The resilience of tropical intertidal seagrass meadows, grazed by dugongs, and the impact of anthropogenic stressors

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Chapter 6

Synthesis

6.1 Relevance of the thesis

It has been estimated that seagrass meadows are being lost at a rate of around 7 % of their surface area annually, equal to two football fields each hour (Unsworth et al., 2018). Anthropogenic-driven developments in coastal areas can have a significant impact on reducing seagrass density and quality in coastal areas (Duarte, 2002; Orth et al., 2006; Short and Escheveria, 2009; Grech et al., 2012; Murphy et al., 2019: Serrano et al., 2020). Grech et al. (2012) concluded that the major threats to seagrasses are largely terrestrial based, as most seagrass meadows are found in inshore waters less than 10 m deep, where their health and survival are influenced by complex natural and human-induced processes. It is in this coastal zone, where land and sea meet, that seagrasses are under pressure from their greatest threats: urban/industrial runoff, urban/port infrastructure development, agricultural runoff, and dredging. Excessive nutrient loads and sedimentation are the most common and significant causes of seagrass decline (Orth et al., 2006).

According to Green and Short (2010) and Kuriandewa et al. (2003), Indonesia has 30,000 km^2 of seagrass, representing at least 5% of the world's total seagrass area. This seagrass area has been decreasing during the past decades (Unsworth et al., 2018). Seagrass meadows in Indonesia have been impacted by various anthropogenic interventions. Coastal development and deforestation resulting in sedimentation are important drivers (Abrams et al., 2016; Unsworth et al., 2016). The impact of sedimentation results in increased suffocation of plant tissue through sediment together with a reduction in light availability due to increased particulates in the water column (Unsworth et al., 2018; Cabaco et al., 2008; Terrados et al., 1998). Estuarine and coastal environments in which seagrass meadows occur are particularly vulnerable to human impacts (Cabaco et al., 2008). Eutrophication has led to increased nutrient and organic matter deposition within estuaries worldwide (Orth et al., 2006). Associated changes in the condition of the sediment and decreased light availability result in additional stresses for benthic organisms (Unsworth et al., 2015; Adams et al., 2016; Chartrand et al., 2016). In addition, contamination in the estuaries can arise from discrete sources (e.g., industrial waste) or diffuse contamination (e.g., catchment runoff). As such, seagrasses growing in shallow coastal areas and also in estuarine habitats can be damaged by shipping traffic, contaminated bilge water, accidental spills, and contaminated by using antifouling compounds (Taylor et al., 2011; Govers et al., 2016)).

Seagrasses themselves seem to tolerate and recover quite well from anthropogenic contamination such as oil spills (Fonseca et al., 2017). Several reports mention that oil spills do not have a significant long term effect on seagrass even though at the beginning of exposure to oil seagrasses experience mass mortality (Zieman et al., 1984; Helen et al., 2011; Kenworthy et al., 2017; Magalhaes et al., 2021). However, as an ecosystem, oil spills have an acute short-term impact on the community of organisms associated with seagrass, i.e. algae, benthic organisms, periphyton, etc (Jacobs et al., 1989; Helen et al., 2011; Kenworthy et al., 2017; Magalhaes et al., 2021).

In the light of the rapid developments in coastal areas, understanding the mechanisms of seagrass resilience to environmental pressures on intertidal seagrass meadows has become of critical importance. It has been suggested that intertidal seagrass communities are less well-studied than subtidal seagrass communities (De Iongh et al., 1998). These intertidal seagrass communities are more strongly exposed to both natural stresses and anthropogenic pressures compared to subtidal seagrass meadows. Apart from this, they form an important food source for dugong a green turtle. As a consequence, the focus of this Ph.D. research has been on the impact of anthropogenic stressors (pollution and sedimentation) on intertidal seagrass communities in Balikpapan Bay and the interaction with dugongs. The main objective of this research is to investigate how seagrasses living in the intertidal area survive and respond to environmental pressures and how this affects dugong grazing. The following research questions were formulated to address the research objectives:

a) What are the ecological characteristics of intertidal seagrass meadows, and how do environmental and biological factors influence dugong grazing behavior? (Chapter 2)
b) How do oil spills affect the survival of seagrass meadows, and what factors influence their recovery and the subsequent impact on dugong grazing behavior? (Chapter3)
c) How do intertidal seagrass meadows respond to sedimentation, and what role does below-ground biomass play in enhancing their resilience? (Chapter 4)
d) How does clonality contribute to the ability of intertidal seagrass meadows to cope with extreme environmental conditions and sediment burial? (Chapter 5)

These questions were addressed in the preceding chapters 2-5 and in combination conceptualizing ed some of the underlying mechanisms related to the anthropogenic impacts on intertidal seagrass survival. The conceptual framework of this study is presented in chapter 1 and each chapter of this PhD research contributed to addressing the subsequent research questions. The current chapter provides the research synthesis, societal and scientific implications of the findings, and recommendations (Fig. 6.1).

