula.html

Piura,Peru	*C. Mydas*	Fish, scraps	Tourists swim in marked provisioning	**(i,j)** https://www.tripadvisor.com/Attraction_Review-g667820-d6406862-Reviews-Nadando_con_Tortugas_en_El_Nuro-Piura_Piura_Region.html
	C. Mydas	Fish, scraps	area with full connection to the sea	https://www.youtube.com/watch?v=9ZvZ2gHCAiY
Puerto Lopez, Ecuador	*C. Mydas*	Lettuce, fruit	Tourist boat tours	https://www.tripadvisor.com/Attraction_Review-g635730-d6415855-Reviews-or20-Aventuras_La_Plata-Puerto_Lopez_Manabi_Province.html#REVIEWS
Green Turtle Cay,	*C. Mydas*	Unknown	Tourist boat tours	https://www.tripadvisor.ca/ShowUserReviews-g147430-d149426-r470123044-Brendal_s_Dive_Center-Green_Turtle_Cay_Abaco_Islands_Out_Islands_Bahamas.html
The Bahamas	*C. Mydas*	Fish		https://www.instagram.com/p/Bi19HBin1hz/?utm_source=ig_web_copy_link
North-Eleuthera,	*C. Mydas*	Squid	Tourist boat tours	*This study*
The Bahamas	*C. Mydas*	Squid		**(c,d)** https://www.tripadvisor.com/Attraction_Review-g5785959-d13817344-Reviews-or5-Da_Salty_Pig_Adventures-Spanish_Wells_Eleuthera_Out_Islands_Bahamas.html
Little Farmers Cay, Exuma,	*C. Mydas*	Fish	Tourist boat tours	https://www.tripadvisor.ca/LocationPhotoDirectLink-g147429-d1059646-i249470113-Fowl_Cay_Resort-Great_Exuma_Out_Islands_Bahamas.html
The Bahamas	*C. Mydas*	Fish		https://www.tripadvisor.com/Attraction_Review-g147429-d8837395-Reviews-Aquadisiac_Adventures-Great_Exuma_Out_Islands_Bahamas.html
Playa Piskado, Curacao	*C. Mydas*	Fish, scraps	Tourist tours,	**(k)** https://www.info-curacao.com/en/tours/grote-knip-beach-and-snorkeling-with-sea-turtles/
	C. Mydas	Fish, scraps	provisioning by fishermen	https://www.viator.com/nl-NL/tours/Curacao/All-west-beach-hopping-tour/d725-74296P1
Barbados	*C. Mydas*	Fish, scraps	Tourist boat tours	https://doi.org/10.7589/52.2S.S104
	C. Mydas	Fish, scraps		(l) https://www.tripadvisor.com/Attraction_Review-g147263-d2202816-Reviews-Barbados_Excursions_Catamaran_Turtle_Snorkeling_Tour-Bridgetown_Saint_Michael_Par.html#REVIEWS

APPENDIX 4.E

Pictures displaying a variety of food offered as a tourist activity to green sea turtles (*Chelonia mydas*, circles), loggerhead turtles (*Caretta caretta*, triangles) and hawsksbill turtles (*Eretmochelys imbricata*, rectangles) globally. Tourists are regularly seen touching or holding turtles while provisioning. In-pictures A-P correspond to sources listed in appendix 4.D. In-Picture C) turtle at lower half of the picture is a resighting of CM2 (ID by carapace injury) at the turtle provisioning site in Eleuthera on Nov 30, 2019, 22 days after camera tag deployment, epoxy nearly dislodged. D) Most likely resighting of CM5 at turtle provisioning site (facial scute ID) at Jul 8, 2018, 430 days before camera tag deployment.



APPENDIX 4.F

Methods daily seagrass intake rate

Seagrass intake rates were calculated by multiplying the amount of bites taken on camera by leaf area (estimated leaf length per bite * averaged leaf width from field measurements) and averaged dry weight cm^{-2} (DW cm^{-2}) from field measurements of the separate seagrass species. Calculated total intake of DW hour^{-1} for each turtle was extrapolated to a projected seagrass intake day^{-1} (12 hours of daylight grazing, Williams, 1988). The projected value was then compared to the range of 30-220 g DW/ day, calculated by Williams 1988 to be needed by similar sized green sea turtles of 4 to 80 kg (Williams 1988, Thayer 198, Bjorndal 1980).

Turtle growth rates and body condition index

Turtle health implications were investigated using former tag data from tag-recapture studies. If a turtle was tagged prior, growth rates were calculated by subtracting former weight and CCL data from current measurements and dividing this by the number of years between tagging events. Body condition index (BCI) was calculated by first converting CCL to SCL using the equation (CCL = -0.414 + 1.039 * SCL), developed by Bjorndal and Bolten, 1989 for similar sized turtles, and then calculating the BCI using the equation (BCI = weight/SCL^3*10000, Bjorndal et al., 2000).

ANIMAL-BORNE VIDEO REVEALS ATYPICAL BEHAVIOUR IN PROVISIONED GREEN TURTLES: A GLOBAL PERSPECTIVE OF A WIDESPREAD TOURIST ACTIVITY

4

CHAPTER 5

Green turtles shape the seascape through grazing patch formation around habitat features: experimental evidence

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ABSTRACT

Understanding how megaherbivores incorporate habitat features into their foraging behavior is key towards understanding how herbivores shape the surrounding landscape. While the role of habitat structure has been studied within the context of predator-prey dynamics and grazing behavior in terrestrial systems, there is a limited understanding how structure influences megaherbivore grazing in marine ecosystems. To investigate the response of megaherbivores (green turtles) to habitat features, we experimentally introduced structure at two spatial scales in a shallow seagrass meadow in The Bahamas. Turtle density increased 50-fold (to 311 turtles ha^{-1}) in response to the structures, and turtles were mainly grazing and resting (low vigilance behavior). This resulted in a grazing patch exceeding the size of the experimental set-up (242 m^{2}), with reduced seagrass shoot density and aboveground biomass. After structure removal, turtle density decreased and vigilance increased (more browsing and shorter surfacing times), while seagrass within the patch partly recovered. Even at a small scale (9 m^{2}), artificial structures altered turtle grazing behavior, resulting in grazing patches in 60% of the plots. Our results demonstrate that marine megaherbivores select habitat features as foraging sites, likely as a predator refuge, resulting in heterogeneity in seagrass bed structure at the landscape scale.

Link to videos

5.1 INTRODUCTION

The physical arrangement of objects in space can determine the movements and grazing behavior of large herbivores (Treydte et al. 2010). Habitat structure may be used as shelter, for orientation, or as a food source, locally increasing the grazing impact and therefore shaping the surrounding landscape (Anderson et al. 2010, Khadka and James 2016). Habitat structure also plays an important role in predator-prey dynamics (Owen-Smith 2019). For example, herbivore prey that are chased down by predators are likely to use habitat features as both a place for shelter as well as to forage, indicated by locally increased grazing and reduced plant biomass (Bakker et al. 2005, Creel et al. 2005). On the other hand, ambush predators may incorporate habitat features such as tree logs or rocky outcrops in their hunting strategy (Podgórski et al. 2008, Smith et al. 2019), causing prey to avoid grazing near these features (van Ginkel et al. 2019). In contrast to terrestrial ecosystems, there is a limited understanding of how habitat features influence megaherbivore grazing behavior in marine ecosystems.

Seagrass ecosystems provide important foraging habitat for large marine grazers, in which patch reefs (e.g. coral boulders) as well as manmade structures (e.g. jetties or wrecks) commonly occur and provide some habitat structure. Green turtles (*Chelonia mydas*) use these shallow seagrass systems as foraging grounds and display high foraging site fidelity (Shimada et al. 2020). Anecdotal evidence describes that turtles may use vertical habitat features as refuge from predation from sharks (Thomson et al. 2011), and that turtles use coral boulders or caves to rest in at night, probably as shelter from predation (Christiansen et al. 2017). Additionally, a preference for safer edge habitats instead of interior shallow banks has been described for turtles in Shark Bay, Australia, with impacts on grazing behavior and vegetation structure (Heithaus et al. 2007, Burkholder et al. 2013). This can be explained by the hunting preference of the main turtle predators, tiger sharks (*Galeocerdo cuvier*), for homogeneous shallow seagrass meadows where escape opportunities for prey are limited (Heithaus et al. 2002a, 2002b). Small marine herbivores such as urchins and fishes use structural features such as coral formations as shelter, increasing grazing pressure around these structures and forming grazing ‘halos’ (DiFiore et al. 2019), however experimental evidence of a similar mechanism for larger marine herbivores is lacking. Therefore, it remains unknown whether large marine grazers, such as turtles, incorporate natural or artificial habitat features in their foraging site selection, and if so, what the specific requirements (e.g., dimensions, number of features) are of those habitat features.

In this study, we assessed if and how green turtles exhibit variation in grazing behavior and impact in response to the presence of habitat features. Additionally, we explore whether this behavior is dependent on the size of an area with habitat features. To this purpose, we experimentally added artificial structures (mesh cages) in both large- and small-scale arrays to a shallow bay with extensive seagrass meadows on Eleuthera, the Bahamas. Based on previous findings that turtles seek shelter near corals at night, as well as their known predator-prey dynamics, we expect turtles to select structures in both the small- and large-scale arrays as their preferred foraging site, resulting in local increases in turtle density, a decrease in vigilant behavior and grazing patch initiation with impacts on seagrass structure.

5.2 MATERIALS AND METHODS

5.2.1 Study site

The experiments were conducted at Bottom Harbour, north Eleuthera, The Bahamas (25.465294, -76.634903) from May 2018 to August 2020. Bottom Harbour is a shallow water inlet of the western Atlantic Ocean with a mean depth of approximately 3.5 meters, dominated by a continuous high-cover *Thalassia testudinum* seagrass meadow. The bay provides a year-round foraging site for sub-adult green turtles (*Chelonia mydas*), and is situated within The Bahamas shark sanctuary (Gallagher et al. 2021). Large numbers of turtle predators (tiger shark, *Galeocerdo cuvier*) have been reported in the region of our study site (Talwar et al. 2020) and others, summarized in Appendix 5.A).

5.2.2. Experimental design

The impact of habitat features on green turtle foraging behavior was tested by establishing arrays of artificial structures at two spatial scales. During the study's initial phase (the large-scale experiment) we tested the turtle response to the presence of refuges/shelter, represented by a group of artificial structures. An experimental array of (partial) cages, interspersed with open plots, was established as part of a larger experiment studying seagrass herbivory, the *Thalassia* Experimental Network (TEN), led by J.E. Campbell. In total, the set-up consisted of a grid of 50 individual 0.5 x 0.5 x 0.5 m (herbivore exclusion) cages and open plots, each separated by 2 m, in an area of 23 x 10.5 m (241.5 m^2), (see Fig. 5.1a and Appendix 5.B for a detailed description). The structures were established on May 2, 2018 and removed March 28, 2019, after 11 months. After removal, four corner poles of the original experimental array were retained to continue measuring the turtle response within the area. At the start of the experiment, a large control area of the same size as the experimental array (23 x 10.5 m) was set up adjacent to the experimental array in an area within a similar continuous seagrass meadow.

Observations of turtle aggregation and grazing in the large-scale experimental array (Appendix 5.C), led to a separate follow-up experiment to study (1) whether this grazing response to the large-scale array depended on the size of the area with these structures and (2) whether turtles aggregate near the structures to rest inside. Therefore, on November 7, 2019, we established five small-scale arrays in a similar dense *T. testudinum* meadow approximately 50 m away from the large-scale experiment, consisting each of four subplots of 0.5 x 0.5 x 0.5 m (9 m^2 per array), marked with 4 corner poles, of which two sides were covered with vexar mesh (mesh size 1.5 cm) (Fig. 5.1e). Mesh was not added to the cage tops, preventing turtles from using the structures to rest and sleep in (as was observed in the larger array, Appendix 5.C).

5.2.3 Turtle density

We conducted aerial surveys using a drone (DJI Phantom 3) to determine the impact of added habitat features on turtle densities at our study site. The drone was flown to a fixed position 20 m above the large-scale experimental array and the control area. Both locations were maximum 2.5 m water depth to ensure turtle detection. Perception bias was minimized by only analyzing videos when glare could be minimized to <20% of the field of view, when water clarity allowed easy viewing of the bottom, both in the tall and grazed seagrass, and by viewing the footage three times (following (Whitman 2018), see Video 5.1 for a turtle moving through both tall and grazed seagrass). For each 10-minute video, the maximum number of turtles observed per given moment was recorded using the MaxN method (Mallet and Pelletier 2014). Turtles were identified visually and by movement (at least once during the deployments). The aerial surveys were not performed within 5 days after structure addition/removal to minimize impacts of human disturbance on turtle densities. Turtle densities were quantified four times while the large-scale array was present (October 2018 to February 2019), seven times after the array was removed (in the period of 2 to 7 months after removal; May to October 2019) and seven times in the control area (October 2018 to October 2019). Turtle densities are expressed as turtles ha^{-1}, consistent with previous studies (Christianen et al. 2014, Rodriguez and Heck 2021).

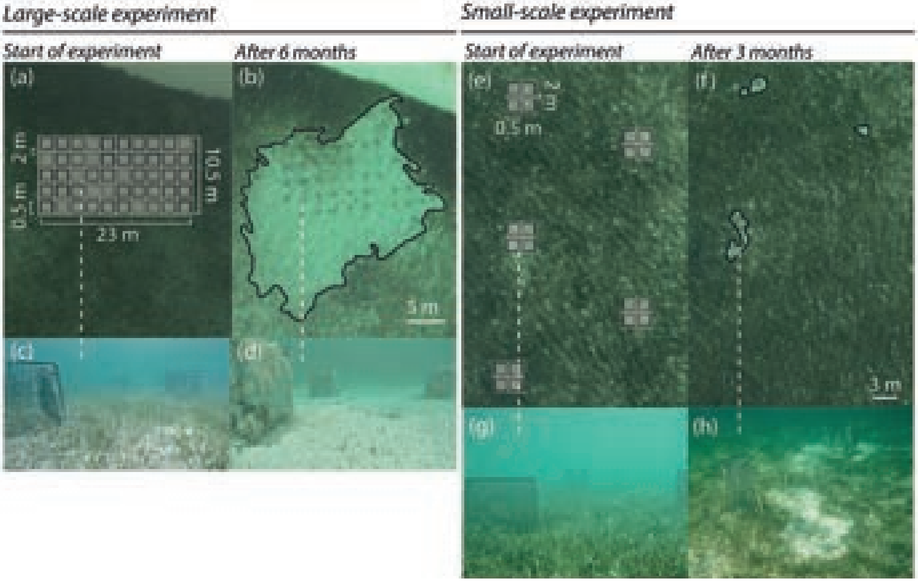

Figure 5.1 The set-up of the experimentally added habitat features and subsequent formation of grazing patches around the large scale (a-d) and small scale (e-h) arrays. Panels a and e are aerial images of the seagrass meadow at the time of structure establishment. The overlay diagrams represent the set-up of the artificial structures added as habitat features to the seagrass habitat (details in Appendix 5.B). Panels c and g are corresponding underwater pictures at plot establishment. Panels b and f show the black outlines of the grazing patches after 6 and 3 months respectively, and d and h are corresponding underwater pictures. Note the short-grazed seagrass around the structures in panels b, d, f and h. Pictures c, d, g made by F.O.H. Smulders, picture h made by O.R. O'Shea.

5.2.4 Turtle grazing behavior and vigilance

In the large-scale experiment, we estimated turtle residence time, grazing strategy and vigilance with and without habitat features using the aerial surveys. Per 10-minute aerial survey, we tracked each individual turtle by labelling it in a video editing program (Wondershare Filmora X10.1.3). In this way, we could quantify the total time (in minutes) each turtle spent within the boundaries of the experimental array. In addition, to describe the behavior for each turtle while inside the array, we calculated the percentage of time each individual turtle spent stationary (grazing/resting in/outside structure), intensively grazing (moving slowly in meandering grazing patterns across the grazing patch), browsing (passing by without intensively grazing and taking occasional bites) and breathing at the water surface. Megaherbivores have been described to decrease both surfacing time (Heithaus and Frid 2003), and time spent foraging (Wirsing et al. 2007a) under the risk of predation. Therefore, in this study we characterized browsing and short surfacing times as high vigilance, while resting and intensively grazing indicated low vigilance. The behavioral characteristics of individual turtles were averaged to obtain a single value per replicate survey.

5.2.5 Turtle grazing impact

To determine the impact of turtle grazing in between the structures of the large-scale array on seagrass structure, we measured *T. testudinum* cover, shoot density (# shoots m^{-2}), LAI (Leaf Area Index, one-sided leaf area m^2/ground area m^2), and leaf biomass (g DW m^{-2}). The seagrass properties were measured from biomass cores (15 cm diameter) taken within open plots and full cages at the moment of structure removal (11 months after plot establishment, n = 4).

The formation of grazing patches was calculated in both the large- and small-scale experimental arrays by using aerial images made monthly using a drone (DJI Phantom 3). We took underwater images after each drone survey to ground-truth the grazing patches, confirming that the difference between intensively grazed and ungrazed habitat was indicated by a light green to dark green color border. For the large-scale experiment, the experimental array was compared to a control area. In ImageJ (ImageJ 1.52q) the grazed area was converted to m^2 with plot size as a scale reference, assuming a homogeneously flat seafloor.

5.2.6 Data analysis

All data were tested for normality and homogeneity of variances (Shapiro Wilk test, Levene's test, $p > 0.05$). The difference in average turtle density, turtle residency time and grazing strategy between the large-scale experiment with structures present versus after structure removal as well as the difference in turtle density between the large-scale experiment with structures present and the control array were analyzed using Welch two-sample t-tests (comparing groups with unequal sample sizes and/or variances) or the Wilcoxon rank-sum test as the non-parametric alternative. The differences in seagrass cover, shoot density, LAI and aboveground biomass between open plots and caged plots were analyzed using two-sample t-tests (Student's t-test for equal variances and Welch's t-test for unequal variances), or the Wilcoxon rank-sum test as the non-parametric alternative. Non-parametric tests were performed on the data with non-normal asymmetric distributions, because of our small sample sizes. All statistical analyses were performed in R (R Core Team 2019), $p < 0.05$. Average values are presented together with standard errors.

5.3 RESULTS

5.3.1 Turtle density

The average turtle density in the large-scale array with structures (310.6 ± 20.7 turtles ha^{-1}, Fig. 5.2, Video 5.2) was significantly higher compared to the control area (5.9 ± 5.9 turtles ha^{-1}, Wilcoxon rank-sum test, W = 28, $p = 0.0049$), and compared to the large-scale array 2 to 7 months after structure removal (53.2 ± 14.9 turtles ha^{-1}, Wilcoxon rank-sum test, W = 28, $p = 0.0084$). There was a clear step-function decline in turtle density after removing the structures (Fig. 5.2a).

5.3.2 Turtle grazing behavior and vigilance

Turtles varied in their residence time and grazing behavior between the treatments. In the control area only one turtle visited the area during the observations (0.1 minutes residence time), prohibiting including the treatment in statistical analysis. Turtles stayed significantly longer in the array with structures present (7.6 minutes ± 0.5, N = 4) compared to the turtles in the array after structure removal (2.6 minutes ± 0.9, N = 6, Welch two-sample t-test, t(7.28) = - 4.90, $p = 0.0016$). Turtles spent significantly more time stationary (grazing or resting within the seagrass meadow) in the array with structures present (51% ± 5) compared to turtles in the array after structure removal (6% ± 4, Wilcoxon rank-sum test, W = 24, $p = 0.013$). Further metrics on behavior either indicating vigilance (browsing, short surfacing times) or non-vigilance (intensive grazing, long surfacing times) are listed in Appendix 5.G.

5.3.3 Turtle grazing impact

The differences in *Thalassia testudinum* seagrass cover, shoot density, LAI and leaf biomass were compared between open and caged plots situated within the large-scale experimental array 11 months after the array was established. All seagrass properties were significantly reduced in the open plots compared to the caged plots (Fig. 5.2d, Appendix 5.D, 5.E)

Grazing patches were formed both in the large-scale array as well as in the follow-up small-scale arrays. In the large-scale array, a single grazing patch of 918 m^2, covering the area of the experimental plots and beyond (348% of the total array) formed around

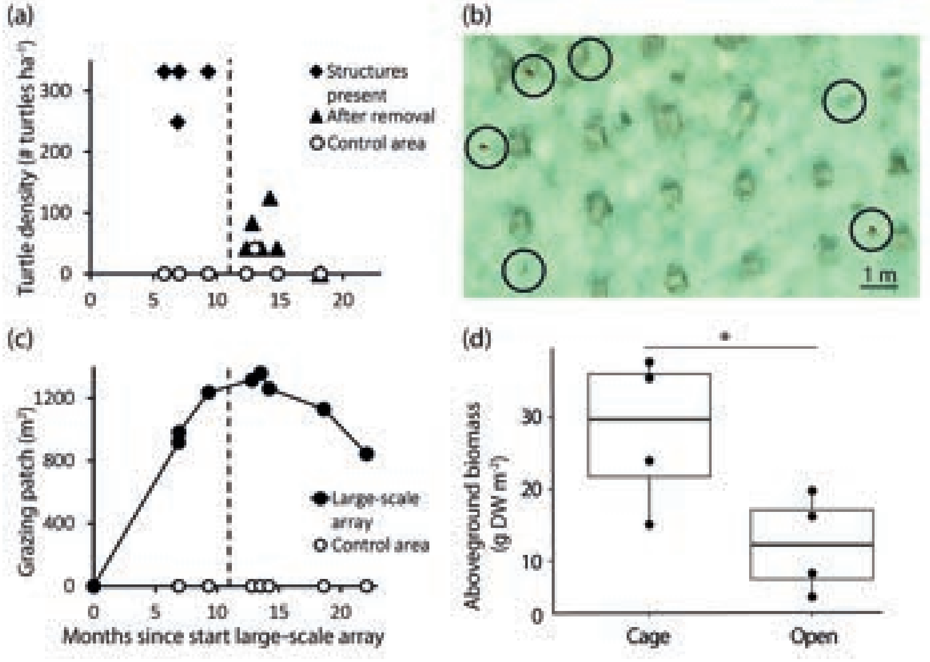

Figure 5.2 The impact of the large-scale experimental array with structures on turtle density (a, b), grazing patch development over time (c) and seagrass aboveground biomass (d). Panel a shows the turtle density (MaxN) over time as measured by the aerial surveys in the control area and in the array before and after structure removal. Structure removal, 11 months after establishment, is indicated by the black dashed line. Panel b is a screenshot of an aerial survey when structures were present, with 6 turtles present in the frame, of which 3 are breathing at the surface. The other three could be recognized because they moved in the video. All seagrass surrounding the structures is heavily grazed. The development of the grazing patch surrounding the experimental array since the establishment of the structures (day 0) is shown in panel c. The black solid line with closed circles indicates the grazed area in the experimental array. Open circles indicate the grazed area in the control area. Structure removal is indicated by the black dashed line. Panel d shows the difference in aboveground biomass of seagrass (*Thalassia testudinum)* between open plots within the array and caged plots at the moment of structure removal (two-sample t-test, t(6) = 2.50, $p = 0.046$). Significant differences between the treatments are indicated with an asterisk (* $p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
Link to videos: https://doi.org/10.4121/264ab2e2-eb36-4647-af52-07e0708142e9.

the structures after 7 months, while no grazing patch was formed in the control area (Fig. 5.1a-d). This patch increased in size to 1359 m^2 (515% of the size of the total array), until the structures were removed after 11 months (Fig. 5.2c). After structure removal, the patch decreased in area to 319% (844 m^2), 22 months since the start of the experiment. In the follow-up small-scale experiment, turtle grazing patches started to form within 3 months in three out of five replicate arrays (Fig. 5.1e-h, Appendix 5.F). Six months after establishment of the structures, on average 14.4% ± 7.6 (1.3 ± 0.7 m^2) of the small-scale experimental arrays was transformed into a grazing patch.

5.4 DISCUSSION

Our study experimentally demonstrates that habitat features can increase green turtle grazing impact, resulting in grazing patches surrounding these features and resultant seascape heterogeneity. Turtles were attracted to both the large- and small-scale experimental arrays with structures and displayed an increase in non-vigilant behavior as resting and intensive grazing between the structures. Our results suggest that habitat features may serve to reduce the risk of predation for megaherbivores.

5.4.1 Impact of habitat features on turtle density and grazing behavior

Habitat features, in this case represented by artificial structures, may play an overlooked role in determining foraging site selection and grazing behavior by marine megaherbivores. We found relatively low turtle density and no grazing patches in the control area. In contrast, adding artificial structures to the seascape in a large-scale array caused a significant local increase in turtle density and their residence time, a significant change of grazing strategy, and the formation of grazing patches, similar to the grazing halos caused by small herbivores (DiFiore et al. 2019). Turtles spent more time resting and grazing within the array compared to the control area and to the array after structure removal. Densities of 331 turtles ha^{-1} within the large-scale array exceeded previous reports of 18-26 turtles ha^{-1} in high-density areas, reaching the carrying capacity of those meadows (Rodriguez and Heck 2021). Indeed, in our study, high turtle density led to a significant decrease in seagrass cover, shoot density, LAI and aboveground biomass in open plots compared to caged plots. Though herbivore group size by itself could also impact vigilance of individuals and their grazing rates (Bauman et al. 2021), turtle densities were reduced and the grazing patch decreased in size once the structures were removed from the large-scale array. Moreover, in the follow-up experiment using small-scale arrays that supported fewer turtles, individual turtles initiated similar – but smaller - grazing patches in the majority of the arrays, suggesting that the main cause of this change in grazing impact was due to presence of the structures (see Video 5.3 where a single turtle directly targets two of the small-scale arrays). Multiple mechanisms may be behind this observed effect of habitat features. Below we discuss the main factors that have been found to affect turtle behavior in relation to habitat features, including predation risk, buoyancy regulation and carapace cleaning.

5.4.2 Habitat features used as predator refuge may mediate grazing impact in a landscape of fear

Habitat features may reduce the predation risk for turtles, in line with other prey with chasing predators (Creel et al. 2005, DiFiore et al. 2019). In contrast to many sites around the globe where turtles live in predator-free environments, our study site was situated in a region with high densities of tiger sharks, the main turtle predator (Whitman 2018, Talwar et al. 2020). Predators can affect prey behavior by creating spatial variation in perceived predation risk through strong non-consumptive effects, forming a landscape of fear (Laundré et al. 2001, Gaynor et al. 2019). Spatial variation in risk can have larger impacts on prey behavior than direct consumption, as shown for tiger sharks and bottlenose dolphins (Heithaus and Dill 2002). We observed non-vigilant grazing behavior near the habitat features, and vigilant behavior increased once structures were removed, suggesting an impact of structures on the risk perception of turtles. Though artificial and of different material, the structures used here were of similar dimensions as coral boulders, which often occur in tropical seagrass meadows and are known to provide protection for turtles at night on coral reefs (Christiansen et al. 2017). Our results suggest that these type of habitat features also provide refuge from predators during the day, impacting grazing behavior and thereby shaping the seascape.

How habitat features impact predation risk remains to be investigated. For sharks which need linear routes of attack (Heithaus et al. 2002a), vertical structures within open habitats may prevent high-speed attacks. Alternatively, natural or man-made structures might deter sharks via other yet unknown mechanisms. For turtles, structures may serve as camouflage to reduce their chances of being visually detected by sharks (Ryan et al. 2022) or limit their need to be vigilant in all directions, as they may be protected from at least one side by the structure, within an otherwise high-risk homogeneous seagrass meadow. To further investigate these complex predator-prey dynamics, future studies can focus on shark movements and hunting strategy as well as turtle risk perception, orientation, and escape behavior in relation to habitat features. Additionally, it is yet unknown whether this type of risk-related behavior is intrinsically incorporated in turtle behavior, or that it is linked to local predator presence, which can be clarified with follow-up studies on the response of turtles to habitat features in low-predator environments. The presence of habitat features may add a new component important in risk-related foraging behavior of turtles in addition to body condition, as turtles in poor health have been found to select riskier foraging areas compared to healthy turtles (Heithaus et al. 2007). For future studies we recommend using high-resolution tracking and animal-borne video to determine the impacts of both body condition and structures on turtle movements, risk perception and grazing behavior (Christiansen et al. 2017, Smulders et al. 2021, Hays et al. 2021).

Apart from predation risk, other factors could explain observed turtle behavior near the structures. The turtles may have used them to regulate their buoyancy while they rest during the day, close to their foraging ground. Because green turtles in water up to 5 m are mostly positively buoyant (Hays et al. 2004), the partial cages may have facilitated resting at this shallow site. Additionally, the structures may have provided substrate for the cleaning of their carapace (Heithaus et al. 2002c). However, in the small-scale experiment, turtles were still attracted to the artificial structures, whereas they could not use these for resting due to the design. Similarly, on the drone videos, mainly grazing and resting was observed, and not cleaning behavior. Therefore, we propose that the structures were likely used for foraging site selection in a landscape of fear.

5.4.3 Implications for future research and nature management

Our findings have implications for other studies on marine grazing behavior. Previously described grazing halos adjacent to natural coral reef structure may partly originate from megaherbivore grazing behavior in addition to mesoherbivores such as fish and urchins (DiFiore et al. 2019) and other (a)biotic processes (Bilodeau et al. 2021). If so, then field studies using a diverse array of (partial) cages and open plots to quantify grazing pressure risk may overestimate local grazing intensity due to the structure effect.

Marine megaherbivores in other (high-risk) areas are likely to increase their density and grazing pressure near (artificial) habitat features. Permanently added structures to a seagrass habitat may therefore cause a decrease and even loss of seagrass habitat. On the other hand, natural resource managers may incorporate artificial structures and/or shelters into their conservation efforts to temporarily concentrate endangered turtle populations in certain areas. Natural structures such as coral boulders may promote local heterogeneity in seagrass structure and therefore ensure a diverse seascape. Our approach and findings provide a novel mechanism that links habitat features and the impact of large marine grazers on the seascape.