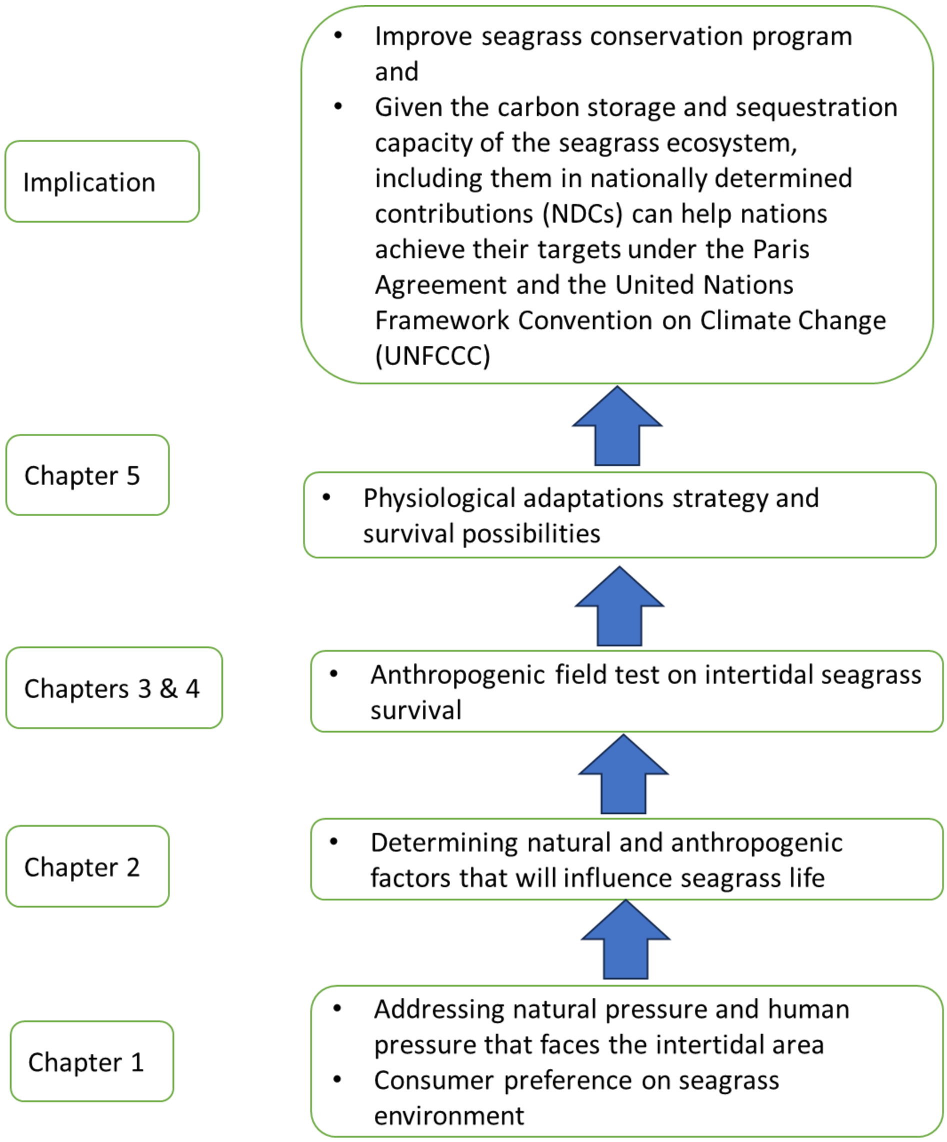

Fig 6.1. Synthesis of this thesis, showing the major outcomes and implications

6.2 The importance of seagrass meadows for dugongs and carbon sequestration

Seagrass habitats are capable of storing carbon in the form of carbohydrates as some species have rhizomes and root mats that are buried for centuries to millennia (Romero et al., 1994; Mateo et al., 1997). However, their slow net biomass increase under contemporary environmental conditions means that seagrasses can only have a relatively small impact on mitigating global CO_2 emissions (e.g., they will only capture 0.1% of emissions globally (Irving et al., 2011)). The reason for this pattern is that seagrasses fix organic carbon, the majority of which enters the food chain through direct consumption by herbivorous organisms as well as through decomposition as detritus. The broken seagrass leaves and shoots partly stay in the sediment and partly are released into the water column, where they are decomposed by microorganisms (Nienhuis et al., 1989). During decomposition, organic materials are directly consumed by detritus feeders. Meanwhile, the particulate detritus in the water column serves as food for filter-feeding organisms. Together, the decomposition and respiration processes recycle most of the carbon within the seagrass meadows. The estimated amount of material of

Indonesian seagrass that is exported to other ecosystems is only 10 %, and the remaining is recycled within the seagrass ecosystem itself (Nienhuis et al., 1989).