ACKNOWLEDGMENTS

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APPENDIX 5.A

Abundance of tiger sharks (turtle predators) as reported in the wider region of Eleuthera. Presence of tiger sharks from studies with data from Eleuthera and neighboring islands. We searched Google Scholar and Web of Science for the key words 'Tiger shark' or '*G. cuvier*' and 'The Bahamas'. Due to limited data, we incorporated both studies on abundance in the region as well as studies where satellite locations of tagged sharks showed that individuals have visited north Eleuthera at least once. From these results, we presented presence of tiger sharks and abundance (in CPUE) if available.

Study	Location	Method	CPUE
Hammerschlag et al., 2015	North Eleuthera	Tagging	
Lea et al., 2015	North Eleuthera	Tagging	
Brooks et al., 2011	South Eleuthera	BRUVS Longline	0.013 0.0023
Talwar et al., 2020	South Eleuthera	Longline	0.005
Gallagher et al., 2021	Great Exuma and New providence	Tagging	
Whitman, 2018	Abaco	BRUVS	0.01-0.1

Brooks, E. J., Sims, D. W., Danylchuk, A. J., & Sloman, K. A. (2013).

Seasonal abundance, philopatry and demographic structure of Caribbean reef shark (Carcharhinus perezi) assemblages in the north-east Exuma Sound, The Bahamas. *Marine biology*, *160*(10), 2535-2546.

Hammerschlag, N., Broderick, A. C., Coker, J. W., Coyne, M. S., Dodd, M., Frick, M. G., ... & Hawkes, L. A. (2015). Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. *Ecology*, *96*(8), 2117-2126

Lea, J. S., Wetherbee, B. M., Queiroz, N., Burnie, N., Aming, C., Sousa, L. L., ... & Shivji, M. S. (2015). Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific reports*, *5*(1), 1-11.

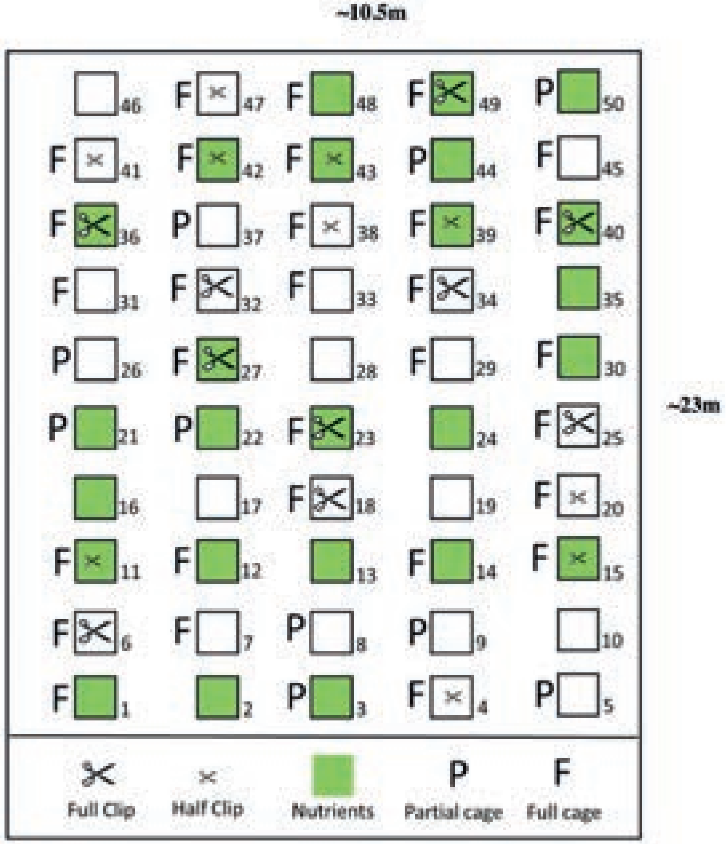
Whitman, E. R. 2018. Factors affecting green turtle foraging ecology across multiple spatial scales. FIU Electronic Theses and Dissertations. 3870.

Talwar, B. S., Stein, J. A., Connett, S. M., Liss, S. A., & Brooks, E. J. (2020). Results of a fishery-independent longline survey targeting coastal sharks in the eastern Bahamas between 1979 and 2013. *Fisheries Research*, *230*, 105683.

Gallagher, A. J., Shipley, O. N., van Zinnicq Bergmann, M. P., Brownscombe, J. W., Dahlgren, C. P., Frisk, M. G., ... & Duarte, C. M. (2021). Spatial connectivity and drivers of shark habitat use within a large marine protected area in the Caribbean, The Bahamas Shark Sanctuary. *Frontiers in Marine Science*, 1223.

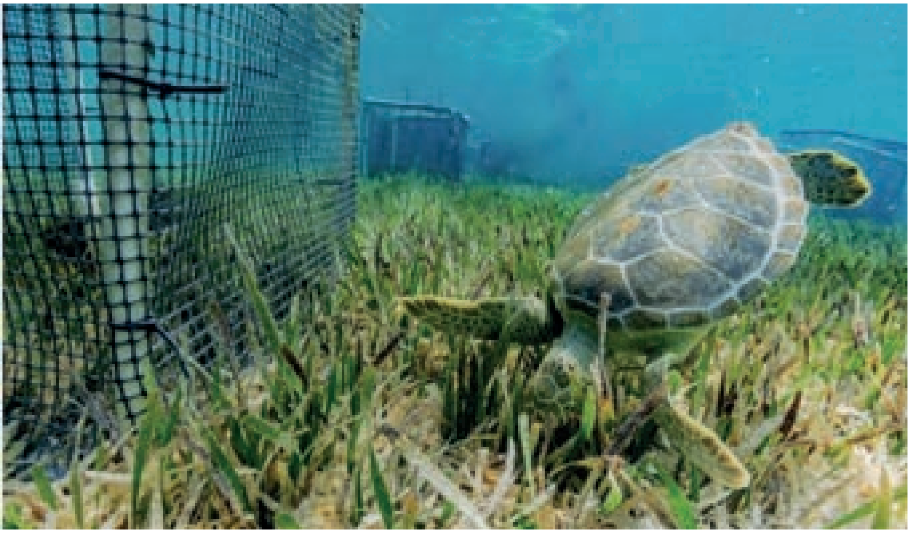
APPENDIX 5.B

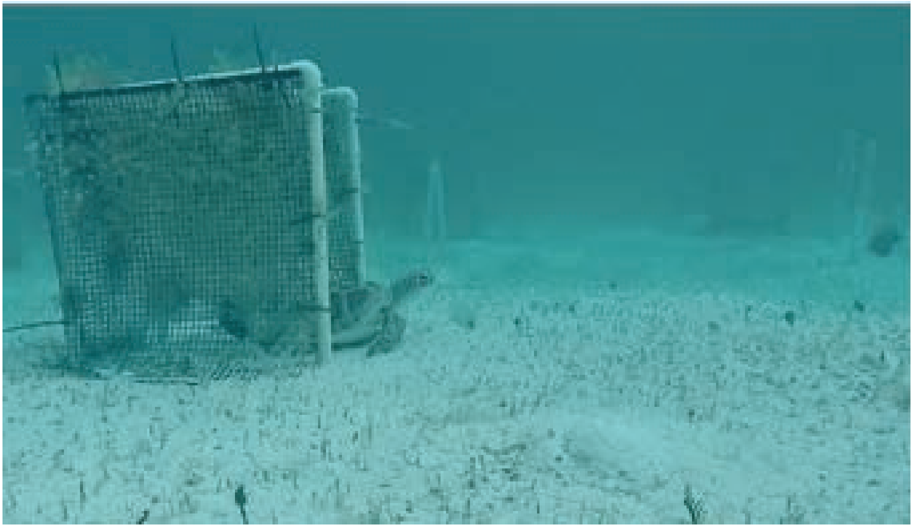
Experimental set-up of the large-scale experimental array, part of the *Thalassia* experimental network (TEN). In total, the set-up consisted of a grid of 50 individual 0.5 x 0.5 x 0.5 m cages and open plots, each separated by 2 m, in an area of 23 x 10.5 m (241.5 m^2). The full cages (n = 30) excluded turtles and consisted of a PVC frame with vexar mesh (mesh size 1.5 cm) on all four sides, and bird mesh on top (mesh size 1.5 cm). Partial cages (n = 10) consisted on the same frame, but with three of the four sides covered in vexar mesh, allowing turtles to occupy the cages. Open plots (n = 10) consisted of four PVC poles marking the base of the frame, without additional poles or mesh on the top or sides. Cage types (and additional treatments, including mimicked grazing and fertilizer addition to plots) were deployed in a fully factorial, randomized design.



APPENDIX 5.C

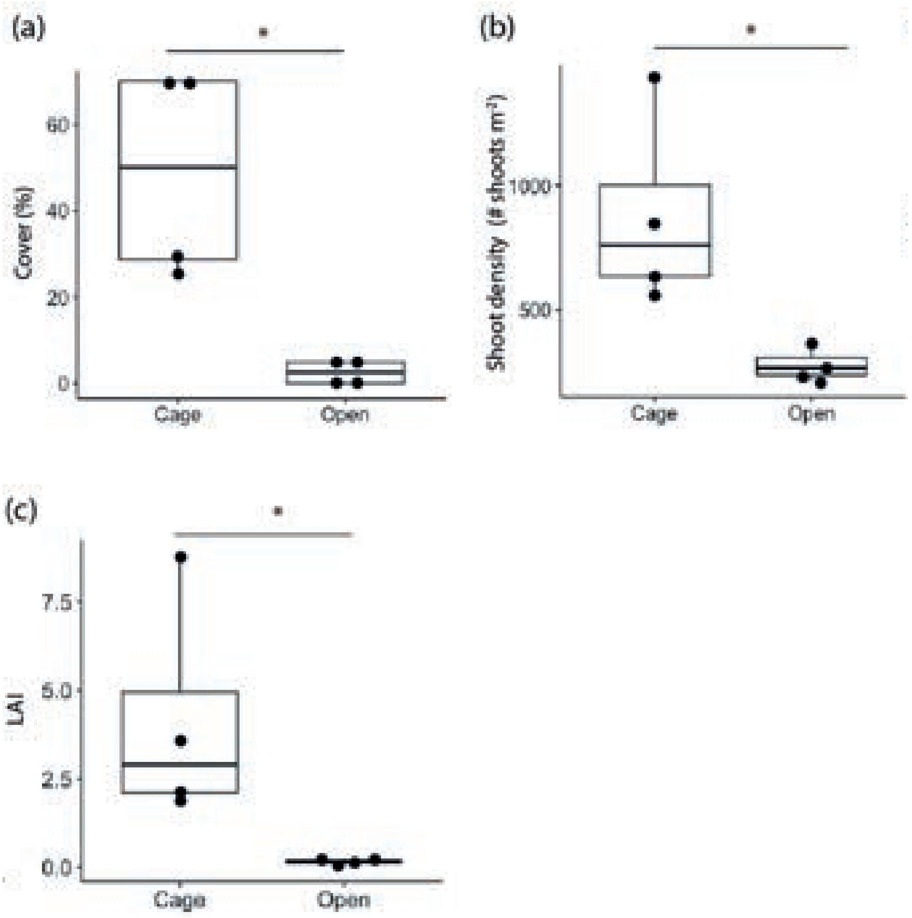
Top picture: green turtles increased in density and started grazing near the structures moments after structure establishment, picture taken 2nd of May 2018 by Shane Gross. Bottom picture: green turtle in a partial cage of the initial large-scale experiment. Surrounding the partial cage a highly grazed meadow confirms high turtle densities. Picture taken 27th October 2018 by F. Smulders.





APPENDIX 5.D.

The impact of cage and open treatments on the following seagrass properties (a) % cover (Wilcoxon rank-sum test, W = 16, *p* = 0.027), (b) shoot density (two-sample t-test, t(6) = 3.05, *p* = 0.023) and (c) Leaf Area Index (LAI) (Wilcoxon rank-sum test, W = 16, *p* = 0.029), 11 months after the establishment of the large-scale experimental array. Significant differences between cage treatments are indicated with an asterisk (* *p* < 0.05, ***p* < 0.01, ****p* < 0.001).



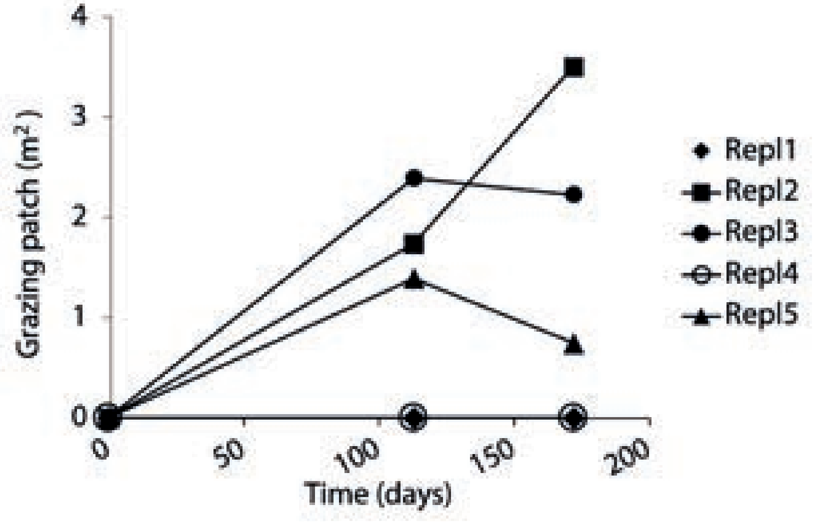
APPENDIX 5.E

Thalassia testudinum seagrass properties as measured at the end (11 months) of the large-scale experiment. Values of cover, shoot density, LAI and leaf biomass were compared between the open and caged plot treatments. P values show significant differences between the seagrass properties in the open and caged plots (* $p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

	Open plots	**Caged plots**	**Test**	**P-value**	**Test statistic**	**df**
Cover (%)	2.5 ± 1.4	48.8 ± 12.3	Wilcoxon rank-sum test	**0.030***	W = 16	
Shoot density (shoots m^{-2})	280.7 ± 34.7	876.3 ± 192.3	Student's two-sample t-test	**0.023***	T = 3.05	6
LAI	0.15 ± 0.04	4.14 ± 1.6	Wilcoxon rank-sum test	**0.029***	W = 16	
Leaf biomass (g DW m^{-2})	12.3 ± 3.4	28.1 ± 5.3	Student's two-sample t-test	**0.046***	T = 2.50	6

APPENDIX 5.F

Development of grazing patches surrounding the small-scale experimental arrays (N = 5) since the establishment of the structures (day 0).



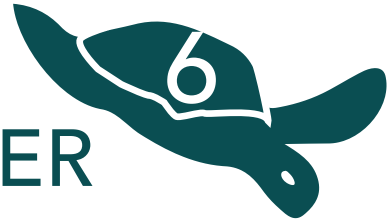
APPENDIX 5.G.

Behavior and grazing strategy of green turtles in the large-scale experimental array with added artificial structures. Presented is the percentage of time spent within the array (% residence time), stationary (grazing or resting within the seagrass meadow), intensive grazing (moving slowly in meandering patterns across the meadow), intensive grazing + stationary (total grazing), browsing (moving in linear direction) and at the water surface (surfacing). The different treatments consist of turtle behavior in the array while structures were present (N = 4), after structure removal (N = 6) and in the control area (N = 1). P values show significant differences between the turtles in the array with structures present and after removal (* $p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

	Residency (minutes)	Stationary (%)	Intensive grazing (%)	Total grazing (%)	Browsing (%)	Surfacing (%)
(a) Structures present	7.6 ± 0.5	51.0 ± 4.9	49.0 ± 4.9	100	0	6.3 ± 2.2
(b) After structure removal	2.5 ± 0.9	6.3 ± 4.1	40.2 ± 15.9	46.5 ± 19.0	53.5 ± 17.8	2.5 ± 1.0
(c) Control	0.1	0	0	0	100	0
Test (comparing a & b)	Welch two-sample t-test	Wilcoxon rank-sum test	Welch two-sample t-test	Wilcoxon rank-sum test	Wilcoxon rank-sum test	Welch two-sample t-test
P-value	**0.0016 ****	**0.013 ***	0.62	0.07	0.07	0.18
Test statistic	t = -4.90	W = 24	t = -0.53	W = 20	W = 4	t = -1.60
df	7.28		5.92			4.27

GREEN TURTLES SHAPE THE SEASCAPE THROUGH GRAZING PATCH FORMATION AROUND HABITAT FEATURES: EXPERIMENTAL EVIDENCE

5



CHAPTER

Seagrass ecosystem multifunctionality under the rise of a flagship marine megaherbivore

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ABSTRACT

Large grazers (megaherbivores) have a profound impact on ecosystem functioning. However, how ecosystem multifunctionality is affected by changes in megaherbivore populations remains poorly understood. Understanding the total impact on ecosystem multifunctionality requires an integrative ecosystem approach, which is especially challenging to obtain in marine systems. We assessed the effects of experimentally simulated grazing intensity scenarios on ecosystem functions and multifunctionality in a tropical Caribbean seagrass ecosystem. As a model, we selected a key marine megaherbivore, the green turtle, whose ecological role is rapidly unfolding in numerous foraging areas where populations are recovering through conservation after centuries of decline, with an increase in recorded overgrazing episodes. To quantify the effects, we employed a novel integrated index of seagrass ecosystem multifunctionality based upon multiple, well-recognized measures of seagrass ecosystem functions that reflect ecosystem services. Experiments revealed that intermediate turtle grazing resulted in the highest rates of nutrient cycling and carbon storage, while sediment stabilization, decomposition rates, epifauna richness, and fish biomass are highest in absence of turtle grazing. In contrast, intense grazing resulted in disproportionally large effects on ecosystem functions and a collapse of multifunctionality. These results imply that *i)* the return of a megaherbivore can exert strong effects on coastal ecosystem functions and multifunctionality, *ii)* conservation efforts that are skewed towards megaherbivores, but ignore their key drivers like predators or habitat, will likely result in overgrazing-induced loss of multifunctionality, and *iii*) the multifunctionality index shows great potential as a quantitative tool to assess ecosystem performance. Considerable and rapid alterations in megaherbivore abundance (both through extinction and conservation) cause an imbalance in ecosystem functioning and substantially alter or even compromise ecosystem services that help to negate global change effects. An integrative ecosystem approach in environmental management is urgently required to protect and enhance ecosystem multifunctionality.

6.1 INTRODUCTION

Humans rely on a multitude of services provided by Earth's ecosystems, such as food, water, and protection as well as climate buffering (Millenium Ecosystem Assessment 2005, Costanza et al. 2014). However, humans are greatly impacting megafauna population numbers, both through overexploiting and degrading entire ecosystems and their fauna (Rockström et al. 2009, Almond et al. 2020) and also through successful conservation and restoration efforts that allow some populations to rebound locally (Lotze et al. 2011, Warren 2011). These changes in megafauna populations can induce large-scale changes in terrestrial, freshwater, and marine ecosystems, which in turn impairs ecosystem functions and services, as found across ecosystems and biogeographic zones, including tundra, savanna and rainforests (Estes et al. 2011, Zimov and Zimov 2014, Dirzo et al. 2014, Galetti et al. 2015, McCauley et al. 2015, Doughty et al. 2016). Additionally, changes to one species can also disrupt the complex equilibrium between trophic levels if predators and their prey are impacted in a different way (e.g. large herbivore recovery in a system where their food source is still in decline) or recovering at different time scales (Duarte et al. 2020). This potential has been illustrated in several classic studies of cascading, top-down effects triggered by megafaunal defaunation through extirpation of sharks, otters, and cetaceans (Estes and Palmisano 1974, Steneck and Sala 2005, Ainley et al. 2006, Heithaus et al. 2008a, Estes et al. 2009, Baum and Worm 2009).

A decrease or increase in marine megafauna populations coincides with changes in key ecosystem functions and services, such as coastal erosion protection (Coverdale et al. 2014), nutrient transport (Doughty et al. 2016), carbon sequestration (Wilmers et al. 2012) and ecosystem resilience (Steneck and Sala 2005, Hughes et al. 2016). However, extrapolating results from a single function to infer the role of marine megafauna in complex systems ignores the interplay among functions, as well as our desire to simultaneously extract multiple goods and services from high-functioning ecosystems. To solve this we need an integrative assessment of the effects of changing megafauna abundance on the entire ecosystem, its functions and services and the interplay among functions, termed ecosystem multifunctionality (Hensel and Silliman 2013, Byrnes et al. 2014), which is currently lacking. Furthermore, there is no evidence of causation, as experimental support for the ecosystem impacts of changes of marine megafaunal on multifunctionality remains absent so far because experimental support for such integrative assessment is challenging to obtain, especially in marine systems.

Here, we assessed the effects of changing megaherbivore populations on ecosystem multifunctionality in a tropical seagrass ecosystem. Undisturbed seagrass ecosystems are hotspots for marine megafauna including sea turtles, sharks, dugongs, dolphins, otters and crocodiles (Sievers et al. 2019), and provide crucial ecosystem services (Nordlund et al. 2018). Seagrasses evolved under grazing pressure by mammalian megaherbivores (sea cows or Sirenians such as dugongs and manatees) and by its dominant megaherbivore, the green turtle (*Chelonia mydas)* (Aragones and Marsh 2000, Domning 2001) and thus, grazed seagrass meadows presumably represent the "natural" state of seagrass ecosystems (Christianen et al. 2021) until overexploitation began centuries ago (Thayer et al. 1984, Jackson et al. 2001). After the decimation of turtle populations, roughly between 1800 and 1990, long before modern ecological investigations began, seagrass meadows were left composed of large, slow-growing climax species with high seagrass biomass (Jackson 1997). Since successful conservation measures to protect nesting areas and international law prohibiting turtle trade were established, an increasing number of seagrass meadows are experiencing a rise in green turtle populations (Chaloupka et al. 2008, Weber et al. 2014, Mazaris et al. 2017). As a result, more and more seagrass meadows are recovering to their natural grazed state in the last decade. This is reflected by acceleration on the number of publications on seagrass, megaherbivores and turtles in peer-reviewed journals over time (Fig. 6.1a). Turtle population growth may be enhanced further by the absence of their main predator (Tiger shark, *Galeocerdo cuvier*) due to shark overfishing (Heithaus et al. 2014) and by the loss of seagrass habitat due to other anthropogenic stressors, which stimulate turtle densities to increase in the remaining habitat (Christianen et al. 2014). This has resulted in an increase in reports of turtles overgrazing the seagrass, i.e., when grazing rates exceed production rates (Williams 1988, Christianen et al. 2014, Fourqurean et al. 2019, Gangal et al. 2021) in some cases leading to seagrass collapse (Christianen et al. 2014, Gangal et al. 2021). The intensity of megaherbivore grazing can thus determine the seagrass biomass, shoot density and canopy structure (Smulders et al. 2023a, Burkholder et al. 2013, Nowicki et al. 2018, Scott et al. 2018), ranging from low seagrass biomass when sea turtles are abundant, to high seagrass biomass when turtles are absent (Fig. 6.3), which may affect ecosystem multifunctionality.

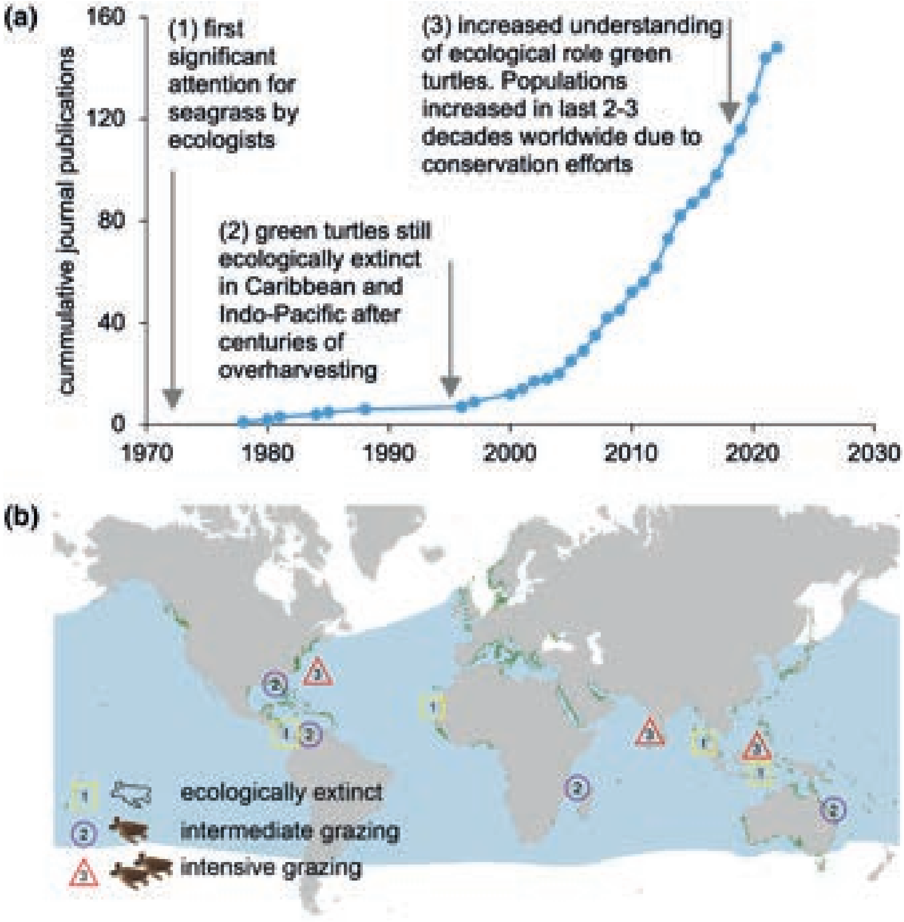

Figure 6.1. (a) The number of publications on seagrass and green turtle grazing in peer-reviewed journals is accelerating over time (Web of Science, Scopus, Google Scholar 1960-2022, Appendix 6.F) mirroring the recovery of green turtle populations. Arrow 1: (McRoy and Helfferich. 1977, Thayer et al. 1977); arrow 2: (Jackson 1997), arrow 3: (Chaloupka et al. 2008, Weber et al. 2014, Mazaris et al. 2017). (b) A selection of sites illustrates that all three different grazing scenarios for green turtles occur in coastal (sub-)tropical seagrass ecosystems around the world, in all three ocean basins where green turtles are found. Green dots: global seagrass distribution (UNEP-WCMC and Short 2021), blue: distribution of the green turtle, *Chelonia mydas,* (Kot et al. 2022). (Scenario 1) (Jackson 1997, van der Laan and Wolff 2006, Vonk et al. 2008, Jones et al. 2018, Gaubert-Boussarie et al. 2021); Scenario 2) (Ballorain et al. 2010, Molina Hernández and van Tussenbroek 2014, Christianen et al. 2019, Rodriguez and Heck 2020, Scott et al. 2020, Gulick et al. 2020); Scenario 3) (Christianen et al. 2014, Fourqurean et al. 2019, Gangal et al. 2021).

We translated these observations into our aim of assessing the impact of increasing megaherbivore densities on key seagrass ecosystem functions and multifunctionality. This was tested in an experimental design in which the seagrass was excluded from turtle grazing (representing absence of turtles), exposed to intermediate turtle grazing (representing the naturally grazed scenario), and lastly, we manipulated the seagrass to mimic a scenario of intensive grazing or overgrazing by turtles by removing plant biomass, based on literature showing this mechanism (Fourqurean et al. 2019, Gangal et al. 2021). After 18 months of experimentation, we measured seven ecosystem functions and captured the overall effects in a novel, integrated seagrass ecosystem multifunctionality index.

6.2. MATERIALS AND METHODS

6.2.1. Study system

The experiment was conducted in a tropical, subtidal seagrass meadow, located within Lac Bay, Bonaire, Caribbean Netherlands (12°06'N 068°14'W). Lac Bay contains ~200 hectares of seagrass and is designated to be a wetland of international importance under the Ramsar Convention. Seagrass meadows were mainly dominated by the native seagrass, *Thalassia testudinum*, and to a lesser extent *Syringodium filiforme*, as well as the invasive seagrass, *Halophila stipulacea* (Christianen et al. 2019) along with beds of the calcareous algae *Halimeda* spp. Today, Lac Bay's seagrass meadows are home to one of the largest green turtle foraging aggregations in the southern Caribbean (Debrot et al. 2012, Rivera-Milán et al. 2019). The abundance of green turtles (*Chelonia mydas*) has been recovering in the leeward Dutch Caribbean islands in recent decades after past depletion due to overharvesting (Jackson 1997). By contrast, overexploited top predators that feed on green turtles, such as tiger sharks have not shown any evidence of recovery in the Caribbean (Ward-Paige et al. 2010), with only occasional observations on Bonaire. The green turtle population in Lac Bay grazed only on seagrass leaves with plenty of seagrass biomass still present. The seagrass meadow can withstand the current grazing pressure and remains a high productivity (Christianen et al. 2019). Hence, we classified the current meadow as being exerted to intermediate grazing pressure. Other foraging areas with very high green turtle abundances are subject to much higher grazing intensities than observed in Lac Bay (Christianen et al. 2014, 2021, Gangal et al. 2021). Other megaherbivores like manatees (*Trichechus manatus*) also feed on seagrass. However, while manatees were abundant in the Southern Caribbean region before the European colonization during the 17th -

19th centuries, they were still absent from the region at the time of the study (Jackson 1997, Debrot et al. 2013). Mesoherbivore fish were abundant in the bay but only in shallower areas (e.g., the mangrove fringe) where the absence of turtle grazing leads to a high canopy that provides food and shelter to a high diversity of fish (Smulders et al. 2022).

6.2.2. Approach and megaherbivore grazing intensity treatments

To assess the impact of megaherbivore grazing intensity on ecosystem multi-functionality, we have experimentally manipulated seagrass biomass and grazing intensity to simulate three progressing grazing intensity scenarios, all of which can be found in three ocean basins (Fig. 6.1b); (1) No turtle grazing, representing the absence of turtles. The absence of turtle grazing (or intensive grazing by smaller herbivores) results in high seagrass biomass as observed in many current modern seagrass meadows where turtles remain ecological extinct (Jackson 1997, van der Laan and Wolff 2006, e.g., Vonk et al. 2010, Jones et al. 2018, Gaubert-Boussarie et al. 2021); (2) Intermediate turtle grazing, representing presence by turtles. Ecosystems were exposed to natural or intermediate grazing intensity resulting in intermediate seagrass biomass, with plenty of leaf biomass still present as observed in meadows with turtles (Molina Hernández and van Tussenbroek 2014, Christianen et al. 2019)*;* (3) Intensive turtle grazing, representing the accumulation of turtles, resulting in very high grazing pressure and sometimes 'overgrazing', i.e. when grazing rates exceed production rates, and very low seagrass biomass as observed in areas with turtle accumulation (Fourqurean et al. 2019, Gangal et al. 2021).

We manipulated the seagrass biomass corresponding with the three different grazing intensity treatments with a combination of exclosure and seagrass removal treatments. In Treatment 1, turtle grazing was excluded from the plots by using underwater cages (1.5 m x 1.5 m x 0.5 m with walls of galvanized 9 mm steel wires and 15 cm mesh size). The cages excluded sea turtles but permitted the movement of small-bodied animals (e.g., fish), did not attract additional fish and did not inhibit light transmission to the seagrass bed (Christianen et al. 2012). The vertical walls of each cage were extended 30 cm into the sediment to prevent subterranean movement and intrusion of large animals. Algae growth on the cages was minimal during the experiment as it was checked every two weeks and removed when necessary. For Treatment 2, the plots were left exposed to intermediate green turtle leaf grazing. Each plot was marked by four galvanized steel pins protruding 10 cm above the sediment and not subjected to any changes. Turtle grazing was constant over the 18 months. In Treatment 3, plots were exposed to high-intensity grazing. Here, all above and below ground seagrass biomass was removed from the plot at the start of the experiment (July 2015) to mimic the effects of high-intensity turtle grazing, observed in areas with a high abundance of sea turtles that induced a shift from *Thalassia* to bare sand (Gangal et al. 2021) or excavated roots (Christianen et al. 2014). The excavating behavior is atypical of the cultivated grazing behavior that has been widely documented in the literature for Caribbean meadows (Bjorndal 1980, Ogden et al. 1983, Gulick et al. 2020), where turtle densities and seagrass species numbers and grazing intensity are typically lower than tropical meadows elsewhere. However, if turtles only intensively graze on aboveground leaves, this can also lead to bare patches as *Thalassia* meadows become depleted and can no longer recover. This has been observed in the Pacific ocean within five years after the arrival of dense turtle aggregations (Gangal et al. 2021). Under continued turtle accumulation, the transition of Thalassia to bare patches is likely to arise elsewhere and has already been observed in Bermuda (Government of Bermuda 2021), Bonaire (Pers. obs. MJAC and FOHS) and the Bahamas (Smulders et al. 2023a). Plots were marked as in Treatment 2, thereby permitting re-colonization by clonal expansion of surrounding seagrass during the experiment while still being exposed to intermediate turtle grazing.

6.2.3 Experiment

The experiment was conducted over a period of 18 months (from July 2015 to February 2017). Fifteen plots (1.5 m x 1.5 m) were selected at similar water depths (2.0 m ± 0.3 m), similar plant biomass, and cover and were deployed over an area of 500 m^2. The three treatments were applied randomly to the chosen plots to avoid potentially confounding effects of small-scale spatial heterogeneity.

The resulting seagrass biomass was quantified at the start of the experiment (to ensure plots had similar biomass) and at the end of the experiment in all experimental plots from a core sample (15.3 cm diameter, 20 cm depth) collected at the center of each plot, together with leaf productivity, shoot density and canopy height. Aboveground plant parts (leaves and sheaths) were separated from belowground parts (roots and rhizomes) before processing and analysis. Aboveground parts were rinsed with water to remove epiphytes and sediment as well as other attached materials. After drying (48 h at 60 °C) the aboveground biomass of *T. testudinum* in each core was quantified as the combined dry weight (DW) of *T. testudinum* leaves and sheaths.

Table 6.1 Methods used to measure seven proxies of seagrass ecosystem services and functions. Ecosystem services reflect benefits (of monetary value) provided to humanity and are underpinned by examples of ecosystem processes and functions, adapted from (Barbier et al. 2011). Sampling timing and frequency are given between brackets. S: start of the experiment, E: end of the experimental period. The proxy measured herein outlines the actual variant(s) of those processes and functions that we quantified.

Ecosystem service	Method	Reference
Ecosystem process and function	Proxy measured herein (Sampling timing)	
Water purification Nutrient cycling	1. Net leaf nitrogen uptake rate, calculated as seagrass leaf production (using plastochrone method) x leaf nitrogen content, measured using elemental analyzer. (S, E)	(Short and Duarte 2001, Christianen et al. 2019)
Carbon sequestration Biochemical activity	2. Decomposition rate, determined from the Tea bag index (over last 61 days of experiment)	(Keuskamp et al. 2013)
	3. Sediment organic carbon content using dry combustion method with the elemental analyzer (E)	(Howard et al. 2014)
Fisheries maintenance Provisioning of habitat, shelter, nursery	4. Fish biomass using stationary-point-count-method and SCUBA. Biomass estimated using species specific weight-length relationships (E)	(Polunin and Roberts 1993)
	5.Macrofauna (invertebrate) richness from sediment cores and net sweeps (E)	(Vonk et al. 2010)
Coastal protection and erosion control Wave attenuation and sediment stabilization	6. Sediment stabilization, measured as threshold shear velocity, from unilateral field flume measurements. (E)	(James et al. 2020)
Tourism, research Maintaining wildlife habitat	7. Invasive species buffering assessed as the area cover of invasive species Halophila stipulacea. A non-preferred species for megafauna. (E)	(Smulders et al. 2017)

6.2.4 Ecosystem functions

We measured seven variables serving as proxies for ecosystem functions and processes underpinning essential seagrass ecosystem services (Table 6.1, Barbier et al. 2011, Nordlund et al. 2018): nutrient cycling, decomposition rates, carbon storage, fish biomass, macroinvertebrate species richness (α diversity), sediment stability and resilience to invasive species. For five processes, the corresponding variables were measured within each plot of the treatments (carbon content, decomposition rate, nutrient cycling, macroinvertebrate species richness, and percentage of invasive seagrass). Fish biomass was estimated after cages were removed to avoid cage effects. Sediment stabilization was estimated in the close vicinity of the experimental plots, in selected plots where biomass measurements confirmed similar aboveground biomass, as the experimental plots contained an insufficient area of undisturbed sediment.

6.2.4.1 Estimation of nutrient cycling

Nutrient cycling was assessed using net aboveground seagrass nitrogen uptake as a proxy and was estimated by multiplying leaf productivity with leaf nitrogen content. Seagrass productivity was assessed using the plastochrone method (Short and Duarte 2001) and the dry weight of new regrowth was measured (48 h at 60 °C) after an eleven-day interval at the start and end of the experimental period. Leaf nitrogen content was estimated from the material used to quantify seagrass aboveground biomass. Dried leaves were ground and subsequently analyzed using an elemental analyzer coupled as described in (Christianen et al. 2019).

6.2.4.2 Estimation of decomposition rates

Organic matter decomposition rates were quantified using the “tea bag” index (Keuskamp et al. 2013). The approach employs commercially available tea bags as a standardized assessment. Five tea bags of two types of tea with different characteristics (rooibos tea, Lipton Inc., EAN: 87 22700 18843 8, and green tea, Lipton Inc., EAN: 87 22700 05552 5) were buried at 8 cm depth in each plot. The tea bags were deployed during the last two months of the field treatments and recovered after 61 days. Soil particles were removed and the tea and bags were dried (48 h at 60 °C) and weighed. The use of tea types with contrasting decomposability served as the basis for the estimation of a decomposition curve from a single temporal sample. The decomposition rate (*k*) was calculated as described by Keuskamp et al. (Keuskamp et al. 2013), using a hydrolysable fraction of 0.552 g g^{-1} and 0.842 g g^{-1} for rooibos tea and green tea, respectively.

6.2.4.3 Estimation of carbon storage

Sediment organic carbon storage was estimated as the percentage of carbon in the sediment. Small sediment cores (22.9 mm diameter, 50 mm depth, yielding a sediment volume of 20.6 cm^3) were collected from the cores used to extract aboveground plant biomass. Sediment samples were dried (48 h at 60 $^{\circ}$C) and weighed to determine the dry bulk density (DBD; mg DW m^{-3}). Corrections for inorganic carbon (i.e., calcium carbonate, $CaCO_3$) were undertaken on subsamples that were incinerated (4 h at 500 $^{\circ}$C) and the resulting ash (containing the inorganic carbon) was weighed. The percentage of carbon in sediment and ash was measured using a Thermo Scientific™ Delta V isotope ratio mass spectrometer coupled with a Thermo Scientific Interscience "Flash" Elemental Analyzer™, series 112 (Thermo Scientific Inc.). Standards were included in every five samples using ISE 946 reference material and the certified calibration standard Acetanilide (OAS certificate 293514). The percentage of inorganic carbon in the ash was subtracted from the estimate of total carbon in the sediment to obtain the percentage of organic carbon in the sediment (Howard et al. 2014).

6.2.4.4 Estimates of fish biomass and macroinvertebrate species richness

Fish biomass and macroinvertebrate species richness were assessed from visual underwater census, stationary point-count-methods (Polunin and Roberts 1993, Dorenbosch et al. 2005), and sediment core samples. Fish biomass was assessed in a quadrat of 1.5 m x 1.5 m. Counts were conducted after a wait time of five minutes to minimize disturbance. During the first seven (of a total of ten) minutes of observation time, fish species identification and counting were conducted from outside the sampling quadrat. During the last three minutes, the observer moved through the quadrat to identify and count smaller fish hiding within the canopy. All macrobenthic invertebrates (epifauna > 1 cm) were identified and counted inside the quadrat during these last three minutes (Vonk et al. 2010). Additionally, infauna was collected and counted from the sediment cores collected for plant biomass analysis (see above) after sieving the sediment (1 mm round mesh). The collected macrobenthic invertebrates were identified to as taxonomic class. Because species richness of both in- and epifauna was highly correlated (Appendix 6.C, R^2 0.72, $p<0.001$) the data of in- and epifauna species richness was combined for each plot and reported per unit area (m^2).

All fish records were classified into 2.5 cm size classes and used to estimate total fish biomass. Estimation of size classes was trained by repeatedly estimating the sizes of objects placed underwater representing all size classes until the observer was able to determine length with a maximum deviation of 2.5 cm for objects less than 20 cm long (Humann and DeLoach 1989). Fish biomass was estimated from the size estimates for each species using species-specific weight-length relationships (WLR), defined as $W = a \times L^b$, where W is fish total dry weight in grams, L is the length in cm, a is a species-specific coefficient that relates to body shape and b is the exponent relating to species-specific growth form (Bouchon-Navaro et al. 2006, Froese et al. 2014). The parameter estimates for a and b were obtained from previously published data (Bouchon-Navaro et al. 2006) based on 50 different fish species collected from seagrass meadows in the Lesser Antilles.

6.2.4.5. Estimation of sediment stability

Sediment stability was quantified by measuring the threshold flow velocity, i.e., the velocity of water at which sediment was mobile, in a portable "unidirectional-flow-flume", the TiDyFLOW flume (James et al. 2019). The portable flume was placed nearby the experimental plots on plots with seagrass biomass comparable to the treatments. Measurements were conducted at three plots for each treatment and at each plot, three measurements were averaged. The unidirectional flow flume generated a current velocity that forced the water through a 1.2 m x 0.25 m x 0.3 m (L x W x H) Perspex tunnel that was placed over the vegetation. The flow velocity was measured with an acoustic Doppler flow sensor (ADV, Nortek AS™ Vectrino Field Probe) that was suspended at 25 cm above the sediment surface within the flume tunnel. Two divers closely observed the sediment surface within the flume tunnel, and the critical erosion threshold was the velocity at which sediment grains situated beneath the ADV began to lift and move along the bed surface. The training was conducted before the measurements to ensure the observations were standardized. Sediment transport is proportional to flow velocity to the power of 3, therefore small changes in velocity lead to large changes in observed sediment dynamics. Visual observation of sediment movement is therefore sufficiently accurate to determine erosion thresholds for ecological studies. See James et al. (James et al. 2020) for an extensive description of the portable unidirectional-flow-flume and experimental setup. To test if grain size differences influence sediment stability among treatments and to test the relative importance of the canopy on the sediment stabilization function, we also analyzed median grain size for all plots using a Malvern Laser Particle Sizer (Appendix 6.D). For this, we used a sub-sample from the sediment cores (taken at 0 – 5 cm depth) collected for carbon storage assessment.

6.2.4.6 Estimation of resilience to invasive species invasion

We estimated the relative rate of colonization in each experimental plot by the invasive seagrass *Halophila stipulacea. H. stipulacea* cover was monitored at the start and end of the experimental period in a 25 x 25 cm frame in the center of each plot. The change in cover between the start and end of the experimental period was taken as a measure of resilience to invasion for the native *T. testidinum* meadows.

6.2.5 Data analysis

All data analyses were performed in R, version 3.3.3 (R Core Team 2017). The average aboveground seagrass (*T. testudinum*) biomass estimated at the end of the experiment was compared among the three different *in situ* treatments (Appendix 6.A, 6.B (Christianen et al. 2022)). The measured response of each ecosystem function was plotted against the aboveground biomass as the explanatory variable to represent the effects of changing megaherbivore grazing intensity. Earlier work has shown that the relationships between the structure and ecosystem functions in coastal habitats can be linear as well as nonlinear being characterized by thresholds and limiting functions (Koch et al. 2009), which in turn is relevant for the nature (thresholds, rate, level) of the response to changing megaherbivore abundance. Accordingly, we assessed the relationship between aboveground seagrass biomass and each response variable individually in five models using the *invFSxfunc* package (Angelini et al. 2015, Ramus et al. 2017). Using nonlinear least squares (Grothendieck 2013), we fitted null, linear, log, hyperbolic, and power relationships for each response using the aboveground seagrass biomass of each plot as the explanatory variable. The selection of the best fitting model was based on the Akaike information criterion, correcting for small sample sizes (AICc) (Grothendieck 2013, Byrnes et al. 2014). For each response variable, we compared the null model with the most probable model using a one-way ANOVA. We reported each treatment, or aboveground seagrass biomass, as the probability (*P*) of each model, given that the null hypothesis was true. The model fit, AICc values, AICc weight, and parameter estimates for each individual ecosystem function and the multifunctionality response variable are tabulated in Appendix 6.E.

To assess if megaherbivore grazing intensity, reflected in treatments on aboveground seagrass biomass, had effects on the seven measured ecosystem functions, we employed the *multifunc* package (version [0.7.0]; https://github.com/jebyrnes/multifunc) as well as the averaging and single threshold approaches to quantify ecosystem multifunctionality (Byrnes et al. 2014). The averaging approach determined the average level of multiple functions by standardizing each function average to a common scale and taking the mean. Realizing that invasive seagrass cover represented a negative contribution to ecosystem multifunctionality the invasive seagrass cover was used as an inverse function. We integrated the overall effect of single ecosystem functions by estimating an average ecosystem multifunctionality index (in percent) for each plot. We assumed that high values for each of the seven functions corresponded to a high level of ecosystem function (i.e., higher values of sediment stability implied a higher performance for this function). The average ecosystem multifunctionality index can be interpreted as the average level of all seven functions. However, this index should not be used to assess whether all functions were being performed simultaneously at a high level, given that functions performed at low levels could be averaged out by those performed at high levels. Thus, we summed up the number of ecosystem functions in each plot for which the standardized estimate was above each of nine thresholds (from 10 % - 90 % of maximum functioning, in increments at 10 %) (Byrnes et al. 2014). Threshold index scores (ranging from zero to seven) denoted the number of ecosystem functions above a specific threshold in each plot.

6.3 RESULTS

The three different megaherbivore grazing intensity scenarios that were simulated by our *in situ* experimental treatments resulted in pronounced differences in aboveground seagrass biomass (Appendix 6.A). Treatment 2 (intermediate turtle grazing intensity) led to reduced aboveground seagrass biomass by 55 % compared to treatment 1 (no turtle grazing). Treatment 3 (intensive turtle grazing) reduced the aboveground seagrass biomass by 96 %.

The relationships between six of the seven ecosystem functions and the aboveground plant biomass (as a proxy for megaherbivore grazing intensity) were highly significant ($P < 0.002$, Fig. 6.2). Nitrogen uptake, decomposition, sediment organic carbon content, fish biomass, macroinvertebrate species richness and sediment stability were all positively related to seagrass biomass (Fig. 6.2). Whereas the percentage invasive species cover seemed negatively related to seagrass biomass, this effect was statistically nonsignificant. We identified both linear and nonlinear relationships between aboveground seagrass biomass and individual ecosystem functions (Fig. 6.2) and found both thresholds and saturations in the provisioning of ecosystem functions under the manipulation of seagrass biomass and grazing intensity. The response of seagrass net nitrogen uptake, underpinning the ecosystem service water purification (Table 6.1) was hyperbolic (Fig. 6.2a). Decomposition and sediment organic carbon content, both functions affecting carbon storage, increased linearly (Fig. 6.2b) and logarithmically (Fig. 6.2c) respectively, with aboveground seagrass biomass.

The response of fish biomass, a function representing the ecosystem service food provisioning, was hyperbolic (Fig. 6.2d). The response of macroinvertebrate species richness, also representing food provisioning, to aboveground seagrass biomass, was logarithmic (Fig. 6.2e). The response of sediment stability, a process that represents erosion control and hence coastal protection (Christianen et al. 2013), was exponential (Fig. 6.2f), and unaffected by median grain size (Appendix 6.D). No significant relationship between aboveground seagrass biomass and invasive species percentage was detected (Fig. 6.2g). Markedly different effects of our treatments on ecosystem functions were also reflected in the relative responses, e.g., the rate of increase in fish biomass was lower compared to the data on macroinvertebrate species richness.

Importantly, the impact of the simulated progressing megaherbivore intensity treatments varied among single ecosystem functions (Fig. 6.2a-g). Under intermediate turtle grazing (Treatment 2), the plant production level was the highest and two out of the seven ecosystem functions (sediment organic carbon content, and nutrient cycling) had the highest measured values. Intense grazing (Treatment 3, representing megaherbivore accumulation) resulted in a collapse of ecosystem functions. Without turtle grazing (Treatment 1), four out of the seven ecosystem functions (sediment stability, fish biomass, macroinvertebrate species richness, and decomposition rate) had the highest values (Fig. 6.2a-g).

Ecosystem multifunctionality, the combined effect of all seven single ecosystem functions, was positively related to aboveground plant biomass (Fig. 6.2h). The effect of aboveground seagrass biomass on ecosystem multifunctionality thresholds was positive (> the 10 % threshold), although the nature of the response differed among threshold values (Fig. 6.2i); a linear relationship was observed at a 20 % threshold, whereas the response was exponential at 30 %, logarithmic at 40 %, hyperbolic at 70 % and linear function at 90 % threshold (Fig. 6.2a-i).

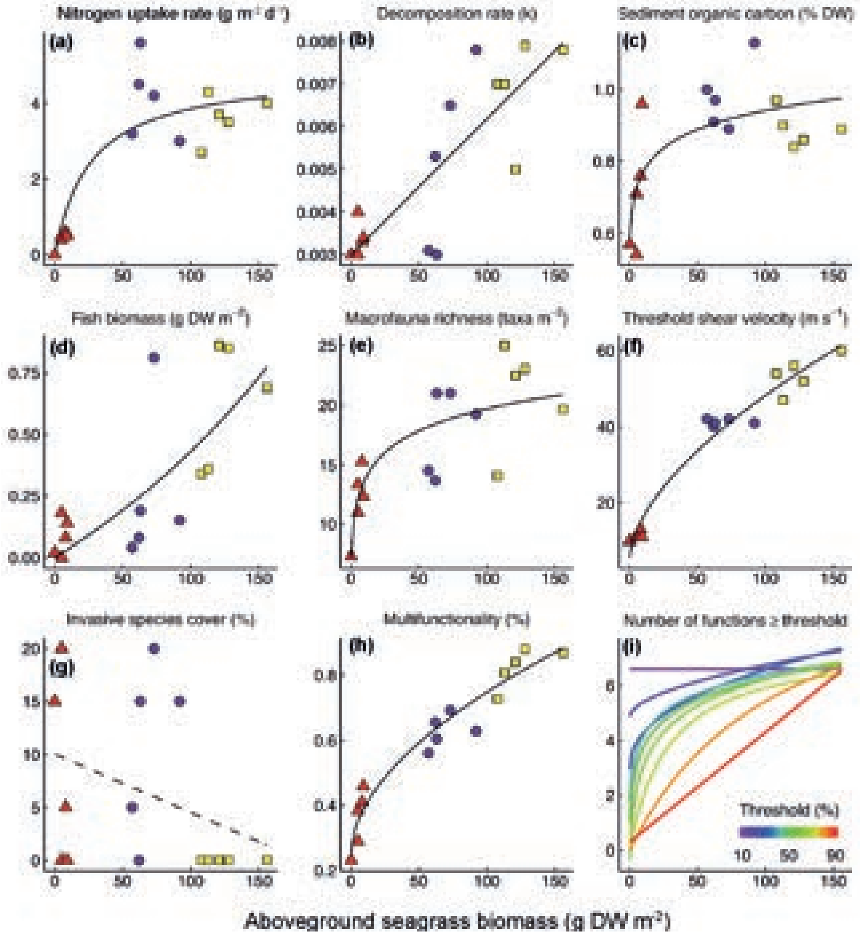

Figure 6.2 Results of experimental manipulation simulating differential megaherbivore grazing intensities on seagrass ecosystem functions and ecosystem multifunctionality, following the three megaherbivore grazing scenarios (Fig. 6.3) with aboveground seagrass biomass as a proxy for the outcome of grazing intensity (x-axis). The best fitting models determined by AICc are shown in Appendix 6.E. (A) Net leaf nitrogen uptake rate, (B) Tea bag decomposition rate. (C) Sediment organic carbon storage. (D) Biomass of fish species (E) The taxonomic richness of macroinvertebrates. (F) Sediment stabilization, measured as threshold shear velocity, the speed at which sediment became mobile in a unidirectional-flow field flume. (G) Resilience against invasive species expansion, measured as change in % cover of the invasive seagrass *Halophila stipulacea (not significant)*. (H) Ecosystem multifunctionality index, the average of the seven standardized functions in percent. (I) Several functions (max seven functions) exceed threshold levels in each plot against aboveground seagrass biomass, for thresholds ranging from 10 % to 90 % of the maximum indicated on the color scale below. Colors and symbols correspond to the three grazing intensities Treatment 1 - no turtle grazing (megaherbivores ecologically extinct, yellow squares), Treatment 2 - intermediate turtle grazing (return of megaherbivores to intermediate levels, purple circles), Treatment 3 - intensive turtle grazing (megaherbivores accumulation, red triangles). Solid line: significant results. Dotted line: results not significant.

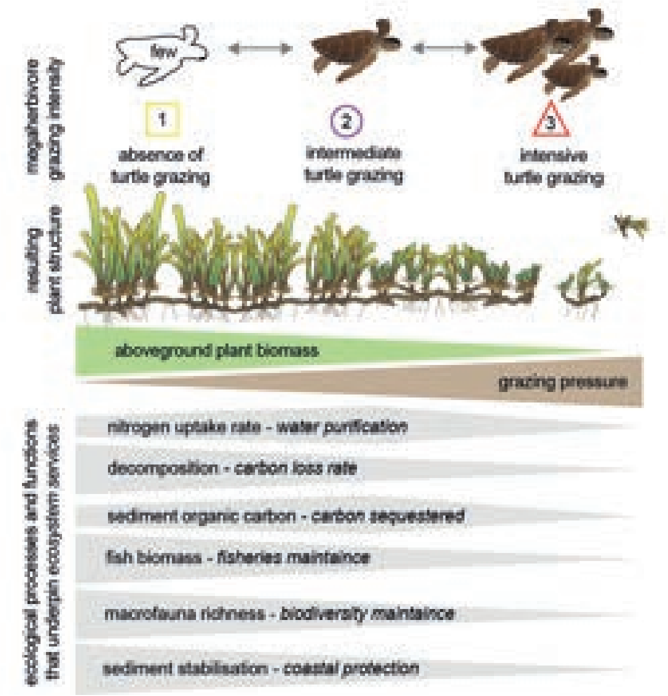

Figure 6.3 Consequences of changing marine megaherbivore densities for ecosystem functioning and services. Three scenarios of megaherbivore grazing intensity, can be observed in tropical seagrass ecosystems with green turtles as megaherbivores across the world (Fig. 6.1b). In a *situ* experiment, three different levels of sea turtle grazing intensity were simulated as found in the literature. Treatment 1 - no turtle grazing (megaherbivores ecologically extinct, yellow squares), Treatment 2 - intermediate turtle grazing (return of megaherbivores to intermediate levels, purple circles), Treatment 3 - intensive turtle grazing (megaherbivores accumulation, red triangles). Megaherbivore grazing intensity affects the seagrass biomass, shoot density, and canopy structure which has implications for ecosystem functioning. The impact of megaherbivore grazing intensity for single ecosystem functions and their integrated overall effect, ecosystem multifunctionality, was determined over the range of remaining seagrass biomass at the end of the 18-mo experimental period and is summarized in grey bars. Image credit (vector graphics): Joanna Woerner, Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/). Images were customized by the authors.

6.4 DISCUSSION

In recent decades, humans have driven megafauna loss in the oceans, but have also helped some populations to rebound through successful conservation and restoration efforts (Lotze et al. 2011, McCauley et al. 2015, Mazaris et al. 2017). So far, the consequences of such changes in marine megaherbivores on ecosystem multifunctionality were poorly understood. The present study provides a novel contribution to evaluating the ecosystem multifunctionality index over a gradient of grazing intensity. We provided the first experimental evidence of strong, contrasting impacts between three different scenarios of grazing intensity on ecosystem multifunctionality by a key marine megaherbivore, the green turtle. The experimental results in one area may not necessarily apply to all seagrass systems. However, our results clearly demonstrated that while intermediate turtle grazing results in shifts in ecosystem functioning compared to turtle absence, intensive turtle grazing pressure has a disproportionally large effect on ecosystem functions and likely will result in overgrazing-induced loss of multifunctionality. In addition, our study provides a basis for projecting historical levels of seagrass multifunctionality before their principal megaherbivores first became ecologically extinct.

6.4.1 Multifunctionality is not necessarily highest for the 'natural state' of ecosystems

There have been different turtle scenarios in history (high abundance, low abundance, now sometimes hyper-abundant), but now all three scenarios occur simultaneously in all three ocean basins where turtles are found (Fig. 6.1b), making the outcome of this experiment globally relevant and urgent. As turtles continue to recover, this has led to the need to assess the impact of current megaherbivore scenarios on ecosystem multifunctionality (Scott et al. 2018), and to predict ecosystem impacts of future shifts. In our experiment, each separate turtle grazing intensity treatment affected ecosystem functions differently in terms of the nature and level of impact. The absence of turtle grazing increased sediment stabilization, decomposition, macrofauna species richness as well as fish biomass, but did not significantly enhance nutrient cycling and carbon storage compared to the natural grazed scenario. The largest impact was observed in the treatment corresponding to intensive grazing, leading to a loss of seagrass biomass and resulting in a simultaneous collapse of all seven ecosystem functions measured in our experimental treatments. This could eventually denude land- or seascape of vegetation.

What are appropriate megaherbivore densities and how close today's turtle populations are to pristine numbers is under considerable debate (Broderick et al. 2006, Christianen et al. 2021, Fløjgaard et al. 2022), but our study provides some basis for projecting historical levels of multifunctionality. Pristine seagrass meadows in the past were likely subjected to a high turtle grazing intensity until overharvesting of megafauna began with the arrival of Europeans in the Caribbean in the 17th Century with population estimations "exceeding the highest recorded wildebeest abundances in the Sergenti" (Jackson 1997), and thus consequently lower standing biomass and higher productivity. The results presented here suggest that ecosystem multifunctionality was likely lower for pristine, grazed meadows in pre-European times compared to contemporary seagrass meadows that are often less intensively grazed (e.g., those in Scenario 1 and 2, Fig. 6.2). However, it should be taken into account that the ecosystem services evaluated (and the loss or gain under different treatments) are based on studies that measures in ecosystems with low presence of megafauna (both sharks and sea turtles) and contradicting effects are found. Examples of contradicting effects include some studies that have documented loss of ecosystem services due to increased grazing by green turtles in seagrass ecosystems (James et al. 2020) while others have found no effect or improvement to ecosystem services in grazed systems, including nutrient cycling, macroalgal diversity, sediment stabilization and erosion, and carbon sequestration (Christianen et al. 2012, Molina Hernández and van Tussenbroek 2014, Johnson et al. 2017, 2019, 2020a).

6.4.2 Drivers of megafauna accumulation and degradation of multifunctionality

Although many ecosystems remain depleted of megafauna (Dirzo et al. 2014), reports of rising megaherbivore populations demonstrate nature's impressive potential for resilience and the potential to reverse these declining trends (Lotze et al. 2011, McCauley et al. 2015). Green turtles are an example. Measures to protect green turtles are resulting in the rise of some populations (Chaloupka et al. 2008, Mazaris et al. 2017). However, these populations may not always find sufficiently productive habitat as local anthropogenic stress is degrading coastal habitat, including seagrass, at accelerating rates worldwide (Waycott et al. 2009, Dunic et al. 2021). In addition, tropicalization, the poleward migration of tropical herbivores due to warming water (Vergés et al. 2014a), may enhance megaherbivore densities to increase or accumulate in remaining habitat and to degradation of multifunctionality. Tropicalization has brought green turtles to subtropical seagrass meadows where they were previously rare or only present in summer (Hyndes et al. 2016, Rodriguez and Heck 2020), and where light conditions result in lower seagrass recovery rates, leading to a risk of overgrazing. Seagrass is also experiencing lower seagrass recovery rates in both tropical as in subtropical areas due to significant anthropogenic impacts to the health and stability of seagrass ecosystems, that could thereby further exacerbate the negative effects of grazing. As a result, reports of megaherbivore accumulation are becoming more frequent in areas where habitat resilience is eroding (Ballorain et al. 2010, Lal et al. 2010, Christianen et al. 2014, Molina Hernández and van Tussenbroek 2014, Fourqurean et al. 2019, Gangal et al. 2021). In these areas megaherbivore recovery not simply alters what humans are accustomed to gaining from an unnatural, ungrazed system, but may even lead to overgrazing and the collapse of multifunctionality. An example has recently emerged in the Lakshadweep Islands where turtle overgrazing caused archipelago-wide functional declines of seagrass meadows, with seagrass recovery being absent or low (primarily by a small pioneer species, Gangal et al. 2021).

The impact that turtle grazing has on their environment is likely accelerated further by the decline in large sharks that continues globally (Ferretti et al. 2010, Queiroz et al. 2019). Reports of seagrass overgrazing by turtles from Bermuda (Fourqurean et al. 2019) and Indonesia (Christianen et al. 2014), both show seagrass meadows where predators are ecologically extinct (Heithaus et al. 2014). Although the top-down regulation of turtles remains a topic of debate, large sharks impact the distribution of turtles and dugongs and can reduce grazing pressure through fear effects (Smulders et al. 2023a, Wirsing et al. 2007a, Heithaus et al. 2008b, Burkholder et al. 2013), and can therefore help prevent herbivore accumulation and improve ecosystem multifunctionality. This mirrors the impact of predators on large herbivores in terrestrial system, such as wolves helping to disperse ungulates in space (Laundré et al. 2001), and in dugong grazed seagrass meadows without tiger sharks, where experiments have shown that grazing can exacerbate effects of extreme climate events on seagrass recovery and community composition (Nowicki et al. 2021). Our results imply that the enhancement of ecosystem multifunctionality requires that all ecosystem components, habitat *and,* top predators and megaherbivores recover in the same direction.

In other aquatic ecosystems ecosystem multifunctionality may be affected by similar interactions with rising megaherbivore populations, underscoring the general applicability of our findings. Examples of megaherbivore impacts include various groups of grazers. Overgrazing by Greylag goose threatened restoration of reed belts (Bakker et al. 2018), and overgrazing by waterfowl may endanger the existence of temperate seagrass meadows (Kollars et al. 2017). Overgrazing by West Indian

Manatees was also shown to hinder efforts to restore submerged macrophyte beds (Hauxwell et al. 2004).

6.4.4 Integrating non-linearity of ecosystem responses

We observed linear as well as non-linear responses among different ecosystem services; differing in slope and saturation point, as observed previously in other coastal ecosystems (Barbier et al. 2008, Koch et al. 2009, Angelini et al. 2015, Ramus et al. 2017). We therefore echo the importance of appreciating the non-linear response previously mentioned (Koch et al. 2009). The non-linear responses justified our approach to measure ecosystem functions along a gradient of realized plant biomass, without which we would have failed to detect optimal responses and thresholds for the sudden collapse. Consequently, realized plant density (or biomass) proved the key parameter in assessing the impact of megaherbivore grazing intensity on ecosystem functions and services. This may likely apply to other exclosure studies as well, which to date have rarely taken into account gradients in grazing pressure or realized plant density.

6.4.5 Potential of the ecosystem multifunctionality index

Our study showcased the large potential in employing the ecosystem multifunctionality index to characterize the current and future performance of the entire ecosystem, by providing a quantitative measure of how change simultaneously influences multiple functions and services. The multifunctionality approach has been developed to investigate the relationship between ecosystem multifunctionality and biodiversity (Byrnes et al. 2014). Multifunctionality has been investigated using different methodologies for example to analyse the impact of simultaneous environmental stressors through impacts on the diversity and biomass of the community (Antiqueira et al. 2018). Here, our results on the relation between ecosystem multifunctionality and seagrass biomass changes driven by megaherbivore grazing intensity, show the potential for wider application of this approach by employing an index of multifunctionality to characterize ecosystem performance beyond biodiversity studies. However, the approach can benefit from additional developments and refinements. We revealed that the response curves differ strongly among specific ecosystem functions. In contrast to the high variability among functions underlying different ecosystem services, a low variability was found between functions underlying the same ecosystem service in our study ecosystem (Appendix 6.C; taxonomic richness of epifauna, infauna and fish that underly fisheries maintenance). Such low variability between functions was also found in coastal ecosystem dominated by algae (Ramus et al. 2017). Thus, the ecosystem multifunctionality index appears to be robust in terms of the choice of the specific ecosystem functions from which the index is composed. An ecosystem multifunctionality index could be applied widely across a range of habitats and ecosystems. Opportunities for further development and expansion of the ecosystem multifunctionality index include integrating a weight of each "sub-index" or "ecosystem function" to the final ecosystem multifunctionality index and adding additional "sub-indexes" including sociocultural and economical aspects (e.g., tourism). Tailoring the ecosystem multifunctionality index to each unique case, both by the choice of sub-indexes as well as the weight of each sub-index, would facilitate the application of a universal, transparent index of ecosystem performance.

6.4.6 Implications for management and conservation

Collectively, our *in-situ* experiments revealed strong, contrasting impacts between three different levels of megaherbivore grazing intensity on ecosystem services and multifunctionality in a seagrass meadow, ultimately affecting human wellbeing. Our results have implications for coastal management and conservation. Building on examples of historical megafaunal declines and trophic downgrading(Estes et al., 2016), our findings make it clear that when integrative conservation approaches, aimed at top predators, megafauna and their habitats, prevent megaherbivore accumulation this may enhance ecosystem multifunctionality and restore the ecosystem functions provided by megafauna and their habitats. Unlike terrestrial systems, where there are many more protected areas but where management is now often retrospectively focused on restoring damaged habitats, in marine systems there is still a unique opportunity to proactively prevent habitat loss and reduce marine hunting to manage our impacts on marine habitats and fauna (McCauley et al. 2015). In addition, management plans need to be feasible within the constraints of the current state-of affairs, rather than applying the pre-European state as a reference (in which meadows could sustain higher numbers of megaherbivores), since this reference is no longer valid due to global decimation of megafauna, and habitat loss (Fløjgaard et al. 2022). Ecosystem interactions and dynamics must be accounted for during both the planning and management of protected areas, focusing beyond the alleviation of pressure on single species (e.g., focusing on whole seagrass ecosystems instead of green turtle conservation, Christianen et al. 2021). To arrive at balanced approaches and updated ecosystem reference states, we need a comprehensive examination of the status of the large predators, the megaherbivores and its habitats in experimental rewilding sites that need to be established. In addition, the development of new conservation and strategies also requires including non-linear responses, habitat connectivity and dynamics, synergetic stressors, and ecosystem multifunctionality. Incorporation of integrative multifunctionality indexes towards a balanced approach to conservation and restoration has the potential to enhance ecosystem multifunctionality.

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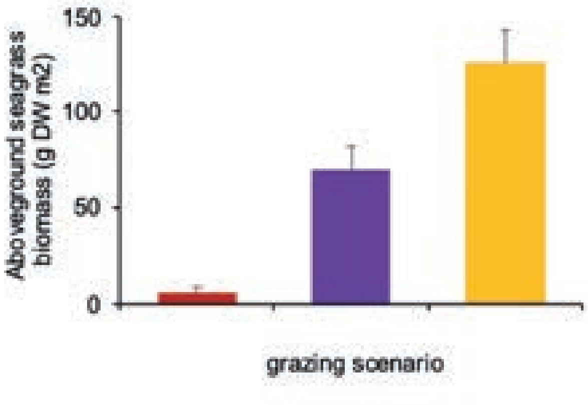
APPENDIX 6.A

The average aboveground seagrass biomass (± SE) measured at the end of the experiment showed significant differences among the three megaherbivore grazing scenarios (ANOVA; $F2,12 = 94.6$, $P < 0.0001$, $R^2 = 0.94$). Yellow - no turtle grazing (megaherbivores ecologically extinct), Purple - intermediate turtle grazing (return of megaherbivores to intermediate levels), Red - intensive turtle grazing.

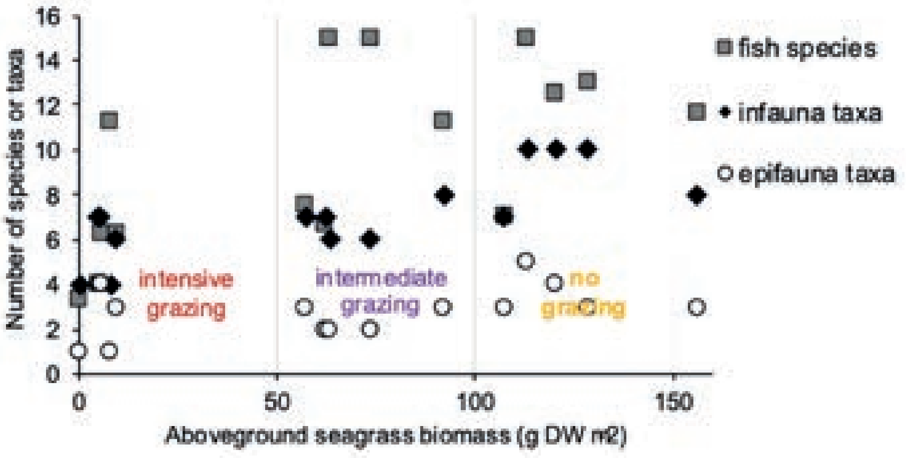


APPENDIX 6.B

Mean plot-level responses used in all analyses. Can be found as 'Dataset S1' at https://doi.org/10.4121/21214229

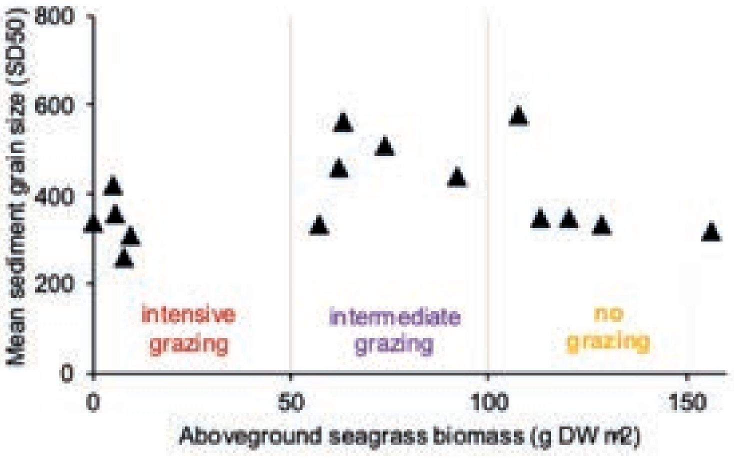
APPENDIX 6.C

The taxonomic richness of fish, infauna, and epifauna taxa along the gradient in seagrass aboveground biomass of the treatments



APPENDIX 6.D

Sediment median grain size was comparable along the seagrass biomass gradient in the treatments ($P > 0.05$, $R^2 = 0.02$). Therefore, sediment grain size appeared uncorrelated with the sediment stabilization proxies ($P > 0.05$) and could not explain the differences in threshold shear velocities (Fig. 6.2f).



APPENDIX 6.E

Model selection tables for all response variables and all models considered. Can be found as 'Dataset S2' at https://doi.org/10.4121/21214229

APPENDIX 6.F

To analyse the number of publications on seagrass and megaherbivores in peer-reviewed journals over time a survey was performed on literature published from 1960 to June 2022 using the search terms "seagrass* AND turtle AND (graz* OR herb*)" using SCOPUS, and Web of Science. 148 peer-reviewed publications were identified that address seagrass and turtle grazing in some way,the first publication is from 1978. Since 1996, more than one publication per year has been published, and the publication rate rapidly increased from 4 per year in 2016 to 16 per year in 2021 (Fig. 6.1a). To illustrate the distribution of the three different grazing scenarios for green turtles, an example of all three scenarios was selected from literature for each of the three ocean basins where green turtles and (sub)tropical seagrass co-occur. And these were presented in a map (Fig. 6.1b). The map is not complete but shows that all three grazing scenarios can currently still be found in multiple ocean basins, making the outcome of our experiment globally relevant and urgent.

CHAPTER 7

Temperature and herbivory drive seagrass recovery potential

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ABSTRACT

Climate-driven shifts in herbivores, nutrient runoff and temperature have been reported to disrupt the functioning of marine primary producers, fueling worries about the future of coastal ecosystems in a warming climate. Here we show that over its (sub) tropical range, seagrass has in fact higher resilience in warmer places. We assessed resilience by studying recovery rates from small-scale (0.018 m^2) perturbations in which we removed all above-and below-ground biomass and applied fertilization treatments in a year-long field experiment. A total of 100 plots at ten sites in the Western Atlantic that span over 20° of latitude were monitored. We show that temperature and grazing pressure are the main driving factors impacting above-and belowground seagrass recovery. Surprisingly, ambient nutrient and light availability and fertilization treatments did not directly affect seagrass recovery, although nutrients did modulate the effect of grazers. Our results suggest that while temperature extremes may still harm seagrass, resilience of this foundational species may increase in gradually warming subtropical parts of its range.

7.1 INTRODUCTION

Global warming and other human-induced stressors are increasingly driving large scale ecosystem loss (Dirzo et al. 2014, IPCC 2022). Seagrass ecosystems, located at the border between land and sea, are amongst the most threatened, as 19-29% of the global monitored area has been lost since 1940 (Waycott et al. 2009, Dunic et al. 2021). Because of their thermal tolerance limits, mass mortality of seagrass is expected under projected global change scenarios (Marbà et al. 2022). Furthermore, direct impacts of warming such as an increase in the frequency and intensity of heatwaves and storms (Knutson et al. 2010, Seidl et al. 2017), may lead to seagrass decline (Serrano et al. 2021). Meanwhile, climate-induced poleward shifts of species, termed tropicalization, can lead to local changes in grazing pressure when herbivores shift their habitat range (Vergés et al. 2014a, 2016, Rodriguez and Heck 2021). Additionally, local impacts include eutrophication due to urban and agricultural nutrient runoff (Lapointe 2019, Horta et al. 2021) which can cause seagrass loss through algal-driven light limitation (Burkholder et al. 2007, Morris et al. 2022). Together, the combined and interacting effects of these factors may drive seagrass loss by compromising their stability and thus their ecological resilience (van Nes and Scheffer 2007, Gissi et al. 2021). For example, seagrass ecosystems weakened by eutrophication may be more vulnerable to heatwaves, increasing the chance of meadow collapse (Ontoria et al. 2019, Pazzaglia et al. 2020). Our understanding of how global change factors are leading to seagrass loss remains limited because empirical studies often assess impacts of single drivers, on small spatial scales, leading to an incomplete understanding of the cumulative impact of multiple environmental drivers on ecosystem resilience across large spatial scales (Borer et al. 2014a).

Field-based methods testing the resilience of foundation species, such as seagrasses, are rapidly developing. In particular, increasing evidence suggests that dynamic indicators, such as the recovery rate after a disturbance, may be better suited to indicate the resilience of an ecosystem compared to static indicators, such as cover or standing biomass (Holling and Gunderson 2002, Cole et al. 2014). Experimental tests of resilience in vegetated habitats with system-wide perturbations of above- and belowground biomass are rarely feasible. Instead, measuring the recovery rate after a small-scale experimental perturbation can serve as a reliable indicator of the resilience of a large-scale ecosystem (Scheffer et al. 2015b, van de Leemput et al. 2018), where a slow recovery may signal vulnerability to a catastrophic shift (van Nes and Scheffer 2007). Disturbance and recovery experiments thereby provide a tool to determine the overall resilience of an ecosystem. In macrophyte dominated ecosystems, the focus is often on measuring aboveground recovery (Macreadie et al. 2014, Smith et al. 2016, Castagno et al. 2021). However, knowledge of belowground dynamics is key for understanding the resilience of these ecosytems (Nyman et al. 2006, Vonk et al. 2015), because belowground biomass includes the carbon reserves important for recovery potential (Hagedorn et al. 2016, Yang and Li 2022) and the root structure that provides stability and resistance to waves and storms (Sasser et al. 2018, Battisti and Griffin 2022, Infantes et al. 2022). Assessing factors that determine both above- and belowground recovery rates is therefore essential to provide management recommendations to conserve and protect coastal ecosystems in times of change and to help build resilience in vulnerable ecosystems facing multiple threats (Senf et al. 2019).

The aim of this study is to investigate the effects of key environmental drivers (temperature, light, nutrient availability and grazing), that vary spatially and are expected to shift because of global change, on the resilience of (sub)tropical seagrass ecosystems. Resilience was assessed by measuring above- and belowground rates of seagrass recovery after a small-scale disturbance (biomass removal) across multiple sites in the North West Atlantic. Since seagrass species traits, as well as the timing and temporal and spatial scale of the disturbance play a large role in determining recovery (Rasheed 2004, Soissons et al. 2018, O'Brien et al. 2018, Sanmartí et al. 2021), we sought to standardize these factors within a regionally coordinated experiment. We focussed on the foundational species *Thalassia testudinum*, as its range extends over a large region in the North West Atlantic and varying recovery times have been reported across studies that varied in site characteristics and their methodology (Dawes et al. 1997, Kenworthy et al. 2002, Hammerstrom et al. 2007). We tested the effect of nutrient fertilization treatments on seagrass recovery by selecting 10 sites across the range of *T. testudinum*, spanning >20° of latitude in a year-long experiment. Additionally, we tested the separate and interactive effects of natural variation in 1) temperature, 2) nutrient availability, 3) light, and 4) fish and turtle grazing on seagrass recovery. We found evidence that both temperature and herbivory – depending on the type of herbivore – can increase seagrass recovery rates and therefore enhance the resilience of (sub)tropical seagrass beds.

7.2 METHODS

7.2.1 Study site

This experiment was part of a larger coordinated research program, the *Thalassia* Experimental Network (TEN) which included experimental sites across the geographic range of *T. testudinum* in the North West Atlantic (9-32 °N) (see Campbell et al. 2023 in press for a detailed set-up of the TEN experiment). At each site, the specific location had the following conditions: a depth of < 4 m, seagrass beds dominated by *T. testudinum* (> 50 % relative abundance), and a minimum seagrass meadow area of 25 m x 25 m. Due to logistics, this experiment could be performed at nine out of the 13 sites that were part of TEN (Appendix 7.A, Fig. 7.1) and we added two sites that were not in the original network: Eleuthera 2 in the Bahamas and Barcadera Bay, Aruba. Eleuthera 2 was added because the original TEN experimental array (Eleuthera 1) became heavily grazed by turtles due to the presence of experimental cages and was therefore not representative of the surrounding seagrass seascape (Smulders et al. 2023a). Therefore, for this experiment, we established a second site (Eleuthera 2) outside of the grazing patch. Additionally, to improve the latitudinal balance of the set-up, Barcadera Bay, Aruba was added as a site.

7.2.2 Experimental design

Identical field experiments were conducted at each site with two treatments, nutrient fertilization and a control (N = 5 per treatment). Ten experimental plots (0.25 x 0.25 m, at least 2 m apart in a randomized design) were established at each site in the fall of 2018 (Sept – Nov, Appendix 7.A) In each plot, a disturbance was created by removing all above – and belowground biomass within a 15 cm diameter circle down to 20 cm in the sediment. After the biomass core was collected, the void was filled with local sediment level to the surrounding sediment, and bamboo skewers (~6 per plot) were used to mark the exact border of where the biomass core had been collected. The seagrass species *T. testudinum* mainly recovers through clonal growth via elongation of horizontal rhizomes (van Tussenbroek et al. 2006). Every two weeks to two months (depending on logistics per site), the number of shoots regrown in the void was counted, to investigate whether the shoot establishment rate was linear throughout the year. After about one year (10-14 months from the experimental disturbance) all biomass that had recovered within the marked void was collected.

Both at the start and end of the experiment, all biomass material was stored in a cooler and processed within 24 hours. The shoots were separated from the belowground biomass, leaves were scraped clean of epiphytes, and the above and belowground material were dried separately in an oven at 60 °C. The number of shoots within the biomass core was recorded as well as the dry weight of the above- and belowground biomass per plot.

Fertilization treatments were established by attaching a fibreglass mesh bag containing 300 g of slow-release Osmocote fertilizer (Everris NPK 14:14:14) 30 cm above the sediment to a pole, at the corner of each plot (following Campbell et al. 2018). Bags were replaced monthly to ensure consistent enrichment.

7.2.3 Environmental drivers of seagrass recovery

We measured several environmental factors at the site level as candidate drivers for seagrass recovery rates. The water temperature was recorded every 6 minutes by loggers (HOBO UA-002064) deployed in the seagrass canopy for the duration of the experiment (spring 2018 to spring 2019). From these daily measurements, an average annual temperature was calculated for each site, as well as the seasonality (SD of temperature among months). Light intensity was measured by a light sensor (Odyssey Submersible PAR Logger) deployed at the same location, with the same measuring interval and duration as the temperature loggers and averaged annually. Since sites may be either P- or N-limited (Fourqurean and Zieman 2002), we used an index to indicate the overall magnitude of nutrient limitation. The Limitation Index (LI) was calculated as the absolute deviation of leaf molar N:P from the balanced 30:1 ratio (Campbell and Fourqurean 2009). LI indicates ambient nutrient availability, where higher values of LI signal a larger degree of either N or P limitation. Ambient leaf N and P content was obtained by analyzing the green leaf tissue from the control (N = 5) plots at the start of the experiment. Additionally, all green leaf material of both control (N = 5) and nutrient-enriched plots (N = 5) obtained at the end of the experiment was analyzed for nutrients to assess the impact of nutrient enrichment on the N and P content of the leaves. Dried leaf material was homogenized to a fine powder using a mortar and pestle. The leaf material was subsequently analyzed for nitrogen content on an elemental analyzer (Thermo Flash 1112), and for phosphorus content on an autoanalyzer (SKALAR San++) after a digestion using sulphuric acid and selenium (following Novozamsky et al. 1983).

Several other environmental drivers were quantified at plot level. To quantify herbivory pressure, we estimated both megaherbivore (turtle) and mesoherbivore (fish) grazing pressure per plot. Fish grazing marks on *T. testudinum* are mostly visible as crescent shaped bitemarks from the sides and top of the leaf (Appendix 7.B). Therefore, fish grazing pressure was estimated by counting the average number of fish (crescent) grazing marks per shoot of (a maximum of) 10 shoots collected in each plot at the end of the experiment (fall 2019). Turtles crop the leaves from above resulting in a straight cut (Appendix 7.B). Therefore, turtle grazing pressure was estimated by calculating the proportion of leaf area that was removed in each of the plots relative to the mean leaf area of the ambient caged plots of the TEN experiment (Campbell et al. 2023 in press). By cross-referencing this calculation with known turtle abundances at the study sites (Pers. obs. LMRB, AMM, FOHS, SAM) this measure was chosen as an accurate estimation of turtle grazing pressure. Estimates were based on seagrass leaf grazing marks instead of known fish or turtle densities in the area because these more accurately represent local grazing impact as within a given meadow there can be local heterogeneity in grazing pressure (Smulders et al. 2022, 2023a).

7.2.4 Data analysis

Our analyses focused on identifying driving factors in *T. testudinum* seagrass recovery rates. We used multi-model inference to examine which local and across-site environmental factors were important for our recovery response variables which were based on measured shoot abundance, aboveground biomass and belowground biomass. Because the timing of the end-harvest varied across sites (between 293 – 433 days after the start of disturbance), the number of shoots, aboveground biomass and belowground biomass recovered at the end of the experiment were standardized to 365 days assuming linear growth, which was confirmed using regression analysis of the shoot abundance data over time after experimental disturbance (Appendix 7.C). The percentage recovered was calculated by dividing the the plot-specific response variables after 1 year by values measured at the start of the disturbance, and multiplying this by 100. Years needed until full recovery was calculated by dividing the start total biomass by the end total biomass, multiplied by the duration of each experiment, and divided by 365 days. Latitude and seasonality were both correlated with average annual temperature and therefore excluded from the main models (Appendix 7.D). For all response variables (shoot, aboveground and belowground recovery), we included the covariates ‘temperature’, ‘fish grazing’, ‘turtle grazing’, ‘light’ and ‘LI’. The models also included fertilization as a fixed factor to observe any significant interactions between fertilization and fish herbivory, turtle herbivory, and LI. We standardized our covariate values by subtracting the mean and dividing by the standard deviation. All covariates had variance inflation factors <5, indicating low collinearity. We fitted the full models for the response variables shoot abundance and above- and belowground biomass using generalized linear mixed models (GLMMs) with site as a random effect and a Tweedie distribution, used for continuous data with non-normal distributions and zero inflation (our response variables had between

13 - 26% zeroes and were tested for zero-inflation using the DHARMa package) using the glmmTMB package. All full models were examined for model fit by plotting the residuals versus the fitted values, the fitted values versus the observed data and the residuals versus the treatment 'fertilization'. The model fit, specifically the ability of the models to cope with the large numbers of zeroes, as well as outliers, dispersion and uniformity were tested using the DHARMa package. We ranked the resulting potential models with AICc using the 'dredge' function in the MuMIn package in R. Because the top models were performing equally well, we performed model averaging to arrive at consistent parameter estimates of the most important explanatory variables in the full GLMM, by averaging a set of top models which share similarly high levels of parsimony. We defined the top models as those that fell within 2 AIC units of the model with the lowest AIC value, as is recommended when factors may have weak interactions with the response (Grueber et al. 2011) with the model.avg function in the MuMIn package, and we present the conditional averages. For data visualization of above- and belowground biomass recovery, we created a dataset using the 'predict' function for each specific significant variable while the remaining variables were set at their average value.

To test whether fertilization increased leaf N and P content, we fitted a linear mixed effects model with a gaussian distribution (using glmmTMB) to plot-specific leaf N and P data, with site as a random effect and fertilization as a fixed factor. Model validation was done as described above.

To test the difference in effect of the environmental factors on traditional static indicators versus dynamic indicators, we compared the response of the aboveground biomass and shoot density (= static) as measured at the start of the experiment to the aboveground biomass recovery and shoot recovery percentages (= dynamic) as obtained at the end of the experiment in the control plots (total of 50 plots). For shoot density and aboveground biomass linear mixed models were used (using lme4 package) and for shoot and aboveground biomass recovery generalized linear mixed models with a Tweedie distribution (using glmmTMB).

To further investigate the relationships among the above and belowground seagrass recovery response variables, we performed correlation analysis using the 'cor' function in R. All data analyses were performed in R, version 2022.12.0 (R Core Team 2022)..

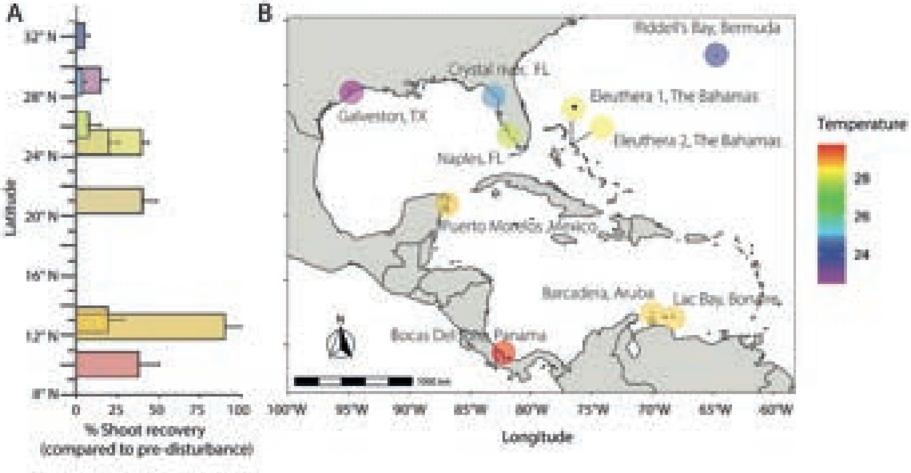

Figure 7.1 (A) Field measurements of seagrass shoot recovery (% compared to pre-disturbance ± SE) in unfertilized plots along a latitudinal gradient, with (B) a map of our study sites. Average annual water temperatures are visualized in color on the bar chart and on the map.

7.3 RESULTS

7.3.1 The effects of fertilization and environmental drivers on seagrass shoot recovery

There was no main effect of fertilization on the percentage of *T. testudinum* shoots recovered after one year (Table 7.1). The percentage of shoot recovery increased with temperature (p = 0.03). Significant interactions were observed between fertilization and both types of grazing pressure. The percentage of recovered shoots increased with increasing fish grazing pressure in the control plots, but not in the fertilized plots (p = 0.002). With increasing turtle grazing pressure, the percentage of recovered shoots decreased in the fertilized plots, while no relationship was found in the control plots (p = 0.013). Fertilization therefore reduced shoot recovery at high grazing pressure for both types of grazers. Figure 7.1 provides an overview of the distribution of our sampling sites and their mean annual temperature, together with associated shoot recovery of the control plots. Results of the latitude and seasonality models are included in Appendix 7.E, 7.F.

Table 7.1 Statistical results for averaged linear mixed models testing the impact of fertilization treatments and environmental drivers on seagrass recovery and nutrient content. The number of top models (≤ Δ2 AICc) is reported, along with the coefficient estimates and standard errors of the standardized regressors. Temperature is the average yearly water temperature at canopy level. Turtle and fish grazing is a grazing index assessed from the leaves. LI is the nutrient limitation index. Light is the yearly average input of light in the system. Nutrient fertilization was simulated by adding both N and P to the water column. Since only one factor, fertilization, was tested against nitrogen and phosphorus content, model averaging was not performed on those two models. Significance codes: ***p<0.0001, **p<0.01, *p<0.05.

Response	Factor	Estimate	SE	P-value
(A) Shoot recovery	**Temperature**	**0.338**	**0.156**	**0.030***
(% Shoots	**Fish grazing**	**0.296**	**0.119**	**0.013***
compared to	**Turtle grazing**	**-0.349**	**0.157**	**0.026***
pre-disturbance)	**Turtle grazing * Fertilization**	**-0.340**	**0.137**	**0.013***
(4 top models)	**Fish grazing * Fertilization**	**-0.253**	**0.081**	**0.002****
	LI * Fertilization	0.214	0.123	0.082
	Light	-0.115	0.134	0.391
	LI	-0.019	0.172	0.598
	Fertilization	0.014	0.010	0.890
(B) Aboveground biomass recovery (% g DW compared to pre-disturbance) (3 top models)	**Temperature**	**0.448**	**0.139**	**0.001****
	Fish grazing	**0.439**	**0.121**	**0.0003*****
	Turtle grazing * Fertilization	**-0.341**	**0.127**	**0.007****
	Fish grazing * Fertilization	**-0.235**	**0.109**	**0.030***
	LI * Fertilization	0.139	0.135	0.299
	Fertilization	-0.018	0.112	0.874
	Turtle grazing	-0.005	0.146	0.970
(C) Belowground biomass recovery (% g DW compared to pre-disturbance) (10 top models)	**Temperature**	**0.524**	**0.202**	**0.009****
	Turtle grazing * Fertilization	**-0.235**	**0.103**	**0.022***
	LI *	**-0.221**	**0.089**	**0.013***
	Fertilization	0.187	0.183	0.306
	Light	0.140	0.142	0.326
	Fish grazing	0.132	0.194	0.497
	LI	-0.124	0.163	0.445
	Turtle grazing	0.044	0.098	0.647
	Fertilization			
(D) % N (DW)	**Fertilization**	**0.228**	**0.048**	**0.000002*****
(E) % P (DW)	Fertilization	-0.001	0.010	0.905

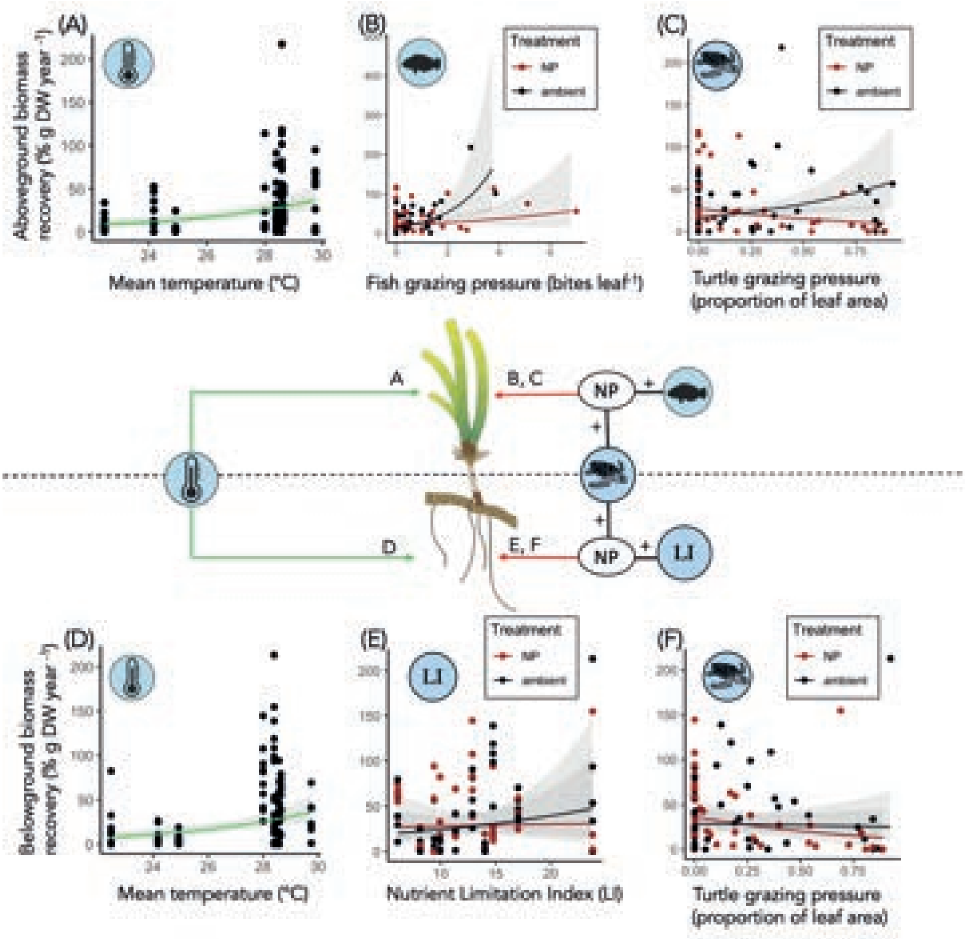

Figure 7.2 Summary of the results of the averaged linear mixed models for above and belowground biomass recovery (% compared to pre-disturbance). The line represents the average value of the model response, with the 95% confidence interval, and is plotted on top of the measured data points. Arrows point from an environmental factor to either above or belowground biomass recovery and indicate a positive (green), negative (red) significant impact on recovery rates either as main effect or in the interaction with fertilization (+ NP) based on the coefficients from the models where p-values < 0.05. Arrow letters correspond to the plots (A-F). Averaged model results are presented in Table 7.1.

7.3.2 The effects of fertilization and environmental drivers on seagrass above- and belowground biomass recovery

Similar to shoot recovery, the percentage of *T. testudinum* aboveground biomass recovered one year after disturbance increased with temperature ($p = 0.001$) (Fig. 7.2, Table 7.1). A significant interaction was observed between fertilization and fish grazing pressure ($p = 0.0003$) and turtle grazing pressure ($p = 0.007$). The positive relationship between fish grazing pressure and aboveground biomass recovery was significantly reduced by fertilization. A negative relationship was found between turtle grazing pressure and aboveground biomass recovery in the fertilized plots, and no relationship in the control plots. Results of the latitude and seasonality models are included in Appendix 7.E, 7.F.

The percentage of belowground biomass recovered one year after disturbance also increased with temperature ($p = 0.009$) (Fig. 7.2, Table 7.1). Additionally, significant interactions were found between the nutrient limitation index (LI) and the fertilization treatment ($p = 0.013$) and between turtle grazing and the fertilization treatment ($p = 0.022$). indicate that fertilization slowed belowground biomass recovery when higher levels of nutrient limitation or turtle grazing were present. The positive relationship found between the nutrient limitation index (LI) and belowground biomass recovery in the control plots was significantly reduced in the fertilized plots. In fertilized plots, a negative relationship was found between turtle grazing pressure and fertilization. The relationship between fish grazing and turtle grazing across sites is displayed in Appendix 7.G. Results of the latitude and seasonality models are included in Appendix 7.E, 7.F.

Fertilization increased leaf N content ($p < 0.0001$), but not leaf P content ($p = 0.91$) (Table 7.1) in seagrass leaves taken from the biomass cores at the end of the experiment. Average values of %N, %P, C:N and C:P are displayed in Appendix 7.G.

When we compared the response of static versus dynamic indicators to the environmental drivers, we found that temperature would not have turned up as an important factor had we focused on static indicators (Appendix 7.J). None of the drivers had a significant impact on static shoot density.

The percentage of shoots and aboveground biomass recovered after one year correlated with the percentage of belowground biomass recovered after one year (Pearson's correlation test, $R^2 = 0.50$, $p = 0.0000001$ and $R^2 = 0.40$, $p = 0.00003$ respectively).

7.3.3 Variation in above- and belowground seagrass recovery rate and recovery time

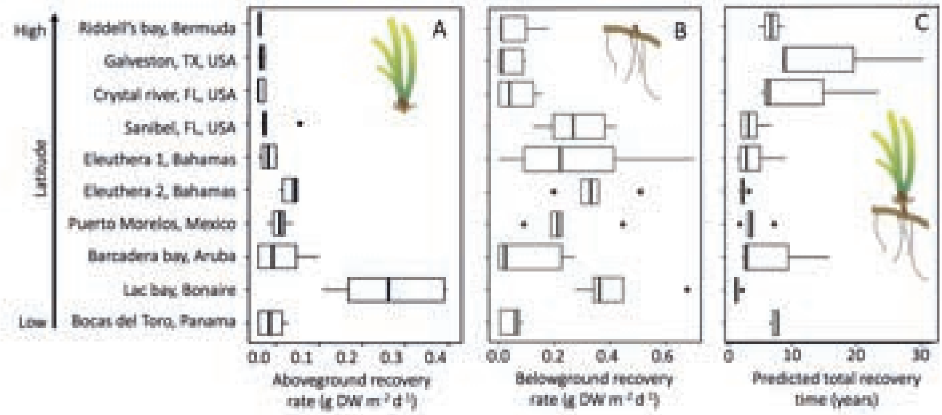

Figure 7.3 Boxplots of (a) aboveground and (b) belowground biomass recovery rates and (c) estimated total recovery time of T. testudinum in unfertilized plots in years. The order of the study sites corresponds to the latitudes from low latitude (bottom) to high latitude (top). Middle vertical lines of the boxes represent boxplot medians, left and right vertical lines represent the 25th and 75th percentiles, whiskers represent the smallest and largest measured values within the 1.5 interquartile range from the box and dots represent the outliers outside the interquartile range.

Aboveground recovery rates (calculated from the biomass cores taken after one year of recovery) in control plots ranged 100-fold from 0.003 ± 0.001 (Bermuda) to 0.30 ± 0.06 (Bonaire) g DW $m^{-2}d^{-1}$ with an overall average of 0.06 ± 0.01 g DW $m^{-2}d^{-1}$ (Fig. 7.3A). Average belowground recovery rates per site ranged 10-fold from 0.04 ± 0.02 (Galveston) to 0.42 ± 0.07 (Bonaire) g DW $m^{-2}d^{-1}$, with an overall average of 0.19 ± 0.03 g DW $m^{-2}d^{-1}$ (Fig. 7.3B).

The percentage of above- and belowground biomass recovered in the control plots after one year was lowest for Crystal river with 2.11 % ± 1.2 and 3.61 ± 1.9 respectively and highest for Bonaire with 195.88 % ± 81.8 and 49.25 ± 6.5 respectively. Comparing above to belowground recovery rates per site and then averaging across sites, we found that aboveground biomass recovers 1.4 times faster back to initial conditions than belowground biomass.

Additionally, we extrapolated the years needed to achieve full recovery (restoring the values from the initial measurements), with a slightly reduced dataset due to removal of the plots that had zero recovery. Years needed for full recovery (both above- and belowground) were lowest for Bonaire (1.5 ± 0.18 years) and highest for Galveston (13.7 ± 3.16 years), with an average of 4.3 years across all sites.

7.4 DISCUSSION

Temperature had a positive effect on the recovery rates of a foundational seagrass across its North West Atlantic geographic range. Our results suggest that cooler temperatures may be limiting the recovery rate of the seagrass *Thalassia testudinum* at subtropical sites, which increases their vulnerability to disturbances and potential collapse (Scheffer et al. 2015a, van de Leemput et al. 2018). These findings are consistent with studies reporting that the resilience of other coastal foundation species such as salt marshes and mangroves can be limited by temperature (Osland et al. 2015, Smith et al. 2022, Reed et al. 2022). Additionally, fish and turtle herbivores altered above and below-ground recovery, depending on local nutrient availability. Increasing grazing pressure due to tropical herbivores expanding their habitat to subtropical latitudes (Vergés et al. 2016) may either positively or negatively impact seagrass resilience depending on herbivore type, grazing intensity and nutrient availability. With our coordinated experimental approach, we showed that temperature and grazing effects are more important in driving (sub)tropical seagrass recovery rates than other environmental drivers such as light. The potential increased resilience due to increasing temperatures may help this seagrass at higher latitudes to resist change and recover after disturbances that are expected under future global change scenarios.

By measuring dynamic indicators (i.e. recovery rates) instead of traditional static indicators (i.e. shoot density, percent cover) we found that a combination of temperature and the interaction between herbivory and fertilization is driving the resilience of this widespread (sub)tropical seagrass species. Temperature was found to increase seagrass recovery, but not seagrass density or aboveground biomass. None of the measured environmental drivers had a significant impact on static shoot density (which, together with cover, is often used as a seagrass response). Therefore, our results provide support from a tropical seagrass system that static and dynamic indicators respond differently to environmental factors, and that dynamic indicators likely reveal future responses of seagrass meadows. We recommend including dynamic indicators to understand the current health and resilience of these coastal foundation species (Lam et al. 2017), and to test whether their resilience may increase over time by adaptations to a changing environment (Cole et al. 2014).

The positive relationship found between temperature and the recovery rates of shoot, above and belowground biomass of (sub)tropical seagrass in this study contrasts with the negative effects of (prolonged) high temperatures that are regularly reported for seagrasses (Thomson et al. 2015, Strydom et al. 2020, Aoki et al. 2021), and other coastal foundation species (Wernberg et al. 2010, Smale 2020). Temperate seagrass meadows have been shown to be especially vulnerable to warming (Seddon et al. 2000, Marbà and Duarte 2010, Shields et al. 2019), but for *T. testudinum*, a species primarily found at tropical latitudes, warming may positively impact growth rates at the edges of its habitat range. Previous work found that under mild temperature increases, seagrass photosynthetic rate increases (Lee et al. 2007), resulting in elevated shoot formation through clonal growth (Lee and Dunton 1996). Above certain temperature thresholds, respiration can exceed photosynthesis, reducing growth rates (Nguyen et al. 2021), which can eventually lead to seagrass collapse (Marbà and Duarte 2010, Marbà et al. 2022). Therefore, seagrasses growing near the upper limits of their thermal distribution in tropical sites may be at elevated risk of increasing sea water temperatures (Wiens 2016), and heatwaves especially. However, within the temperature range examined in our study, which did not include heatwave effects, we found that slight increases in mean annual sea water temperature may benefit the recovery potential of subtropical seagrasses, just as has been found for salt marsh plants in a warming experiment (Smith et al. 2022). Experimental testing of effects of increasing temperatures on the resilience of subtropical seagrasss resilience are needed to confirm the correlative relationships found in this study.

Apart from a lower average annual temperature, subtropical sites experience higher seasonality and therefore a shorter growing season (Tussenbroek et al. 2014). Indeed, we found that higher annual temperature variability – similar to lower annual temperature - drives reduced above and belowground recovery rates. Seagrass growth is likely reduced during winter because of a combination of low surface irradiance and temperatures (Dunton 1994, Tussenbroek et al. 2014, Soissons et al. 2018). A longer growing season due to increasing global temperatures may therefore increase seagrass resilience at subtropical latitudes, depending on local grazing pressure and light and nutrient availability.

Our results highlight that it is important to distinguish types of grazers as well as how grazing intensity can impact recovery rates, corresponding to findings from a single-site experiment (O'Dea et al. 2022). We found that fish grazing pressure can positively impact aboveground recovery rates, likely due to compensatory growth or by fish controlling competitive algae (Vergés et al. 2008, Duffy et al. 2015, Valentine and Heck 2021). An alternative explanation is that, similar to terrestrial grasslands, grazing may open up the canopy thereby increasing light availability for growth of shorter statured vegetation (Borer et al. 2014b). Migrating fishes from tropical sites to subtropical sites may therefore increase local meadow resilience, up to a herbivore density limit where intensive grazing prevents regrowth (Yamaguchi 2010, Vergés et al. 2014b, Bennett et al. 2015). For larger herbivores such as green turtles, we did not find this positive effect of grazing on seagrass resilience, only a negative relationship between turtle grazing pressure and above- and belowground biomass recovery in fertilized plots. In heavily grazed meadows, the carbohydrates may be depleted over time, reducing the capacity for new shoot formation (Fourqurean et al. 2010, López et al. 2019). One of our sites on Eleuthera became heavily grazed by turtles because of the experimental design (Smulders et al. 2023a) resulting in > 50 % reduction of shoot recovery. Our results, together with reports of turtles increasing in densities and/or several overgrazing events at subtropical sites in the Western Atlantic (Fourqurean et al. 2019, Rodriguez and Heck 2021), could indicate reduced meadow resilience and ecosystem functioning in turtle-dense environments (Christianen et al. 2014, 2023, Gangal et al. 2021).

Grazing impact will likely increase, especially in the subtropics, because of the indirect effects of rising temperatures on herbivore habitat range and metabolism (Vergés et al. 2014a, Kumagai et al. 2018, Zarco-Perello et al. 2020). It is unknown whether primary producers will be able to keep up with increasing grazing pressure, as range edge populations experience a shorter growing season with less light (Kirwan et al. 2009, Tussenbroek et al. 2014, Vergés et al. 2016, Soissons et al. 2018). Recently, reduced carbohydrates reserves were found to decrease the tolerance *T. testudinum* to herbivores in the subtropics (Campbell et al. 2023 in press). In addition in our study, grazing (by both turtles and fish) was found to reduce the recovery of shoots and aboveground biomass in fertilized plots. This is likely due to local increased grazing pressure on nutrient enriched leaves, limiting aboveground recovery (Mutchler and Hoffman 2017, Campbell et al. 2018, Smulders et al. 2022). Fertilization-induced grazing pressure by turtles even led to decreased belowground recovery rates. This means that as high latitude sites may currently be less resilient due to temperature and seasonality effects, they are likely more vulnerable to consumer pressure fueled by eutrophication, as was found for other coastal wetlands (He and Silliman 2015). Therefore, it is important to monitor how subtropical seagrasses respond to expected increases in temperature and grazing pressures as well as to assess their carbohydrate reserves and (seasonal) light availability to determine if they will be able to maintain resilience under high grazing pressure (Soissons et al. 2018, Campbell et al. 2023 in press).

Theory suggests that the capacity of plant communities to recover after disturbances likely depends on local nutrient status (Boada et al. 2017, Wasson et al. 2017). Seagrass allocates more biomass to leaf tissue when nutrients are abundant and more to belowground tissue when nutrients are limited (Lee and Dunton 2000, Romero et al. 2006), but it was unknown if this applied to seagrass recovery. In our study, the positive impact of nutrient limitation on belowground biomass recovery found in the control plots was significantly reduced by the fertilization treatment, probably because seagrass invests less in the recovery of belowground biomass when nutrients are abundant (Romero et al. 2006, Olsen and Valiela 2010). Surprisingly, no main effects of the fertilization treatment on shoot and above- or belowground biomass recovery were found, even though we did find a significant increase in nitrogen levels in the nutrient-enriched seagrass leaves. In another study within the same sites, fertilization was found to decrease seagrass leaf productivity (Campbell et al. 2023 in press). Rhizome turnover rates are approximately 10 times lower than leaf turnover rates (Vonk et al. 2015). Therefore, one year was possibly too short a time to distinguish impacts of fertilization on clonal recovery rates at some locations.

Our results can be used to identify vulnerable sites which show lower recovery than expected based on their average seawater temperature. These regions should be the focus of conservation efforts as they may be more vulnerable to collapse (El-Hacen et al. 2018, van de Leemput et al. 2018). Our average of 4.3 years needed until full recovery falls within reported values of 2-9.5 years for *T. testudinum* to recover from (experimental) propellor scars to pre-disturbance conditions (Dawes et al. 1997, Kenworthy et al. 2002, Hammerstrom et al. 2007), and to our knowledge our study includes for the first time belowground biomass recovery measurements to this prediction. We found average recovery rates of 0.06-0.36 g DW belowground biomass m^{-2} day^{-1}. These rates can be used to predict the recovery rate of *T. testudinum* in meadow scars initiated by propellers or anchors, or under heavy turtle grazing pressure, and to estimate the recovery of important ecosystem services such as sediment stability and carbon storage after disturbance. We found that aboveground biomass recovered on average 1.4 times faster than belowground biomass, indicating that aboveground biomass production is likely followed by belowground biomass recovery. For future research on seagrass recovery rates, we want to highlight that in our study, shoot recovery responded similarly to aboveground biomass recovery in response to temperature related drivers, but not to belowground biomass recovery. Therefore, dynamic responses of aboveground variables may not be representative of the whole plant, and for future studies it is important to include measures of belowground biomass recovery to be able to comprehensively study resilience indicators.

In conclusion, our study shows that 1) temperature is a main predictor of increased resilience of (sub)tropical seagrasses, 2) the interaction between nutrient fertilization and fish or turtle herbivory has the potential to decrease seagrass meadow resilience, and 3) measuring the response and recovery rate of belowground biomass in addition to aboveground biomass is essential towards understanding seagrass resilience and estimating ecosystem recovery after perturbations. Our study highlights the importance of dynamic indicators such as recovery rate to estimate the resilience of foundation species, and shows how small-scale experiments replicated across large spatial scales can reveal responses of foundation species to important global drivers. Ecologically based strategies are needed to improve the resilience of these valuable coastal ecosystems and to maintain their role as ecosystem engineers in a changing world.

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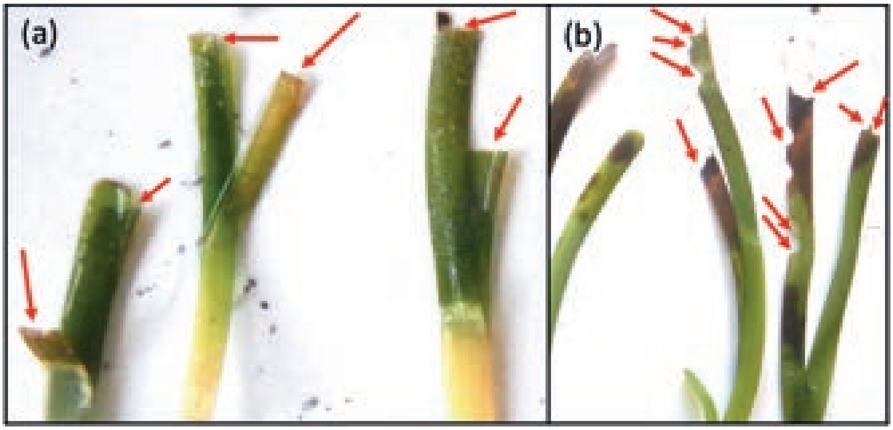
APPENDIX 7.A

Table of the experimental sites with the location, start date, end date and duration of the experiment.

Site	Country	Latitude	Longitude	Start date	End date	Duration (days)
Riddell's Bay	Bermuda	32°15′49.9″N	64°49′50.5″W	14 Sept '18	7 Aug '19	327
Galveston	Texas, USA	29°02′41.8″N	95°10′15.7″W	2 Oct '18	12 Sept '19	433
Crystal river	Florida, USA	28°42′50.4″N	82°49′08.4″W	11 Sept '18	23 July '19	315
Sanibel	Florida, USA	26°29′48.6″N	82°09′40.0″W	15 Sept '18	6 Aug '19	325
Eleuthera 1	The Bahamas	25°27′53.5″N	76°37′35.8″W	24 Nov '18	10 Nov '19	351
Eleuthera 2	The Bahamas	25°27′53.7″N	76°37′35.3″W	28 Nov '18	6 Nov '19	343
Puerto Morelos	Mexico	20°52′04.5″N	86°51′35.4″W	19 Sept '18	1 Aug '19	316
Barcadera Bay	Aruba	12°28′33.2″N	69°59′24.0″W	16 July '18	17 Apr '19	305
Lac Bay	Bonaire, NL	12°06′44.3″N	68°13′42.0″W	12 Sept '18	16 Oct '19	399
Bocas del Toro	Panama	9°21′05.8″N	82°15′27.8″W	26 Sept '18	16 July '19	293

APPENDIX 7.B

Differences between green sea turtle grazing and fish grazing (a) *Thalassia testudinum* seagrass shoots that have been grazed by turtles resulting in straight cuts. (b) *T. testudinum* shoots that have been grazed by fish, resulting in crescent shaped bite marks.



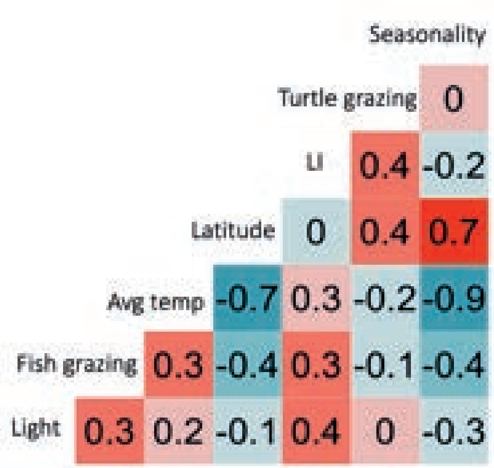
APPENDIX 7.C

Results of the regression analysis testing the linear average shoot recovery in control plots over time

Location	Estimate	SE	t value	P value	R^2
Riddell's bay, Bermuda	0.002	0.0008	2.587	0.036*	0.49
Galveston, TX, USA	0.003	0.001	2.561	0.043*	0.52
Crystal river, FL, USA	0.014	0.006	2.222	0.048*	0.68
Sanibel, FL, USA	0.006	0.003	2.323	0.033*	0.29
Eleuthera 1, Bahamas	0.116	0.010	11.30	0.011*	0.99
Eleuthera 2, Bahamas	0.009	0.004	2.359	0.078	0.58
Puerto Morelos, Mexico	0.014	0.001	9.541	0.0000006***	0.88
Barcadera bay, Aruba	0.005	0.0007	7.029	0.00001***	0.80
Lac bay, Bonaire	0.026	0.003	8.442	0.00006***	0.91
Bocas del Toro, Panama	0.010	0.002	5.990	0.0002***	0.80

APPENDIX 7.D

Pearson correlation matrix showing correlation coefficients between candidate environmental drivers of recovery rates. Latitude and seasonality were excluded from the multi-model inference because r > 0.50 with temperature.



	Fish grazing	Avg temp	Latitude	LI	Turtle grazing	Seasonality
Turtle grazing						0
LI					0.4	-0.2
Latitude				0	0.4	0.7
Avg temp			-0.7	0.3	-0.2	-0.9
Fish grazing		0.3	-0.4	0.3	-0.1	-0.4
Light	0.3	0.2	-0.1	0.4	0	-0.3

APPENDIX 7.E

Statistical results for averaged linear mixed models testing the impact of fertilization treatments and environmental drivers on seagrass recovery and nutrient content. In this model the effect of seasonality was included instead of the effect of average annual temperature that is presented in the main text. The number of top models (≤ Δ2 AICc) is reported, along with the coefficient estimates and standard errors of the standardized regressors. Seasonality is the SD of temperature among months. Turtle and fish grazing is a grazing index assessed from the leaves. LI is the nutrient limitation index. Light is the yearly average input of light in the system. Nutrient fertilization was simulated by adding both N and P to the water column. Significance codes: ***p<0.0001, **p<0.01, *p<0.05.

Response	Factor	Estimate	SE	P-value
(A) Shoot recovery	**Seasonality**	**-0.371**	**0.140**	**0.010***
(% Shoots	**Fish grazing**	**0.294**	**0.114**	**0.011***
compared to	**Turtle grazing**	**-0.381**	**0.147**	**0.026***
pre-disturbance)	**Turtle grazing * Fertilization**	**-0.340**	**0.137**	**0.010****
(3 top models)	**Fish grazing * Fertilization**	**-0.257**	**0.081**	**0.002****
	LI * Fertilization	0.215	0.122	0.078
	Light	-0.149	0.121	0.219
	LI	-0.064	0.162	0.695
	Fertilization	0.013	0.010	0.897
(B) Aboveground biomass recovery (% g DW compared to pre-disturbance) (3 top models)	**Seasonality**	**-0.523**	**0.139**	**0.0002*****
	Fish grazing	**0.398**	**0.119**	**0.0002*****
	Turtle grazing * Fertilization	**-0.348**	**0.125**	**0.005****
	Fish grazing * Fertilization	**-0.233**	**0.107**	**0.030***
	LI	-0.181	0.135	0.178
	LI * Fertilization	0.149	0.133	0.263
	Fertilization	-0.023	0.110	0.834
	Turtle grazing	-0.075	0.134	0.57
(C) Belowground biomass recovery (% g DW compared to pre-disturbance) (11 top models)	**Seasonality**	**-0.605**	**0.170**	**0.0009*****
	Turtle grazing * Fertilization	**-0.239**	**0.102**	**0.020***
	LI * Fertilization	**-0.219**	**0.089**	**0.014***
	Light	0.135	0.168	0.421
	Fish grazing	0.108	0.140	0.439
	LI	0.158	0.177	0.371
	Turtle grazing	-0.179	0.158	0.257
	Fertilization	0.037	0.010	0.708

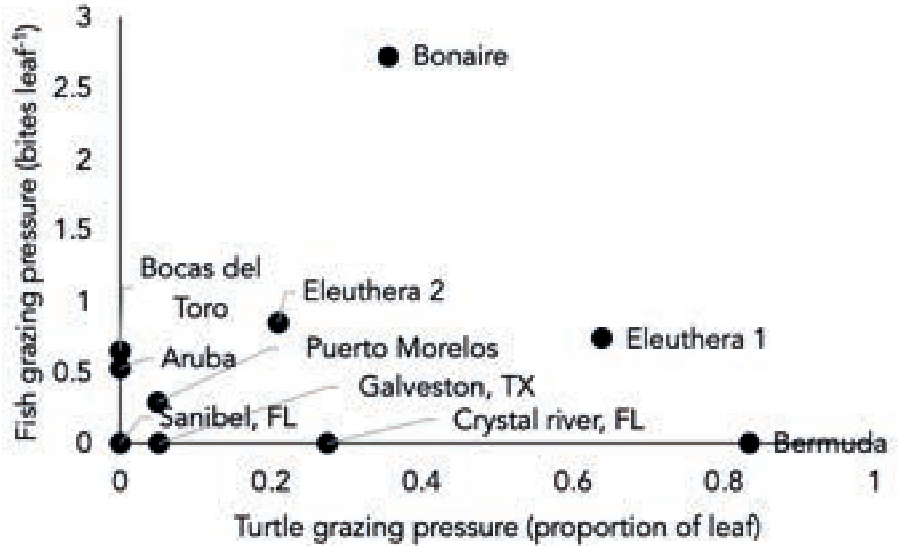
APPENDIX 7.F

Statistical results for averaged linear mixed models testing the impact of fertilization treatments and environmental drivers on seagrass recovery and nutrient content. In this model the effect of latitude was included instead of the effect of average annual temperature that is presented in the main text. The number of top models (≤ Δ2 AICc) is reported, along with the coefficient estimates and standard errors of the standardized regressors. Seasonality is the SD of temperature among months. Turtle and fish grazing is a grazing index assessed from the leaves. LI is the nutrient limitation index. Light is the yearly average input of light in the system. Nutrient fertilization was simulated by adding both N and P to the water column. Significance codes: ***p<0.0001, **p<0.01, *p<0.05.

Response	Factor	Estimate	SE	P-value
(A) Shoot recovery (% Shoots compared to pre-disturbance) (2 top models)	Latitude	-0.249	**0.188**	**0.185***
	Fish grazing	**0.282**	**0.127**	**0.027***
	Turtle grazing	**-0.333**	**0.170**	**0.042***
	Turtle grazing * Fertilization	**-0.311**	**0.128**	**0.015***
	Fish grazing * Fertilization	**-0.236**	**0.075**	**0.002****
	Fertilization	0.013	0.101	0.897
(B) Aboveground biomass recovery (% g DW compared to pre-disturbance) (10 top models)	**Latitude**	**-0.489**	**0.182**	**0.007****
	Fish grazing	0.256	0.170	0.132
	Turtle grazing * Fertilization	**-0.294**	**0.123**	**0.017***
	Fish grazing * Fertilization	-0.193	0.108	0.073
	Fertilization	-0.021	0.113	0.856
	Turtle grazing	0.087	0.167	0.604
	Light	0.183	0.142	0.198
(C) Belowground biomass recovery (% g DW compared to pre-disturbance) (11 top models)	Latitude	-0.231	0.249	0.353
	Turtle grazing * Fertilization	**-0.232**	**0.102**	**0.024***
	LI * Fertilization	**-0.216**	**0.090**	**0.017***
	Light	0.277	0.241	0.250
	Fish grazing	0.253	0.167	0.129
	LI	0.260	0.252	0.302
	Turtle grazing	-0.236	0.180	0.190
	Fertilization	0.029	0.099	0.768

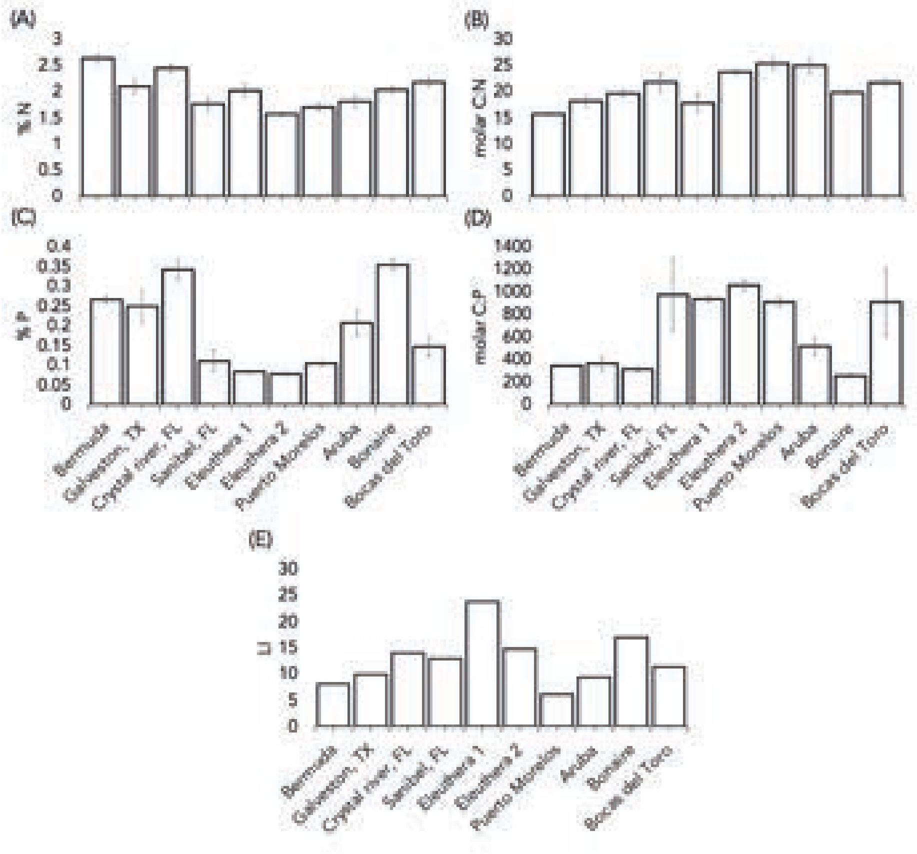
APPENDIX 7.G

Herbivory grazing pressure across sites. Site means for fish grazing pressure (number of bites per leaf) and turtle grazing pressure (proportion of leaf removed) ± SE.



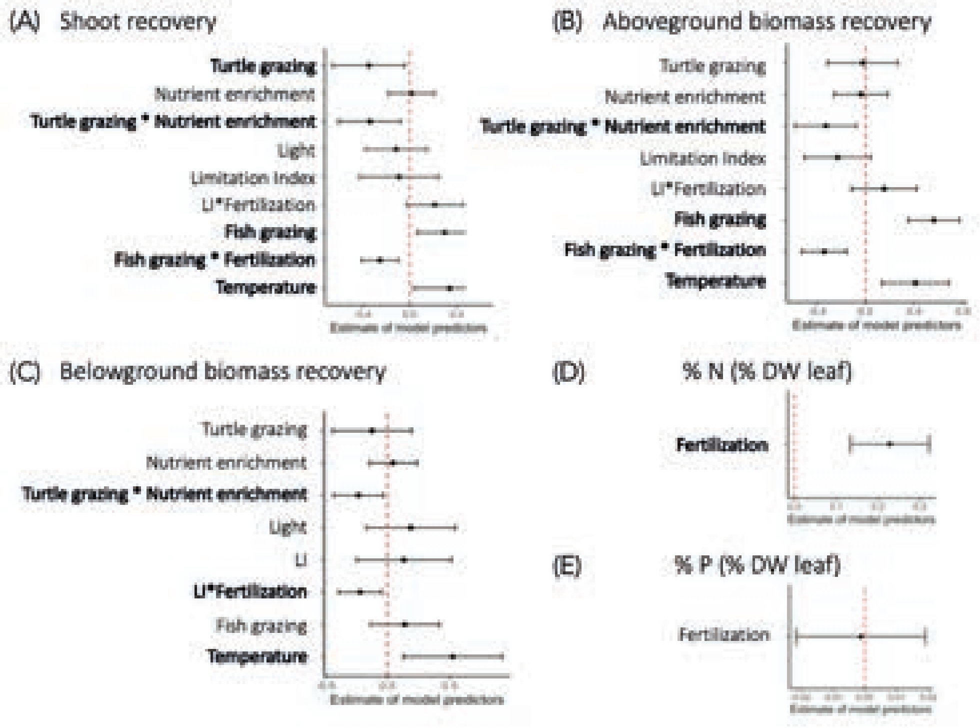
APPENDIX 7.H

Trends in leaf (A) %N, (B) molar C:N, (C) %P, (D) molar C:P and (E) Nutrient limitation index across sites ± SE.



APPENDIX 7.I

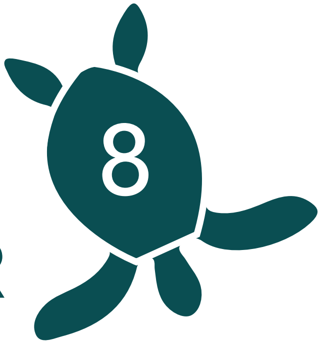
Standardized coefficient plots displaying model estimates and lines present 95% confidence intervals of the averaged models of (A) shoot recovery, (B) aboveground biomass recovery, (C) belowground biomass recovery, (D) Nitrogen and (E) phosphorus. Significant coefficients are displayed in bold.



APPENDIX 7.J

The response of static indicators (measured at one point in time) versus dynamic indicators (% recovery over time) of both shoot density and aboveground biomass to environmental drivers. To analyze this, we compared the unfertilized plots of the recovery experiment to the aboveground biomass and shoot density values as measured at the start of the experiment (N = 5, total of 50 plots) using the same generalized mixed model approach as described in our method section.

	Response measured	Significant variable	Estimate ± SE	p-value
Static indicators				
	Shoot density (shoots m^{-2})	--	--	--
	Aboveground biomass (g DW m^{-2})			
		Turtle grazing	**-0.624 ± 0.144**	**0.0003*** **
		LI	**0.302 ± 0.232**	**0.03***
Dynamic indicators				
	Shoot recovery (%)			
		Temperature	**0.361 ± 0.169**	**0.03**
		Fish grazing	**0.660 ± 0.161**	**0.00004*** **
	Aboveground biomass recovery (%)			
		Temperature	**0.612 ± 0.215**	**0.004 ** **
		Fish grazing	**0.944 ± 0.148**	**<0.001*** **
		Turtle grazing	0.442 ± 0.175	**0.01 ***
		LI	-0.418 ± 0.18	**0.02 ***



CHAPTER 8

General discussion: herbivores determine the form, function and future of tropical seagrass ecosystems

Multiple stressors are threatening seagrass ecosystems worldwide (Dunic et al. 2021). Eutrophication, coastal development, and the introduction of invasive species can cause seagrass meadows to decline or species composition to shift with impacts on ecosystem functioning. Herbivores may respond to these stressors and either reduce or enlarge their effects. Similar to terrestrial grasslands, herbivores shape underwater seagrass meadows (Heck and Valentine 2006, Bakker et al. 2016b). The role of herbivores in tropical seagrass ecosystems is increasingly recognized and marine plant-herbivore impacts are expected to strengthen in certain regions of the world; partly due to warming oceans, partly due to rising populations of large herbivores as a result of successful conservation efforts (Rodriguez and Heck 2021, Valentine and Heck 2021).

In this thesis I focused on the impact of invasive seagrass (**Chapter 2,3**), the return of large herbivores (**Chapter 4,5,6**) and global warming related drivers (**Chapter 7**) on the form and functioning of Caribbean seagrass ecosystems. All studies had an experimental approach and were performed in Caribbean seagrass meadows. This chapter integrates the most important findings of this thesis, unravelling knowledge gaps about marine plant-herbivore interactions in a future changing world.

Link to videos

8.1 HERBIVORES DETERMINE THE FORM OF TROPICAL SEAGRASS MEADOWS

8.1.1 Herbivore grazing preference contributes to the expansion success of invasive seagrass.

We found that herbivore grazing preference can shift the seagrass species composition and species dominance (= form) of seagrass meadows, thereby impacting the expansion of an invasive seagrass species. These results corroborate previous findings that intensive grazing by large herbivores can result in a shift from climax to pioneer seagrass species (Preen 1995b, Hernández and Van Tussenbroek 2014, Christianen 2021). As invasive macrophytes are often fast-growing pioneers, grazing can benefit invasive seagrass, depending on herbivore preference (Kimbro et al. 2013). The native herbivore community may facilitate the expansion of invasive macrophytes by excluding the new food source from their diet (enemy-release hypothesis; Keane and Crawley 2002, Gollan and Wright 2006, Vermeij et al. 2009), or form biotic resistance by including the exotics in their diet (Levine et al. 2004, Cebrian et al. 2011, Ribas et al. 2017). In this thesis I describe that even within one bay, differential grazing impact by green turtles preferring native seagrass (Box 1.2, Video 8.1) and by generalist fish grazing on invasive seagrass (Chapter 2, Smulders et al. 2022) can determine the spatial distribution of native and invasive seagrass (Fig. 8.1).

In Lac Bay on Bonaire, green turtles provide enemy release in the center of the bay by preferring native seagrass (Fig. 8.2a), thereby cropping the native seagrass *Thalassia testudinum* short and causing the invasive *Halophila stipulacea* to spread rapidly since 2010 (Box 1.2). Near the edge of the bay, where turtles do not graze, tall canopy *T. testudinum* provides a habitat for a high density and diversity of herbivore fish (Fig. 8.2b). Our experiments in Chapter 2 showed that invasive seagrass expansion was limited by fish grazing (Fig. 8.2c), and the seagrass distribution maps in Box 1.2 and Figure 8.1 show a near absence of invasive seagrass near the edge of the bay. While *H. stipulacea* can grow in an understory of *Thalassia testudinum* (Willette et al. 2014), and invasive seagrass fragments remain viable and can disperse throughout the bay (Box 1.1), *H. stipulacea* does not occur at the edges of Lac Bay as an understory of *T. testudinum* and this is likely caused by high local fish grazing pressure. Native *T. testudinum* can withstand high (fish) grazing pressure and therefore persists (van Tussenbroek et al. 2006). Fish counts in Chapter 2 and fish grazing pressure in Chapter 7 further supports the finding that Bonaire has a relatively high fish grazing pressure compared to other Caribbean sites, likely because of its protection status (Debrot et al. 2012, Video 8.2). The seagrass system on Bonaire therefore provides an ideal opportunity to study marine plant-herbivore interactions compared to other areas that have historically been subjected to (over) fishing. Fish herbivore impact on seagrass species dominance is described in literature to be minimal compared to large herbivores (Heck and Valentine 2006). Still, I provide evidence that fish can limit invasive seagrass in certain areas and therefore should be considered as important drivers of seagrass species distribution.

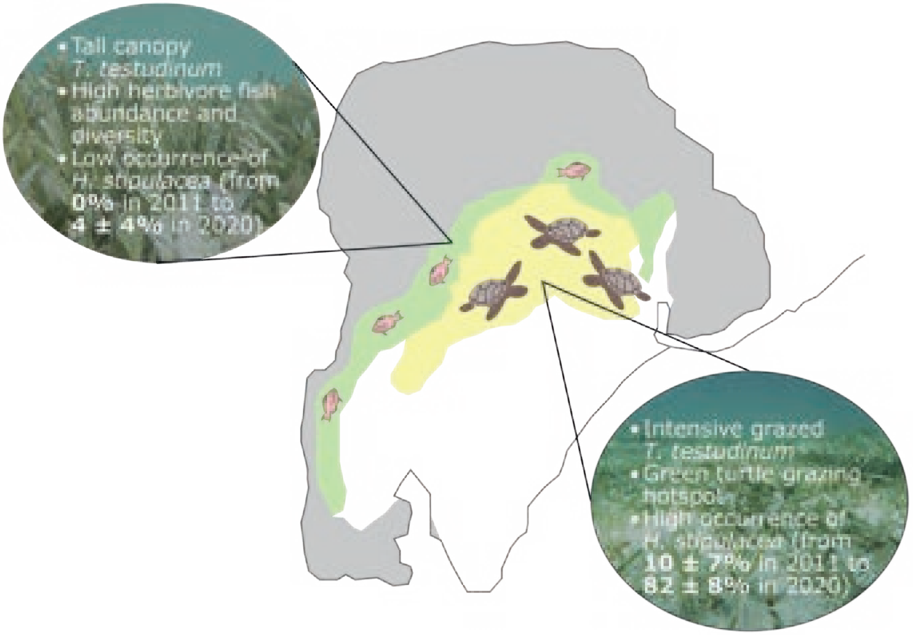


Figure 8.1 Map of Lac Bay on Bonaire. Depicted in grey is the mangrove area, in green the tall canopy *T. testudinum* meadow with high densities of herbivore fish and in yellow the area (turtle density hotspot, (Schut and Simal 2020)) where turtle grazing has led to a vast increase in *H. stipulacea,* ten years since its arrival in the bay. Unpublished results of 2020 are added to compare invasive seagrass distribution between 2011 and 2020. Photos by F. Smulders

Since the start of the Caribbean invasion of *H. stipulacea*, we now know that specialist herbivores initially prefer native seagrass over invasive (Box 1.2, Whitman et al. 2019, Siegwalt et al. 2022), that generalist herbivores provide biotic resistance (Chapter 2), and that the nutritional quality of native seagrass is higher (Box 1.2, Chapter 2). To fill in the remaining gaps, studies are needed that 1) investigate preference of the various important herbivores over time 2) the chemical defenses and 3) physical properties such as tensile strength of native versus invasive seagrass to determine what ultimately drives grazer species preference and seagrass species composition in invaded seagrass ecosystems (Tomas et al. 2011, Enge et al. 2012, Santamaría et al. 2022, Mabey et al. 2022).

8.1.2 Seascape dynamics in invaded ecosystems

Herbivore grazing preference can have cascading effects on other fauna and seascape dynamics. In Chapter 3, I report that on Bonaire, in the areas where intensive turtle

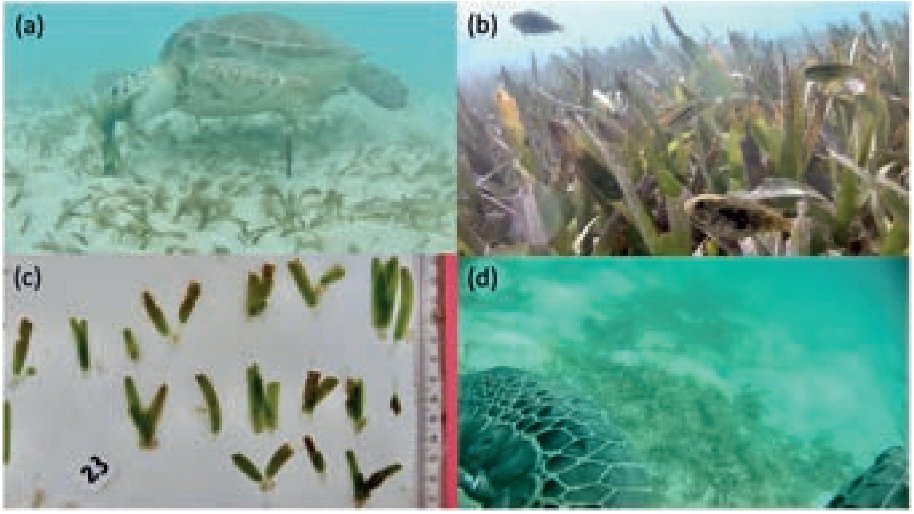


Figure 8.2 (a) Preference of green turtles for native *T. testudinum* over invasive *H. stipulacea* in a food choice experiment (Video 8.1). (b) High herbivore fish abundance and fish grazing marks in tall canopy *T. testudinum* in Lac Bay, Bonaire (Video 8.2). (c) Fish grazing marks on invasive *H. stipulacea* leaves. (d) Long-term invaded seagrass area on Bonaire shows a high abundance of bioturbation mounds (Video 8.3). Photo a-c by F. Smulders, screenshot in d by a green turtle fitted with an animal-borne camera by our team (unpublished results). Videos accessible via https://doi.org/10.4121/6001e291-3c9e-4d33-9513-3581eeaeaf84

grazing on native seagrass led to the dominance of invasive seagrass (Box 1.2), there was an increase in bioturbation activity (Fig. 8.1d). These bioturbation mounds, created by burrowing infauna such as shrimp, worms, and sea cucumbers, likely further negatively impact native seagrass, which is smothered by the sediment and cannot overgrow these mounds (Suchanek 1983, Dumbauld and Wyllie-Echeverria 2003). At the same time, bioturbation opens up the native seagrass canopy, facilitating invasive seagrass (Chapter 3, Smulders et al. 2023b). Invasive seagrass fragments (Box 1.1) that float through the water column can use these mounds as starting point for further colonization, and surrounding invasive seagrass can quickly cover the bioturbation mounds. The mechanism found is especially relevant given that *H. stipulacea* does not currently reproduce sexually within the Caribbean (Smulders et al. 2020), and is therefore dependent on fragmentation for colonizing new areas (Box 1.1).

With experiments on Curaçao, we show that on the bioturbation mounds, the invasive seagrass outcompeted the native photosynthesizing upside-down jellyfish that are dependent on high light availability (Chapter 3). Therefore herbivore-driven shifts in seagrass species composition can further disrupt species dynamics within the ecosystem. There is a possible mutualistic interaction: bioturbators likely thrive in invaded seagrass meadows because of the less complex root structure of *H. stipulacea* compared to *T. testudinum* (Video 8.3). Conversely, *H. stipulacea* uses bioturbation activity to colonize new habitats. Similar positive feedback between burrowing animals and fast-growing plants has been observed in terrestrial habitats for gopher (Tilman 1983) and squirrel (Blank et al. 2013) mounds. Further research can illuminate whether invasive seagrass and bioturbators indeed facilitate each other's environment in marine systems, which species of burrowing infauna are especially relevant in our found dynamics, and which conditions may facilitate a return to a more stable seagrass system with valuable climax species.

8.2 CASCADING EFFECTS OF HERBIVORES ON THE FUNCTIONING OF CARIBBEAN SEAGRASS MEADOWS

8.2.1 Ecosystem functioning of invaded seagrass meadows

Herbivores will impact not only the seagrass morphology and species distribution but also the ecosystem services the meadow provides. By comparing the ecosystem value of native versus invasive seagrass meadows, the economical and societal impact of the species invasion can be assessed, and outcomes can be used in management (Grosholz et al. 2009, Weidenhamer and Callaway 2010). The shift from native to invasive seagrass dominated meadows that are reported at multiple sites across the Caribbean (Winters et al. 2020), has been shown to lower fish abundance and diversity (Becking et al. 2012, Olinger et al. 2017) and reduce resistance to storms (James et al. 2020). However, others report no impact on different trophic groups (Willette and Ambrose 2012, Muthukrishnan et al. 2020), nor on the metabolic productivity (Johnson et al. 2020a). Other effects are likely such as an increase in predation risk because invasive meadows are less structurally complex (as seen in terrestrial grasslands: Norbury and van Overmeire 2019).

In this thesis, I report that *H. stipulacea* provides lower nutritional quality food for consumers compared to *T. testudinum* (Box 1.2), which was confirmed by other studies (Muthukrishnan et al. 2020, Siegwalt et al. 2022). However, we did find evidence of grazing by fish (Chapter 2), and use of habitat by infauna (Chapter 3) further supported by a higher abundance of burrowing shrimps and crabs in *H. stipulacea* meadows compared to *T. testudinum* (pers. obs). We also found an increase in certain areas of invasive seagrass occupying previously bare habitat (Box 1.1, Chapter 3), which likely increases ecosystem value (Viana et al. 2019a). Lastly, we found that the organic carbon stored in surface sediments of *H. stipulacea* meadows was lower than in tall canopy *T. testudinum* sediments, but similar to *T. testudinum* meadows grazed by turtles (Box 8.1). This is in line with previous assessments that fast-growing species (e.g. *H. stipulacea*), and species with higher turnover rates (e.g. *T. testudinum* cropped by turtles), contribute less to carbon accumulation compared to slow growing species (Cebrián and Duarte 1995). Because surface sediments only reflect recent carbon storage, long-term and higher depth resolution studies are needed to assess the impact of a species shift on blue carbon storage (Ellison and Beasy 2018, Wu et al. 2020). In addition to the short-term timescale, the different ecosystem services of *H. stipulacea* reported in literature have been measured at different locations. Therefore, drawing conclusions about the general ecosystem value of invaded seagrass meadows is challenging. There is a need to assess multiple ecosystem functions within one invaded ecosystem, for example, with a multifunctionality index (Chapter 6) and to repeat these measurements over time (Lundholm 2015, Liu et al. 2022).

8.2.2 Tourist-turtle interactions may impact ecosystem functioning

In this thesis, I describe that the presence of humans or predators in a seagrass ecosystem can impact sea turtle (grazing) behavior and subsequent seagrass ecosystem functioning. Provisioning of green turtles by tourists can disturb natural grazing dynamics, as we found intensified grazing close to the provisioning site (Chapter 4, Video 8.4, Smulders et al. 2021). This shift to intensive grazing is associated with reduced ecosystem services such as invertebrate and fish abundance (Johnson et al. 2020b, Inoue et al. 2021), coastal protection (James et al. 2020), and carbon storage (Box 8.1). In addition, we observed altered food intake: provisioned turtles ingested more animal protein, similar to other reports of provisioned turtles (Stewart et al. 2016, Monzón-Argüello et al. 2018), but in addition we found that they grazed less seagrass (Chapter 4). The return of large herbivores (Chapter 6) will likely lead to increases in tourist-turtle interactions. A sustainable form of wildlife tourism may prevent the risk of boat strikes, biting accidents, turtle disease and cascading impacts on ecosystem functioning (Stewart et al. 2016, Murray et al. 2016). A halt to provisioning – as has been done for other (terrestrial) feeding activities – can restore natural (grazing) behavior (Orams 2002). There is a need to study the impact of human activity on marine megaherbivore spatial and temporal movements within their foraging habitat and how this cascades to the functioning of their primary resource. Similar to terrestrial studies that report on impacts of human activity on deer movement and foraging behavior (Ciuti et al. 2012, Mols et al. 2022), it is essential to find out when and where sea turtles feel at risk and when safe, and if human activity could either attract turtles or replace fear effects induced by predators in the seascape. Our novel method to investigate this using animal-borne video (Chapter 4, Fig. 3a, Video 8.4) provides an opportunity to document interactions between humans and wildlife, natural grazing behavior, and potential predator-prey interactions.

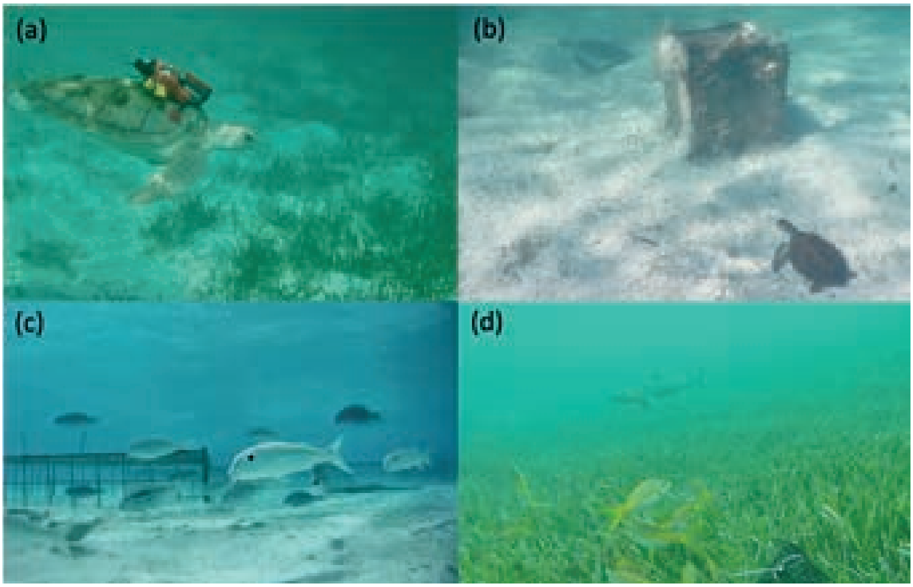
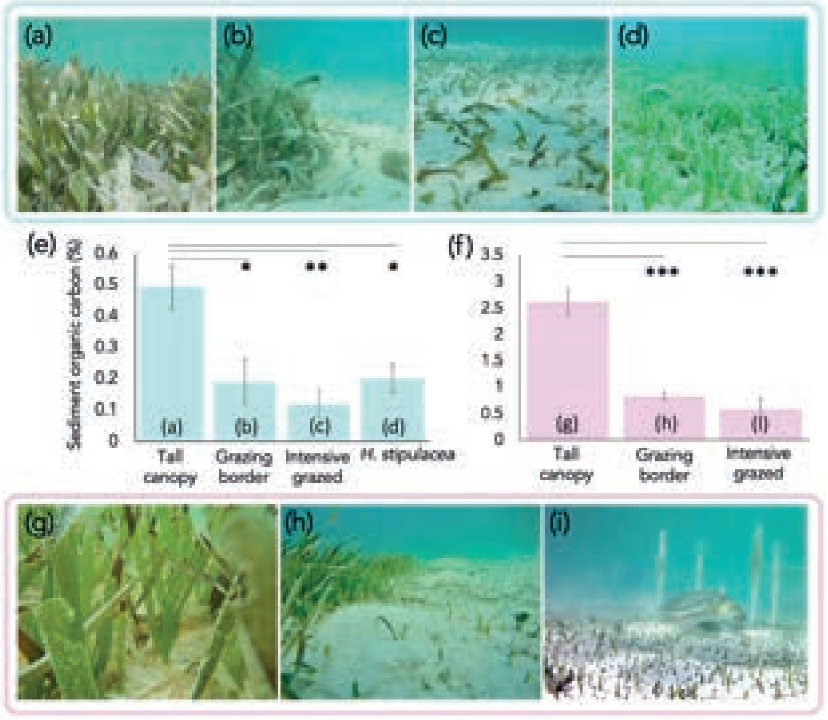


Figure 8.3 (a) Animal-borne video provides an opportunity to study human-wildlife interactions and natural (grazing) behavior (Video 8.4). (b) Sea turtles in a high-predator environment prefer to graze near physical structures, likely as a refuge (Video 8.5). (c) Fish are attracted to (turtle) exclosures, feeding in the proximity or using it as a refuge. (d) A Caribbean reef shark is roaming the tall-canopy seagrass area, creating a landscape of fear. Photos by F. Smulders. Videos accessible via https://doi.org/10.4121/6001e291-3c9e-4d33-9513-3581eeaeaf84

Box 8.1 Seagrass sediment organic carbon content under seagrass invasion and turtle grazing pressure

Intensive turtle grazing can alter the morphology of *T. testudinum* seagrass meadows and impact the ecosystem services the meadow provides (see chapter 6). At two study sites, we looked at the impact of turtle grazing on carbon storage in the sediment. On Bonaire, we compared surface sediments of tall seagrass (Fig. a, n = 4) to the border between tall and intensively grazed seagrass (= grazing border, fig. b, n = 5) to intensively grazed seagrass (> 3 years, Fig. c, n = 5) and invaded seagrass (Fig. d, n = 5). On Eleuthera, we compared sediments of tall seagrass (Fig. g, n = 3) to the grazing border (Fig. h, n = 5) and intensively grazed seagrass (8 months, n = 4) surrounding the experimental structures of chapter 5 (Fig. i).



On Bonaire (Fig. e), we found that the percentage of organic carbon stored at the sediment surface was significantly reduced at the grazing border, in intensively grazed meadows and in *H. stipulacea* meadows compared to ungrazed seagrass (F = 7.198, $p < 0.01$). Similarly, on Eleuthera (Fig. f) we found a significant higher amount of organic carbon in surface sediments of tall canopy seagrass compared to the grazing border and intensive grazed seagrass (F = 41.807, $p < 0.001$). Tall canopy seagrass likely traps more organic matter (for instance in the form of decaying leaves, Fig. g), leading to slowly decomposing detritus which acts as as a carbon sink (Cebrián and Duarte 1995), while fast growing or cropped seagrass (species) and sediments along the grazing border have quick turnover rates and are more prone to erosion (James et al., 2020). These results stress that both seagrass invasion and grazing by sea turtles can significantly alter not only carbon metabolism (Johnson et al., 2020a) but also the amount of organic carbon present in seagrass sediments, that can contribute to long-term carbon storage.

8.2.3. Cascading effects of predator presence on ecosystem functioning

In a high-predator environment, marine megaherbivores base their foraging strategy on their health (Heithaus et al. 2007) and on the shape of the seagrass meadow (Wirsing et al. 2007a, Burkholder et al. 2013). Dugongs have been shown to use an intensive root-digging grazing strategy in safe habitats and a cropping grazing strategy in risky habitats (Wirsing et al. 2007c). In Chapter 5, I describe a novel type of risk-avoidance behavior; sea turtles were attracted to physical structures in their high-predator habitat and subsequently reduced their vigilance and increased their grazing pressure near these structures (Fig. 8.3b, Video 8.5, Smulders et al. 2023a). A similar mechanism has been described for mesoherbivores creating halos around coral structures in high-predator environments (Madin et al. 2011, DiFiore et al. 2019), but not yet for megaherbivores. This type of behavior leads to heterogeneity and locally intensive grazed seagrass meadows, with a decrease in seagrass morphology and biomass (Chapter 5) and in percentage of organic carbon stored in the surface sediment (Box 8.1). Additionally, this reduction in biomass likely affects other services, such as provisioning of habitat for fauna (Vonk et al. 2010) and general ecosystem multifunctionality (Chapter 6). Chapter 5 provides support that green turtles, similar to dugongs, can switch from a vigilant grazing strategy in risky environments to an intensive grazing strategy in safe environments. Therefore, in areas where top predators are lost, turtles may revert to an intensive grazing strategy with impacts on ecosystem functioning (Heithaus et al. 2014). Determining the causal effects of predator and habitat-driven alterations in sea turtle grazing behavior is important as a next step. When do turtles switch from a risky to an intensive grazing strategy, and what exactly is the impact on ecosystem functioning?

8.2.4 Experimental assessment of ecosystem (multi)functionality

For future studies, it is important to note that the physical structure of experimental cages can have an impact on herbivore grazing behavior. Sea turtles prefer to graze near the structures in a landscape of fear, and therefore this may overestimate the grazing pressure in nearby open control plots (Chapter 5). During our herbivore exclusion experiments, I found that fish are generally attracted to experimental cages, with fish densities increasing over the duration of the experiment (pers. obs, Fig. 8.3c). A solution is to carefully select the site, e.g., for turtle exclosures not near areas with high densities of fish, to monitor grazing pressure throughout your experiment and be aware of the local predator abundance potentially impacting your results. In addition, because of the spatial variation in grazing behavior, general herbivore densities cannot be directly linked to local grazing pressure (Chapter 5). Similarly, it is likely not accurate to extrapolate ecosystem services such as the carbon burial capacity of a large seagrass meadow with high herbivore abundance without knowledge of the variation in local grazing pressure. Repeated measures of grazing pressure are needed to quantify both the resilience and ecosystem services of a seagrass meadow (Box 8.1).

Intensive grazing pressure associated with a low-risk grazing strategy (Chapter 5) may lead to a collapse of ecosystem multifunctionality, as found in Chapter 6 (Christianen et al. 2023). Intermediate grazing pressure increased carbon storage and nutrient cycling, but the other ecosystem services were reduced compared to seagrass ungrazed by sea turtles (see Video 8.6 for a comparison between intermediate and absence of turtle grazing pressure). In contrast to the fear effects found in the Bahamas in Chapter 5, the experiments in Chapter 6 were performed in a system without predators, where intermediate or intensive turtle grazing led to a loss of ecosystem services. Therefore, the return of predators could potentially lead to a system with high herbivore densities and the preservation of ecosystem multifunctionality (Fig. 8.3, Heithaus et al. 2014). Herbivores such as sea turtles are needed to maintain biodiversity and structure in the seascape, but a system does not benefit from prolonged intensive grazing (Fløjgaard et al. 2022). Therefore, it is vital to include the predator presence while assessing ecosystem multifunctionality.

8.3 HERBIVORES SHAPE THE FUTURE OF TROPICAL SEAGRASS MEADOWS

Worldwide, the value of coastal ecosystems is increasingly being recognized in light of climate change (He and Silliman 2019). Coastal ecosystems such as salt marshes, mangroves, and seagrasses can mitigate climate change impacts by providing coastal protection and removing carbon dioxide from the atmosphere (Macreadie et al. 2017, Gattuso et al. 2018, Temmink et al. 2022). At the same time, global declines in coastal areas and specifically seagrass meadows due to anthropogenic stressors (Dunic et al. 2021) warrant the need for conservation, restoration and research to better understand complex ecosystem dynamics (van Katwijk et al. 2016). This thesis highlights the critical role of herbivores in shaping seagrass ecosystems, how this role may increase, and their impact managed in the near future.

8.3.1 Species dynamics in invaded seagrass meadows

Seagrass meadows invaded by the non-native *H. stipulacea* or other invasive macrophytes likely benefit from a diverse generalist herbivore community (Chapter 3). Even if the main herbivore in a system, in this case, a green turtle, is a specialist that prefers native seagrass (Box 1.2, Christianen et al. 2019, Siegwalt et al. 2022), the presence of other smaller herbivores can still resist invasion in certain areas and provide a refuge for native seagrass (Chapter 3). Future protection of these herbivores can form the key in building future-resistant seagrass meadows, and specialist herbivores may adapt and incorporate the exotics in their diet over time (Santamaría et al. 2022). As we found that fish grazing pressure may additionally increase the resilience of *T. testudinum* (Chapter 7), expanding ranges of tropical herbivores to subtropical areas (Fodrie et al. 2010, Vergés et al. 2014a, Zarco-Perello et al. 2020) may benefit the balance between native and invasive seagrass.

An important finding from our experiments is that invasive seagrass makes use of disturbance instead of active competition to replace native seagrass species. *Halophila stipulacea* is an opportunistic fast-growing species that was found to increase under intensive turtle grazing pressure (Box 1.2), and to quickly occupy new habitat in the form of bioturbation mounds (Chapter 3). As *H. stipulacea* is expanding fastly throughout the Caribbean, and literature often describes that *T. testudinum* or *S. filiforme* have been outcompeted and replaced by *H. stipulacea* (Willette and Ambrose 2012, Steiner and Willette 2015a, Winters et al. 2020), we investigated whether active competition takes place. Our transplantation experiment revealed no negative effects of invasive seagrass expansion on native seagrass density over time (Chapter 3). Additionally, we performed a nutrient uptake experiment in a controlled laboratory environment to compare the root uptake rate rates between various Caribbean seagrass species. We found no significant differences between native and invasive seagrass uptake rates of ammonia (the preferred nitrogen source of tropical seagrass, Lee and Dunton 2000, Viana et al. 2019a). However, we did find that the initial uptake efficiency k_m of *T. testudinum* was higher than that of *H. stipulacea,* and that the maximum uptake rate of *H. stipulacea* is higher compared to *T. testudinum* (Box 8.2). Together, these findings suggest that *H. stipulacea* needs some sort of disturbance to outcompete the native climax species *T. testudinum*, which complies with their growth strategy as respectively a pioneer and a climax species (O'Brien et al. 2018). This mechanism is similar to e.g., invasive Caulerpa in the Mediterranean that benefitted from both overgrazing of native seagrass by fish and mechanical disturbances (Tamburello et al. 2014). In contrast to previous reports (Winters et al. 2020), I find it more likely that native seagrass declines because of other stressors and that *H. stipulacea* benefits from the same stressors by quickly filling up available niches, either by clonal expansion or by fragmentation (Box 1.1). Earlier research that links *H. stipulacea* to hurricane events (Hernández-Delgado et al. 2020) supports this hypothesis.

Predator presence may also play an important role in providing biotic resistance to invasive seagrass. Based on Chapter 5, predator presence likely results in a less intensive grazing strategy by sea turtles. This would result in less space for the invasive seagrass to settle and grow within high predator seagrass meadows. This may be confirmed by future research investigating invasive seagrass success in high-predator environments. For nature management, it is important to place the invasion in full ecosystem community context, including the interaction between predators and herbivores that may or may not eat the invaders (Smith et al. 2015).

8.3.2 Interplay between nutrients and herbivory

Nutrient enrichment or eutrophication is an important anthropogenic stressor impacting seagrass meadows (Nixon 1995, Burkholder et al. 2007). In this thesis I found evidence that local nutrient enrichment of nitrogen and phosphorus can enhance top-down control, both in invasive (Chapter 2) and native (Chapter 7) seagrass, by both turtles and fish (Chapter 7). This effect has been found before for herbivore fish (Jiménez-Ramos et al. 2017, Campbell et al. 2018), and in our study we found evidence of the underlying mechanism that nutrient-enriched leaves attract herbivores which subsequently reduce seagrass growth rates (Chapter 2). Herbivore and nutrient effects should therefore be considered together in experimental set-ups, otherwise the direct effect of nutrient enrichment on plant physiology and growth may be clouded over by herbivory. However, it is challenging to experimentally exclude small herbivore fish using mesh exclosures and some were still able to enter the fish exclosures used in Chapter 2. Therefore, laboratory experiments can form a solution to study nutrient effects and separate above- from belowground enrichment. Without herbivore presence, we indeed measured a higher maximum root uptake rate for invasive seagrass compared to native climax species (Box 8.2). In systems with low herbivore densities, nutrient loading is likely an extra type of disturbance that can tip the balance from native seagrass dominance to invasive seagrass dominance. Therefore, in systems with low levels of herbivores, it is important to keep the input of nutrients at a minimum, to prevent invasive seagrass thriving on abundant nutrients (Ceccherelli and Cinelli 1997, Gennaro and Piazzi 2011, Teixeira et al. 2017).

Box 8.2 Ammonium uptake rates by above- and belowground structures of native and invasive Caribbean seagrass species

Fast-growing invasive seagrass may benefit from increases in nutrient concentrations in Caribbean seagrass meadows. However, nutrient uptake rates and translocation of invasive seagrass have not yet been compared to native species. In a controlled laboratory environment, the belowground ammonium uptake rate was investigated in invasive *H. stipulacea* and native *T. testudinum*, *H. wrightii*, and *S. filiforme* by tracing 15N uptake in a novel set-up that separated above- and belowground nutrient environments (Fig. a).

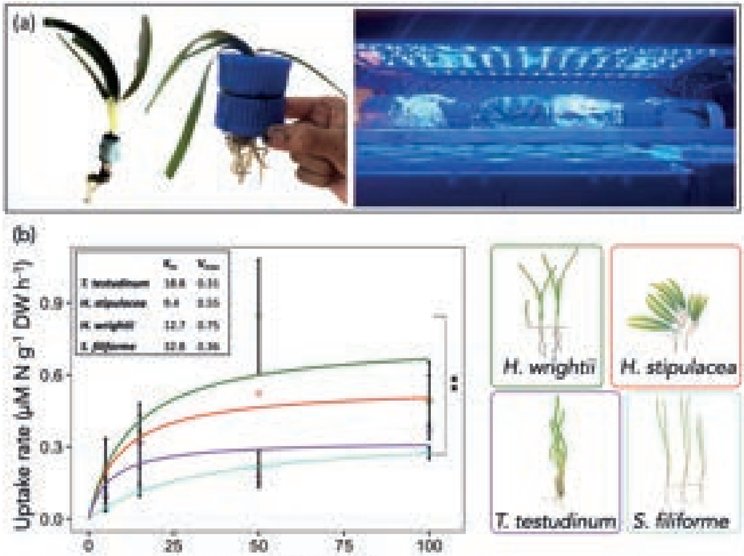


Figure b shows the measured uptake rates (± SE) and the lines correspond to the best fit of the Michaelis-Menten model. The inset shows the Michaelis-Menten parameters derived from the models. At low ammonium concentrations, the climax species *T. testudinum* and *S. filiforme* were most efficient at taking up nutrients via the roots (highest Km). However, the maximum root uptake efficiency (Vmax) was found for the native pioneer species *H. wrightii*, followed by the invasive *H. stipulacea*. Of our measured uptake rates, we found a significant effect of species on the root uptake rates ($F = 5.695$, $p < 0.01$) and post-hoc pairwise comparisons revealed that *H. wrightii* had higher uptake rates compared to *S. filiforme* ($p < 0.01$). Our results indicate that invasive seagrass may benefit slightly over native climax species in high-nutrient environments. However, the uptake rates of the invasive seagrass are comparable to the other native pioneer species. Nutrient enrichment may shift the species balance to pioneer-dominated seagrass systems in (invaded) ecosystems.

8.3.3 What do our results mean for the future of invaded seagrass meadows?

Successful invasion may lead to long-term unstable seagrass meadows. Even though it can regrow quickly, it was shown earlier that invasive seagrass is less resistant to storms compared to native species (Hernández-Delgado et al. 2020, James et al. 2020). In this thesis, I found that sea turtles facilitate invasive seagrass (Box 1.2), and invasive seagrass may facilitate bioturbation activity (Chapter 3) which will likely keep the system in an unstable state (Eriksson et al. 2010, Suykerbuyk et al. 2012). Compared to the native seagrass pre-invasion and pre-disturbance, seagrass ecosystem value will likely be reduced in invaded seagrass meadows (Box 8.1, Christianen et al. 2019, Johnson et al. 2020a, James et al. 2020). In systems where nutrient levels are rising (as is the case for many systems in the Caribbean, see Lapointe 2019, Horta et al. 2021), *H. stipulacea* may develop a competitive advantage because of its nutrient uptake dynamics (Box 8.2). A diverse herbivore community can mitigate this effect (Chapter 2). Biotic resistance may even increase over time; for example on Bonaire, instead of turtles abandoning the invaded seagrass meadow, their population is increasing (Rivera-Milán et al. 2019) together with an increase in green turtles eating invasive seagrass (pers. obs.). An increase in biotic resistance matches with the reports from other coastal ecosystems: for macroalgae in the Caribbean (Santamaría et al. 2022), and sargassum in the UK (Kurr and Davies 2018).

The invasive seagrass *H. stipulacea* is expected to expand to a large area, especially under future ocean warming scenarios (Wesselmann et al. 2021a). Apart from reduced functioning compared to native seagrasses, the species could positively impact ecosystem functioning compared to bare sediment (Box 1.1, Chapter 2, (Davidson et al. 2018, Viana et al. 2019b). Therefore, areas where native seagrass is declining or lost due to intensive grazing, hurricanes, sargassum events, or water pollution, will likely benefit from the arrival of this fast-growing species. And since there is evidence of mesoherbivores (Chapter 2) but also megaherbivores (Siegwalt et al. 2022, Khamis et al. 2022) consuming *H. stipulacea,* expanding ranges of *H. stipulacea* may be much needed given the increase in turtle populations throughout the Caribbean (Chaloupka et al. 2008, Mazaris et al. 2017) and the manatees that are currently starving of food shortage in Florida (Allen et al. 2022) because native seagrass has disappeared. Whether the invasive seagrass will be able to withstand high grazing pressure expected under tropicalization will be an important area of future research.

8.3.4 Future outlook on herbivory in seagrass meadows

Local high densities of sea turtles overgrazing seagrass meadows are reported globally (Chapter 5, Christianen et al. 2014, Fourqurean et al. 2019, Gangal et al. 2021) and overgrazing events are expected to increase under tropicalization (Rodriguez and Heck 2021). Subtropical meadows are, therefore, likely to experience increased grazing pressure because of ocean warming. It remains an open question whether subtropical meadows will be able to maintain their productivity: in this thesis, I show that turtle grazing has a negative impact on the recovery rate of *T. testudinum* shoots, while fish grazing may have a positive effect (Chapter 7). Overall, subtropical seagrass could experience an increase in resilience as a result of rising temperatures. Our method to assess resilience using small-scale recovery experiments (Chapter 7) helps pinpoint vulnerable sites that may be close to collapse and evaluate and compare seagrass resilience (Van Nes and Scheffer 2007, van de Leemput et al. 2018). In addition, our study provides evidence that dynamic indicators (i.e. recovery rate) signal different responses to environmental stressors compared to traditional static indicators (i.e. cover), and are a valuable tool to assess the health of an ecosystem and predict its response to future changes in the environment (Chapter 7). Given the importance of herbivores in shaping seagrass ecosystems (Chapter 2, 5, 6, 7) the effect of increasing temperatures and increases in grazing pressure of large and smaller herbivores on seagrass resilience should be the focus of further investigation.

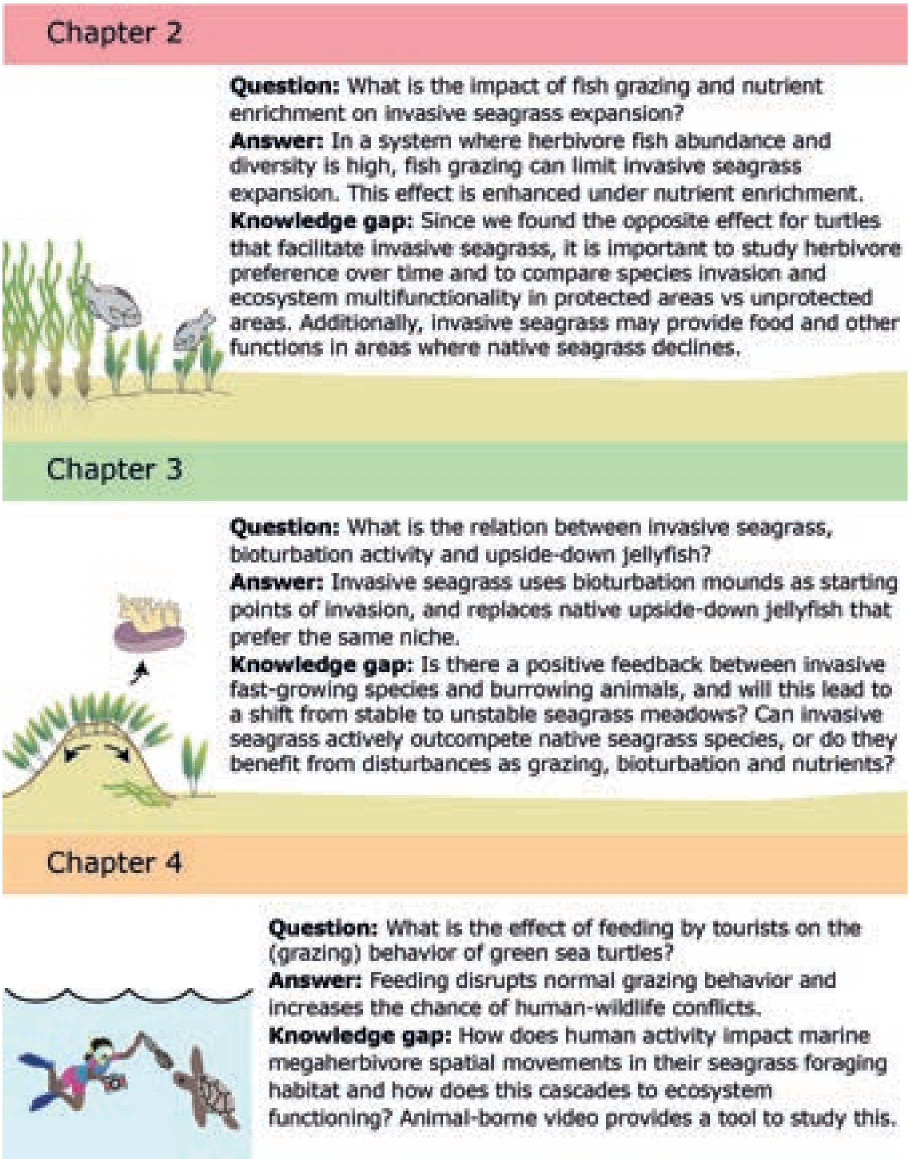
Balanced ecosystems with intact foodwebs contribute to high ecosystem functionality (Chapter 6, Schmitz et al. 2023). We found that predators likely impact multiple ecosystem services, most importantly, blue carbon storage through cascading grazing effects (Chapter 5, Box 8.1). Similar to research on coral reefs (Atwood et al. 2018), risky areas likely have more organic carbon stored. A next step would be to investigate how predators impact turtle grazing behavior and subsequently meadow resilience and ecosystem services. In areas where top predators are conserved or return, predators may help to increase ecosystem value (Atwood et al. 2015, Schmitz et al. 2023). Additionally, protection of seagrass habitat is a vital component in the conservation of charismatic megafauna. There is an urgent need to increase the awareness of the value of seagrass ecosystems through science communication, since seagrasses are among the least protected marine habitat worldwide (United Nations Environment Programme 2020). Increased effort in media outreach by seagrass researchers has shown to be reciprocated with an increase in interest by national and international media platforms (see Curriculum Vitae section in this thesis). Protection of green turtles and conservation efforts have proven successful (Chaloupka et al. 2008, Mazaris et al.

2017), and should be expanded to include the protection of seagrass habitat and their top predators to ensure a balanced ecosystem.

8.4 CONCLUDING REMARKS

Finally, the experiments described in this thesis provide evidence of the ever-increasing role of herbivores in shaping tropical seagrass meadows. Just as in terrestrial grasslands, large and small herbivores together determine a large part of the functioning of seagrass meadows. Seagrass meadows are globally needed to ensure biodiverse, climate resilient coastal zones. Current challenges include shifting species ranges, local stressors and disbalanced trophic chains. Protecting not only flagship turtles but also mesoherbivores (**Chapter 2**), the seagrass habitat (**Chapters 3, 4, 5, 6, 7**) and top predators (**Chapter 5**) will contribute to building biotic resistance as well as high ecosystem functioning (**Chapter 6**) and resilience (**Chapter 7**) of future seagrass meadows (Box 8.3).

Box 8.3 Summary of research questions, answers and knowledge gaps



Chapter 2

Question: What is the impact of fish grazing and nutrient enrichment on invasive seagrass expansion?

Answer: In a system where herbivore fish abundance and diversity is high, fish grazing can limit invasive seagrass expansion. This effect is enhanced under nutrient enrichment.

Knowledge gap: Since we found the opposite effect for turtles that facilitate invasive seagrass, it is important to study herbivore preference over time and to compare species invasion and ecosystem multifunctionality in protected areas vs unprotected areas. Additionally, invasive seagrass may provide food and other functions in areas where native seagrass declines.

Chapter 3

Question: What is the relation between invasive seagrass, bioturbation activity and upside-down jellyfish?

Answer: Invasive seagrass uses bioturbation mounds as starting points of invasion, and replaces native upside-down jellyfish that prefer the same niche.

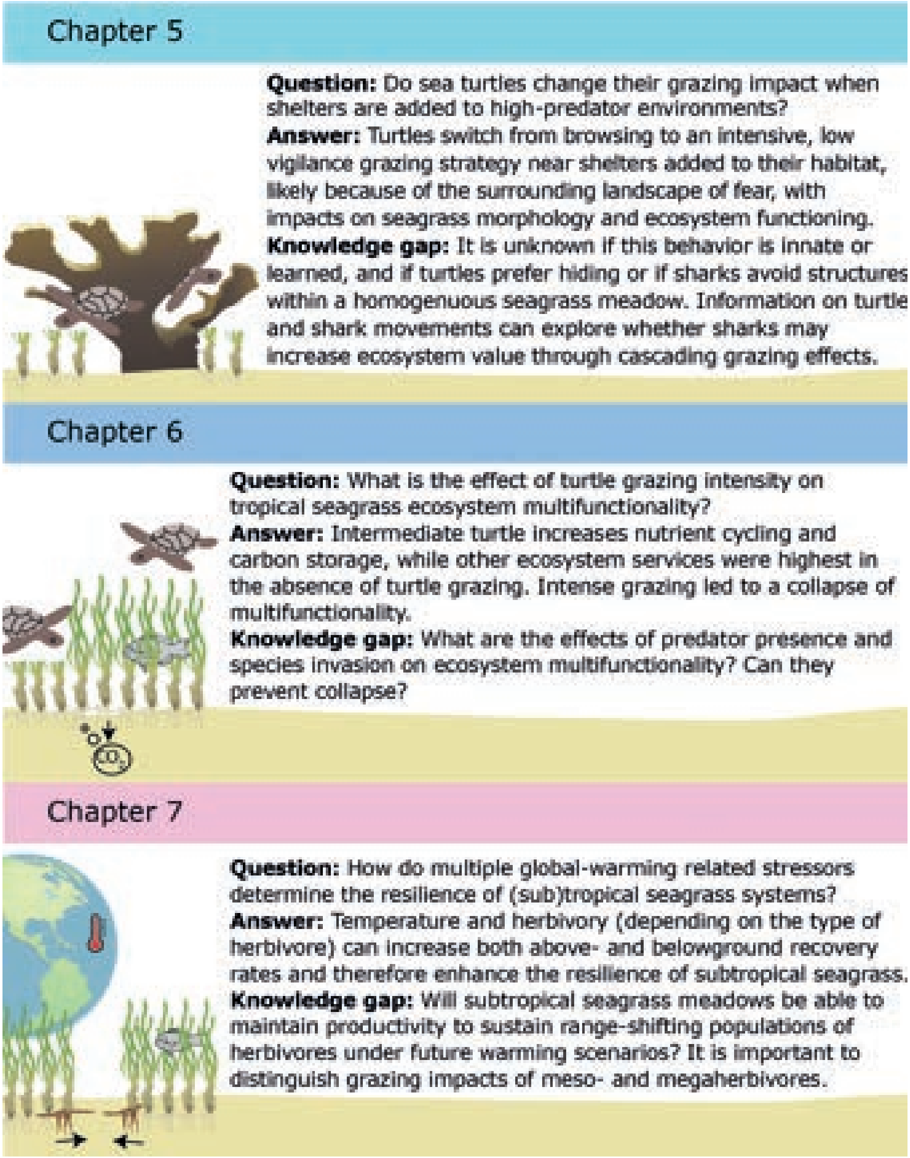
Knowledge gap: Is there a positive feedback between invasive fast-growing species and burrowing animals, and will this lead to a shift from stable to unstable seagrass meadows? Can invasive seagrass actively outcompete native seagrass species, or do they benefit from disturbances as grazing, bioturbation and nutrients?

Chapter 4

Question: What is the effect of feeding by tourists on the (grazing) behavior of green sea turtles?

Answer: Feeding disrupts normal grazing behavior and increases the chance of human-wildlife conflicts.

Knowledge gap: How does human activity impact marine megaherbivore spatial movements in their seagrass foraging habitat and how does this cascades to ecosystem functioning? Animal-borne video provides a tool to study this.



Chapter 5

Question: Do sea turtles change their grazing impact when shelters are added to high-predator environments?
Answer: Turtles switch from browsing to an intensive, low vigilance grazing strategy near shelters added to their habitat, likely because of the surrounding landscape of fear, with impacts on seagrass morphology and ecosystem functioning.
Knowledge gap: It is unknown if this behavior is innate or learned, and if turtles prefer hiding or if sharks avoid structures within a homogenuous seagrass meadow. Information on turtle and shark movements can explore whether sharks may increase ecosystem value through cascading grazing effects.

Chapter 6

Question: What is the effect of turtle grazing intensity on tropical seagrass ecosystem multifunctionality?
Answer: Intermediate turtle increases nutrient cycling and carbon storage, while other ecosystem services were highest in the absence of turtle grazing. Intense grazing led to a collapse of multifunctionality.
Knowledge gap: What are the effects of predator presence and species invasion on ecosystem multifunctionality? Can they prevent collapse?

Chapter 7

Question: How do multiple global-warming related stressors determine the resilience of (sub)tropical seagrass systems?
Answer: Temperature and herbivory (depending on the type of herbivore) can increase both above- and belowground recovery rates and therefore enhance the resilience of subtropical seagrass.
Knowledge gap: Will subtropical seagrass meadows be able to maintain productivity to sustain range-shifting populations of herbivores under future warming scenarios? It is important to distinguish grazing impacts of meso- and megaherbivores.

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Summary

SUMMARY

Seagrass meadows are a vital component of the world's coastal zones. In the past decades, their immense ecosystem value has been increasingly recognized and explored, while at the same time human activities are causing global declines. Therefore, seagrass ecology is a fast-growing and developing field with scientists simultaneously mapping seagrass meadows, exploring fundamental ecological interactions, experimenting with impacts of stressors and restoring degraded areas. Herbivores play a large role in structuring tropical seagrass meadows, and this role is increasing due to conservation efforts of sea turtles combined with herbivore range shifts due to global warming. By building an understanding of herbivore behaviour (**Chapter 2, 4, 5**) and marine plant-herbivore interactions within the seagrass ecosystem (**Chapter 2, 5, 6**), this work aims to identify how herbivores impact the functioning and resilience of tropical seagrass systems in a changing world (**Chapter 3, 6, 7, 8**).

Caribbean seagrass meadows are often dominated by the valuable climax species *Thalassia testudinum*, a species that provides a habitat and food for a wide range of species. However, this species is under increasing pressure of eutrophication, coastal development, overgrazing by sea turtles and the invasion of the exotic seagrass *Halophila stipulacea*. Native herbivores can form biotic resistance to invasive macrophytes, as was described in this thesis for herbivore fish limiting H. stipulacea expansion and providing a refuge for native seagrass (**Chapter 2**). We are the first to identify several native fish species grazing on *H. stipulacea* (**Chapter 2**). As we know from our previous research that sea turtles can facilitate expansion of H. stipulacea by preferring native *T. testudinum* seagrass, the combination of the various preferences of both small and large herbivores were found to explain the distribution of native and invasive seagrass within one Caribbean bay (**Chapter 2, 8**). Additionally, the invasive seagrass dominated seascape as a result of green turtle grazing was found to increase the amount of bioturbation activity (**Chapter 3**). On bioturbation mounds, invasive seagrass can outcompete native upside-down jellyfish for space and thus disrupt the species interactions within seagrass meadows (**Chapter 3**). Diverse and abundant herbivore communities can therefore play an important role in limiting invasion success and the conservation of these species may serve as a tool to slow down seagrass invasion and mitigate potential negative effects of invasive plants on the ecosystem community.

Local nutrient enrichment of nitrogen and phosphorus can enhance top-down control of seagrass by herbivores preferring nutrient-rich leaves. Both fish and turtle herbivores were found to increase their grazing pressure when nutrients were added (**Chapter 2**, **7**), and this enhanced the biotic resistance to *H. stipulacea* (**Chapter 2**), while slightly reducing the resilience of *T. testudinum* (**Chapter 7**). H. stipulacea was found to have a higher nutrient uptake rate compared to T. testudinum (**Chapter 8**). Therefore, in systems with low herbivore abundance, excess nutrients could favour invasive over native seagrass.

Large herbivores as green turtles can shape seagrass meadows depending on top-down impacts from humans or predators. In systems where humans are offering alternative food sources, as described in **Chapter 4** where tourists feed turtles, sea turtles switch from a seagrass-dominated diet to a protein dominated diet and greatly alter their (grazing) behavior, with impacts on seagrass functioning. Additionally, we found that in a seagrass habitat with high predator abundance, turtles select habitat features as foraging sites, likely as a predator refuge, resulting in grazing halos surrounding structures added to their habitat (**Chapter 5**). This result implies that turtles show an intensive grazing strategy when they feel safe, while predator presence results in a browsing grazing strategy, with a positive impact on ecosystem functioning; such as the amount of carbon stored in seagrass sediments (**Chapter 8**). Experimental manipulation of turtle grazing pressure revealed that moderate grazing can increase some ecosystem functions such as nutrient cycling and carbon storage (**Chapter 6**). In contrast, intensive grazing, associated with a low-risk grazing strategy, can lead to a collapse of ecosystem multifunctionality.

Sea turtle grazing may limit the recovery rates of seagrass, while moderate fish grazing can improve seagrass resilience (**Chapter 7**). Due to the positive effect of temperature on both above- and belowground seagrass recovery rates, gradual warming may increase the resilience of seagrass in subtropical parts of its range (**Chapter 7**). However, because subtropical seagrasses are subject to increasing grazing pressure, the carrying capacity of these meadows in respect to grazing should be closely monitored in the future (**Chapter 8**). Overall, conservation and restoration efforts should not only include megaherbivores but also key components like mesoherbivores, predators and their habitat, to ensure high-value and balanced ecosystems that are resilient to future change.

Samenvatting

SAMENVATTING

Zeegrasvelden zijn wereldwijd een essentieel onderdeel van kustgebieden. In de afgelopen decennia is hun ecosysteemwaarde steeds meer erkend en onderzocht. Tegelijkertijd is menselijke activiteit verantwoordelijk voor de mondiale afname van zeegrasgebied. Zeegrasecologie is een snelgroeiend en ontwikkelend onderzoeksgebied, waarbij wetenschappers in hoog tempo zeegrasvelden in kaart brengen, en daarnaast ook fundamentele ecologische interacties verkennen, de impact van stressfactoren onderzoeken en zeegrasgebied herstellen. Herbivoren spelen een grote rol in het vormgeven van tropische zeegrasvelden. Deze rol neemt steeds verder toe door verschillende processen: populaties van een belangrijke grote grazer, de groene zeeschildpad, groeien door succesvolle bescherming, en daarnaast breiden herbivoren hun leefgebied uit als gevolg van de opwarming van de aarde. Door inzicht te krijgen in het gedrag van herbivoren (**Hoofdstuk 2, 4, 5**) en mariene plant-herbivoor interacties binnen het zeegrasecosysteem (**Hoofdstuk 2, 5, 6**), tracht dit proefschrift te identificeren hoe herbivoren van invloed zijn op het functioneren en de veerkracht van tropische zeegrasecosystemen in een veranderende wereld (**Hoofdstuk 3, 6, 7, 8**).

Caribische zeegrasvelden worden doorgaans gedomineerd door de waardevolle climax-soort *Thalassia testudinum*. Deze soort verschaft leefgebied en voedsel aan een breed scala aan dieren. Maar helaas staat *T. testudinu*m onder toenemende druk van eutrofiëring, kustontwikkeling, overbegrazing door zeeschildpadden en de invasie van de exotische zeegrassoort Halophila stipulacea. Inheemse herbivoren kunnen helpen om invasieve (zeegras)soorten te bestrijden. Wij ontdekten dat plantenetende vissen de uitbreiding van *H. stipulacea* beperkten en zo een toevluchtsoord boden aan het inheemse zeegras (**Hoofdstuk 2**). We hebben uit ons eerdere onderzoek geleerd dat zeeschildpadden de uitbreiding van H. stipulacea kunnen bevorderen door de voorkeur te geven aan het inheemse *T. testudinu*m zeegras. De verschillende voorkeuren, van zowel kleine als grote herbivoren, vormen een verklaring voor de verdeling van inheems en invasief zeegras in een Caribische baai (**Hoofdstuk 2, 8**). Daarnaast bleek dat in het invasieve zeegraslandschap, als gevolg van schildpadbegrazing, de hoeveelheid bioturbatie-activiteit groter werd (**Hoofdstuk 3**). Op de bioturbatie-heuvels kan het invasieve zeegras de inheemse 'onderstebovenkwallen' verjagen in de strijd om ruimte en licht, waardoor dus interacties tussen de soorten in de zeegrasvelden verstoord worden (**Hoofdstuk 3**). De hoeveelheid en diversiteit van herbivoren kan dus een belangrijke rol spelen bij het beperken van plantinvasies. Bescherming en behoud van deze dieren kan een middel zijn om de invasie van zeegras te vertragen en de mogelijke negatieve effecten van invasieve planten op het ecosysteem te verminderen.

Bij de experimentele toevoeging van voedingsstoffen (zoals stikstof en fosfor) in de buurt van zeegras, bleek dat herbivore vissen en schildpadden de voorkeur geven aan het eten van zeegras waaraan deze voedingsstoffen zijn toegevoegd. Hun impact op het zeegras werd dus sterker bij extra voedingsstoffen in het systeem (**Hoofdstuk 2, 7**). Dit zorgde ervoor dat de groei van het invasief zeegras *H. stipulacea* extra werd geremd (**Hoofdstuk 2**), en zorgde voor een kleine reductie in de veerkracht van het inheemse zeegras *T. testudinum*. Ook ontdekten we dat H. stipulacea in hoger tempo voedingsstoffen op kan nemen dan *T. testudinum* (**Hoofdstuk 8**). Daarom concluderen we dat onderzoekers altijd rekening moeten houden met grazers als ze de impact van voedingsstoffen in natuurlijke zeegrasvelden onderzoeken. Bovendien kan extra input van voedingsstoffen de groei van invasief zeegras bevorderen ten opzichte van inheems zeegras, vooral in gebieden met weinig herbivoren.

Grote herbivoren, zoals groene zeeschildpadden, kunnen zeegrasvelden vormgeven. Dit is in grote mate afhankelijk van de aanwezigheid van mensen of roofdieren. In gebieden waar mensen alternatieve voedselbronnen aanbieden, zoals beschreven in **Hoofdstuk 4** waar toeristen schildpadden voeren, schakelen de schildpadden over van een zeegrasdieet naar een dieet met veel eiwitten. Hierdoor verandert hun graasgedrag, wat invloed heeft op de vorm van het zeegraslandschap. Daarnaast ontdekten we dat, in een zeegrasgebied met veel roofdieren, schildpadden een voorkeur hadden voor bepaalde schuilplekken in hun habitat. Dit komt waarschijnlijk omdat ze zich daar veilig voelden. Hierdoor ontstonden graastuintjes rondom structuren die we in het zeegrasveld hadden geplaatst (**Hoofdstuk 5**). Dit experiment laat zien dat schildpadden voor een intensieve graasstrategie kiezen als ze zich veilig voelen, terwijl de aanwezigheid van roofdieren leidt tot een strategie waarbij ze willekeuriger grazen. Die laatste tactiek heeft een positieve invloed op het ecosysteem, bijvoorbeeld op de hoeveelheid koolstof die in de zeegrasbodem wordt opgeslagen (**Hoofdstuk 8**). Onderzoek waarbij we de graasdruk van schildpadden experimenteel veranderde, liet zien dat een gemiddelde graasdruk bepaalde ecosysteemdiensten kan verbeteren, zoals het recyclen van voedingsstoffen en koolstofopslag (**Hoofdstuk 6**). Intensief grazen kan daarentegen leiden tot een ineenstorting van de vele functies die het ecosysteem biedt (= multifunctionaliteit) (**Hoofdstuk 6**).

Schildpadbegrazing kan er bovendien voor zorgen dat zeegras minder snel hersteld, terwijl visbegrazing het herstelvermogen van zeegras juist kan verbeteren (**Hoofdstuk 7**). Door de positieve invloed van temperatuur op zowel het bovengrondse als ondergrondse herstelvermogen van zeegras, kan een geleidelijke opwarming van h**et zeewater de veerkracht van zeegras in subtropische gebieden mogelijk vergroten (Hoofdstuk 7**). Maar omdat subtropische gebieden ook steeds meer onder druk komen te staan van intensieve begrazing, is het belangrijk om de draagkracht van deze zeegrasvelden onder deze toenemende graasdruk goed in de gaten te houden (**Hoofdstuk 8**).

Concluderend zullen de inspanningen om zeeschildpadden te beschermen hand in hand moeten gaan met de het behoud en herstel van kleinere herbivoren, grote roofdieren en hun leefgebied, het zeegras. Op die manier kunnen we ervoor zorgen dat deze ecosystemen hun balans terugvinden, hun waarde niet verliezen, en voldoende bestand zijn tegen toekomstige veranderingen.

Resúmen

RESUMEN

Kama di yerba di lamannan rònt mundu ta forma un parti esensial di e área di kosta. Den e último dékadanan, nan balor pa e ekosistema a bira mas i mas rekonosé i investigá. Na mes momentu, aktividat humano ta responsabel pa e redukshon global di e área di yerba di laman. Ekologia di yerba di laman ta un kampo di investigashon ku ta kresiendo rápidamente i den desaroyo, den esaki sientífikonan ta eksplorando rápidamente áreanan di yerba di laman, i ademas ta eksplorando interakshonnan ekológiko fundamental, investigando e impakto di faktornan di strès i restorando áreanan di yerba di laman. Hèrbivornan tin un papel importante den e modelashon di áreanan tropikal di yerba di laman. E papel akí ta oumentando konstantemente debí na vários proseso: e populashonnan di un gran komedó di yerba, e turtuga di laman blanku, ta kresiendo pa kousa di protekshon eksitoso, i tambe hèrbivornan ta ekspandiendo nan habitat komo resultado di keintamentu di mundu. Dor di haña konosementu di e komportashon di hèrbivor (**Kapítulo 2, 4, 5**) i interakshon entre mata marino ku hèrbivor den e ekosistema di yerba di laman (**Kapítulo 2, 5, 6**), e tésis akí ta purba di identifiká kon hèrbivornan ta afektá e funshonamentu i e resiliensia di e ekosistema tropikal di yerba di laman den un mundu kambiando (**Kapítulo 3, 6, 7, 8**).

Kama di yerba di lamannan den Karibe ta dominá generalmente pa e balioso espesie klimaks *Thalassia testudinum (Yerba di Turtuga).* E espesie akí ta proveé habitat i kuminda pa un variedat grandi di animal. Pero desafortunadamente, *T. testudinum* ta bou di preshon kresiente di eutrofikashon, desaroyo na kosta, komementu eksesivo di yerba dor di turtuga di laman i invashon di e espesie eksótiko di yerba di laman *Halophila stipulacea*. Hèrbivornan nativo por yuda kombatí espesienan invasivo di yerba di laman. Nos a deskubrí ku pisṡká hèrbivor a restringí e ekspanshon di *H. stipulacea* i asina a proveé un refugio pa e yerba di laman nativo (**Kapítulo 2**). Nos a siña di nos investigashon anterior ku turtuga di laman por promové ekspanshon di *H. stipulacea* dor di duna preferensia na e yerba di laman nativo *T. testudinum* E diferente preferensianan, tantu di hèrbivor chikitu komo esun grandi, ta splika e distribushon di yerba di laman nativo i di esun invasivo den un bahia di karibense (**Kapítulo 2, 8**). Ademas, a resultá ku den e áreanan di yerba di laman invasivo, debí na komementu dor di turtuga, e kantidat di aktividat di bioturbashon a oumentá (**Kapítulo 3**). Riba e serunan di bioturbashon, e yerba di laman invasivo por kore ku *e kwalnan 'kabes abou' nativo* den e bataya pa espasio i klaridat, i asina ta kousa estorbo di interakshon entre e espesienan den e kamanan di yerba di laman **(Kapítulo 3).** E kantidat i diversidat di hèrbivornan por hunga un papel importante den limitashon di invashon di mata.

Protekshon i konservashon di e animalnan akí por ta un medio pa retrasá e invashon di yerba di laman i pa redusí e posibel efektonan negativo di mata invasivo pa e ekosistema.

Den kaso di añadidura eksperimental di nutrientenan (manera nitrógeno i fòsfòr) den besindario di yerba di laman, a resultá ku piská hèrbivor i turtuga ta preferá kome yerba di laman na kual a agregá e nutrientenan akí. Pues nan impakto riba e yerba di laman a bira mas fuerte ora ku a agregá èkstra nutriente na e sistema (**Kapítulo 2, 7**). Esaki a kousa ku tabata frena e kresementu di e yerba di laman invasivo *H. stipulacea* adishonalmente (**Kapítulo 2**), i tabata kousa un redukshon chikitu den e resilensia di e yerba di laman nativo *T. testudinum*. Tambe nos a deskubrí ku *H. stipulacea* por apsorbé nutriente na un velosidat mas haltu ku *T. testudinum* (**Kapítulo 8**). Dor di esaki, nos ta konkluí ku investigadónan semper mester tene kuenta ku e komedó di yerbanan ora nan ta investigá e impakto di nutriente den áreanan natural di yerba di laman. Ademas input èkstra di nutriente por promové e kresementu di yerba di laman invasivo kompará ku yerba di laman nativo, prinsipalmente den áreanan ku tin tiki hèrbivor.

Hèrbivornan grandi, manera turtuga di laman blanku, por modelá kama di yerba di laman. Esaki ta dependé grandemente di e presensia di hende òf animal yagdó. Den áreanan kaminda hende ta ofresé fuentenan di kuminda alternativo, manera ta deskribí den **Kapítulo 4** na unda turistanan ta duna turtuga kuminda, e turtuganan ta kambia di un dieta di yerba di laman pa un dieta ku hopi proteina. Komo resultado di esaki, nan kondukta di kome yerba ta kambia, loke ta afektá e modelo di e paisahe di yerba di laman. Ademas, nos a deskubrí ku, den un área di yerba di laman ku hopi animal yagdó, turtuga tabata preferá sierto sitio di refugio den nan habitat. Esaki probablemente ta bini dor ku nan ta sinti nan mes safe ei. Dor di esaki a krea hòfi pa kome yerba bèrdè rònt di e strukturanan ku nos a pone den e kama di yerba di laman (**Kapítulo 5**). E eksperimento akí ta demostrá ku turtuga ta skohe pa un strategia intensivo di kome yerba ora nan ta sinti nan mes safe, miéntras ku presensia di animal yagdó ta kondusí na un strategia unda nan ta bai kome yerba mas arbitrariamente. E último táktika akí tin un impakto positivo riba e ekosistema, por ehèmpel riba e kantidat di karbon ku ta almasená den e fòndu di yerba di laman (**Kapítulo 8**). Investigashon den kua eksperimentalmente nos a kambia e preshon di komementu di yerba dor e di turtuganan a demonstrá ku un preshon averahe di komementu di yerba por mehorá sierto servisio di ekosistema, manera resiklahe di nutriente i almasenamentu di karbon (**Kapítulo 6**). Komementu di yerba di forma intensivo, di otro banda, por kondusí na un kolèps di e hopi funshonnan ku e ekosistema ta ofresé (= multifunshonalidat) (**Kapítulo 6**).

Komementu di yerba dor di turtuga ademas por kousa ku yerba di laman ta rekuperá ménos lihé, miéntras ku komementu di yerba dor di piská sinembargo por mehorá e kapasidat di rekuperá di e yerba di laman (**Kapítulo 7**). Dor di e influensia positivo di temperatura, e kapasidat di rekuperá di yerba di laman riba tantu, e kapasidat di riba suela komo esun di bou di suela, un keintamentu gradual di e awa di laman por oumentá posiblemente e resiliensia di yerba di laman den áreanan suptropikal (**Kapítulo 7**). Pero komo ku e áreanan suptropikal tambe ta bini kada bes, mas bou di preshon di komementu di yerba di laman intensivo, ta importante pa tene un bon bista riba e kapasidat di karga di e kama di yerba di lamannan akí bou di e preshon kresiente di komementu di yerba di laman (**Kapítulo 7**).

E konklushon ta, ku e esfuersonan pa protehá turtuga di laman lo mester bai man den man ku e konservashon i restourashon di hèrbivornan mas chikitu, animal yagdónan grandi i nan habitat, i e yerba di laman. Di e forma akí nos por sòru ku e ekosistemanan akí ta rekuperá nan balansa, no ta pèrdè nan balor, i ta sufisientemente resistente na kambionan den futuro.

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In 2015 I met Marjolijn when she trusted me enough to go to Bonaire to start a Msc thesis project, even though we were both not yet familiar with the island. During a single scuba-gear-loaded-kayak trip through the waves together to our experimental site in the middle of Lac Bay, she boosted my field-confidence in such a way and gave me a crash course in seagrass research methods that afterwards I was able to perform the whole experiment on my own. This was the start of our journey of working together, and I was thrilled when I could continue on my favorite research subject by starting my PhD project in 2018.

Marjolijn, I feel like you are the perfect example of someone who makes the impossible possible. With minimal resources and a great batch of creativity, perseverance, and optimism, you've taught me how each setback can be tackled and learned from and how to answer complex research questions with elegant and simple (field) experiments. I feel very thankful for the trust you had in me to explore some academic side trails, which led to interesting discoveries and new research questions. As well as encouraging me to coordinate big experiments with many international collaborators and guiding me through the process of fund raising, budgeting, logistics, and communication. I also feel like we make a great team, you as the visionary and supportive captain, me as first mate a bit more on the conservative side, serving as a manager, memory and planner. You have been there for me throughout and I hope we can continue working together for many years to come.

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I'm very thankful for all the Bsc and Msc students I had under my supervision. I learned a lot from all of you guys, you contributed to my thesis and helped me grew into the academic I am today. **Mark, Julia,** you worked relentlessly on the first experiment of my PhD. Julia we had a lot of fun during loooong field days, where we stretched our tanks to 3 hr dives. Your enthusiasm is super affectious and I still laugh when I think about our discovery that the supersoft alarm originated from your bright yellow truck or the tiny premade alufoil bag to store seagrass. **Tatiana**, we instantly connected from the first moment we met, you starting your Msc project and me my PhD. Your intrinsic love for and knowledge of marine ecosystems inspires me, always willing to do additional experiments or join new projects. The wildlife and ecosystems of Aruba are lucky to have you in their corner. **Liesa, Mickey, Dave and Wout**, with a whole team we travelled to Bonaire to assess sharks, turtles and seagrasses. Together we fitted cameratags on sea turtles, which unfortunately were impossible to find back… Mickey – next to the many field experiments we set up together for your thesis with great teamwork - you were the only one of us who was brave enough to steer the questionable boat (rented from the one eyed retired turtle poacher) we used to look for the cameras, we stranded several times. At night we went out with kayaks through the mangroves to look for the flickering light attached to the cameratags. In 2020, Liesa you escaped to Bonaire during the pandemic related travel restrictions and I eventually managed to join you and we spend a couple of great weeks working closely together, processing a LOT of seagrass samples and struggling to remove 20 1.5 by 1.5 m heavy rebar cages from the turbid water (with help of Hans & Jannie). **Muriel and Naomi**, you had to completely change your plans because of COVID and you managed to push through and complete your thesis projects very successfully on Curacao, which was only possible because of your organizational skills and independence (and by help of CARMABI!). **Divya**, I really enjoyed working together with Ingrid, Egbert and you on a modelling project, and learned a lot. After, we continued working closely together on a laboratory experiment, and had some fun in the long lab hours pushing through all the challenges thrown our way with the COVID restrictions. Near the end of my PhD I had the opportunity to join two more field trips to Bonaire centered around seagrass and mangrove restoration using biodegradable sediment stabilizing structures. **Anniek, Shamyi**, **Laura** and **Josien** you are all very driven to learn and make the world a better place. It was a great experience to work with you and with **Tjisse** & **Karin** and to 'give back' to the wonderful island of Bonaire by giving a seagrass training to the STINAPA rangers and restoring patches of seagrass. It's a great feeling to still be in contact with so many of the students I supervised, I sense there is a great batch of (female!) academics on the rise, ready for a revolution :).

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The past 5.5 years have been challenging to say the least: working in the field of environmental sciences in times of a biodiversity crisis, climate crisis and a pandemic threw many obstacles in my way, and sometimes it was hard to reconcile flying to the Caribbean and spending time there while being aware of my own impact of travelling as well as witnessing how booming tourist business affects these islands. Therefore, I'm very grateful for our collaborations with local partners (special thanks to **Brigit, Isis, Sarah and Yvonne**) that made it possible to design & perform experiments from-a-distance as well the opportunities I got to ensure scientific results were communicated and used in nature conservation. I'm very motivated to use the knowledge gained in this thesis to protect these ecosystems and put **seagrass** more in the spotlight!

Most importantly, I'd like to thank my close support network of friends and family: My **parents**, **sister** and **Eva** for always reading and understanding my work, listening to complaints and being my cheerleaders. With your support I can take on the world! Creating the most encouraging environment I could wish for (my parents), helping me clean cages on Bonaire and being my paranimf (Marisha) and spreading seagrass awareness throughout the Dutch police force (Eva). Thanks to **Karen, Sacha, Cathleen, my family in law** and my other friends and family for keeping me sane. A special thanks to both **my strong grandmothers** who worried sometimes over me travelling and spending so much time underwater but were also so proud of the opportunities I got, which are so different compared to the times they grew up in. This product is as much theirs as it is mine.

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Curriculum Vitae

CURRICULUM VITAE

Fee Smulders, born on the 1st of April 1993 in Amsterdam, has always been fascinated by nature and told people from the age of 8 that she would become a biologist. This developed from reading lots of books and spending time in gardens and on the water, via a very enthusiastic team of biology teachers during high school, to eventually her first diving experience with her husband Milan in Vietnam. The discovery of the underwater world unlocked a curiosity that led her (after becoming a Bsc in Biology) to complete the Msc Limnology & Oceanography at the University of Amsterdam with two Msc thesis projects: one on red algae and cyanobacteria on Curaçao, the other on sea turtle grazing impacts on Bonaire. Spending hours and hours underwater in the seagrass meadows of Bonaire she became captivated by this ecosystem and via the research presented in this thesis as well as by media outreach and mentoring students, continues to make it her mission to better understand, protect and conserve seagrass ecosystems worldwide.

LIST OF SCIENTIFIC PUBLICATIONS

- Fourqurean, J. W., Campbell, J. E., Rhoades, O. K., Munson, C. J., Krause, J. R., Altieri, A. H., ... **Smulders, F. O. H.**, … & Wilson, S. S. (2023). Seagrass Abundance Predicts Surficial Soil Organic Carbon Stocks Across the Range of *Thalassia testudinum* in the Western North Atlantic. *Estuaries and Coasts*, 1-22.
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Scientific outreach

- Educational videoclip & podcast: 'Dit vergeten plantje gaat de wereld redden, 6 August 2023, Universiteit van Nederland
- Educational videoclip: 'Welke rol spelen ecosystemen in ons klimaat?', 3 April 2023, NESSC Tipping point ahead/SchoolTV
- Radio interview: 'Fee Smulders over het belang van wereld zeegrasdag', 1 March 2023, NOS Radio 1 Journaal
- Newspaper interview: 'Zeekoe aan het vloggen: 'Belangrijk om steeds meer te leren over onze dieren'', 11 January 2023, de Telegraaf
- TV news interview: 'Zeekoeien in Burgers' Zoo krijgen camera's', 10 January 2023, NOS Jeugdjournaal
- News article: 'Zeekoeien in Burgers' Zoo gaan 'vloggen' voor onderzoek naar zeegras', 10 January 2023, NU.nl
- Radio interview: 'Haaien beschermen belangrijke zeegrasvelden', 13 November 2022, Vroege Vogels
- Newspaper interview: 'Zeegras evolueerde net als de walvis terug naar zee', 7 October 2022, NRC
- Popular science magazine interview: 'Naar de haaien', October 2022, Kijk magazine
- Newspaper article: 'Grazende vissen kunnen invasief zeegras helpen bestrijden', 13 November 2021, Amigoe
- Newspaper interview: 'The price they pay for your perfect vacation photo', 11 May 2021, The New York Times
- News article: 'Bijvoeren door toeristen maakt schildpadden agressief', 1st February 2021, NU.nl
- 'Global Defaunation and Plant Invasion: Cascading Effects on Seagrass Ecosystem Services', 2018, DCNA Bionews

- Presentation about our seagrass research with Marjolijn Christianen, Justin Campbell and Olivier Kramer, August 2018, Bonaire, Connecting people with nature series.
- 2018 – 2023: Giving yearly lectures to 5th and 6th year scholars at the St Ignatius gymnasium in Amsterdam
- 2018 – 2023: Maintaining a personal research blog: www.feesmulders.com

Made by artist Emma Rehn to illustrate the research presented in this thesis.

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- Research in context activity: 'Educate and engage: from local high school to The New York Times' (2020)

Selection of Other PhD and Advanced MSc Courses

- Scientific Artwork, Data visualisation and Infographics, Wageningen university (2021)
- Zero inflated GLMs and GLMMs with R, Highland Statistics (2022)
- Communication with the Media and the General Public, Wageningen University (2022)
- Science Journalism, Wageningen University (2023)

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Management and Didactic Skills Training

- Supervising Bsc/Msc course fieldtrips to Texel (2018, 2019)
- Yearly lectures to high school students Ignatius Gymnasium (2018-2021)
- Supervising 2 BSc students with thesis (2019)
- Supervising 13 MSc students with thesis (2018-2023)
- Maintaining blog: www.feesmulders.com (2018-2023)
- Multiple interviews by newspapers, radio and mediaplatforms to communicate results NRC, NYT, KIJK, Telegraaf, Vroege Vogels, SchoolTV, Jeugdjournaal (2020-2023)
- Lecture in BSc course on seagrass systems (IMEE) (2021, 2022, 2023)

Selection of Oral Presentations

- *Interactions between nutrient enrichment and biotic resistance in invaded seagrass meadows.* CERF, 1-11 November, 2021, Online
- *Herbivory as a driving force of seagrass species composition and resilience in Caribbean seagrass ecosystems.* International Seagrass Biology Workshop, 7-13 August 2022, Annapolis USA
- *How herbivores drive seagrass species composition and seascape morphology in (sub)tropical seagrass meadows.* NERN NAEM 2022, 20-21 September 2022, Lunteren, The Netherlands
- *Green turtles shape the seascape through grazing patch formation around habitat features in high-predator seagrass ecosystems.* British Annual Ecology Meeting, 19-21 December 2022, Edingburgh, UK

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