Herbivory is done through a variety of organisms, among which mega-herbivores like green turtle (*Chelonia mydas*) and dugong (*Dugong dugong*). The dugong is the only marine herbivore mammal and the largest mega-herbivore that is highly dependent on seagrass as food source (Marsh et al., 2018). Through a cultivating grazing pattern known as "cultivation grazing", dugongs show rotational grazing on so called grazing swards and both rhizomes and leaves of the seagrass are consumed (De Iongh et al., 1998). It is suggested that dugong feces may contribute to organic fertilization of seagrass meadows (Marsh et al., 2018).

Aragones et al. (2006) suggested that dugong feces decomposes more slowly than the original plant material. As a result, dugong grazing and its feces may increase the capacity of seagrass meadows as carbon storage. However, the migration patterns related to dugong grazing are not fully understood, and especially in relation to seagrass meadows in intertidal areas that often intersect with human activities there are few studies available (De Iongh et al., 1998).

Fig 6.2. Massive grazing tracks in Balikpapan Bay showing Dugongs present in the bay

My study showed that dugong grazing is influenced by several factors such as i) location of the seagrass meadow, ii) season, iii) impact of oil pollution, and iv) impact of other forms of human disturbance (see Fig 6.2). I found that food availability and food quality of seagrass in Balikpapan Bay as a food source for dugongs is good and that seagrass is abundant in Balikpapan Bay, offering a suitable habitat for dugongs. The availability of seagrass biomass and carbohydrates are important factors for dugongs to forage (De Iongh, 1996). In addition, dugongs need shelter and protection from the open sea during the monsoon seasons when there are strong winds and high waves. Finally, I observed that dugongs prefer intertidal areas with less disturbance by human activity, which has important implications for its preservation (see "implications" section).

6.3. Intertidal seagrass meadows and impacts of oil spill

An anthropogenic impact that often occurs in coastal areas is the occurrence of oil spills (Fonseca et al., 2017). Oil spills might happen due to ship accidents, pipeline leaks, and ship repair workshop activities. The impact of oil spills on seagrasses has been widely studied by experts. Many studies have examined the effects of oil spills on seagrasses (e.g., den Hartog and Jacobs, 1980; Hatcher and Larkum, 1982; Zieman et al., 1984; Thorhaug et al., 1986). However, in these studies there is no consensus on the short term and long-term impacts of oil spills on the overall health of seagrass, due to a high degree of variability in oil spill scenarios and the different responses among seagrass species (Zieman et al., 1984; Helen et al., 2011; Kenworthy et al., 2017; Magalhaes et al., 2021). Moreover, most studies so far lacked a good baseline measurement of the seagrasses prior to the oil spill, which added to the major uncertainties in the responses. Our research had the 'fortunate' coincidence that a major oil spill happened just after we had finished our baseline observations on the seagrass meadows of Balikpapan bay. This allowed for a unique set-up for investigating the impacts of oil spills on seagrass meadows by comparing the situation before- and after the oil spill.

Prior to the 1980s it appears that the general belief was that seagrasses were not highly susceptible to the effects of oil spills, except when physically covered with oil or when dispersants were used (Thorhaug and Marcus, 1987). More recent studies suggest that when oil is in direct contact with seagrasses it can lead to leaf and shoot mortality (Jackson et al., 1989; Marshall, 1990; Fonseca et al. 2017). In addition to short term mortality, the long term impact of oil exposure on shoot density and photosynthesis performance has been reported in several studies (Fonseca et al., 2017; Kenworthy et al., 2017; Wilson and Ralph, 2012; Kenworthy et al., 1993; Durako et al., 1993; Jackson et al., 1989). Because photosynthesis is reduced, the carbon balance of seagrasses, which is determined by the carbon gain (photosynthesis) and carbon demand (respiration and growth), can become negative (Alcoverro et al., 2001; 1999). During this stressful period, seagrasses become dependent on their carbohydrate reserves in the rhizome /root system (Alcoverro et al., 1999; Brun et al., 2008; Zimmerman et al., 1995). For seagrasses, the most important non-soluble carbohydrate for long-term storage is starch (Pirc, 1989). Starch is the energy source of a plant and, mainly stored in the rhizomes, and produced in periods with a positive carbon balance (Olive et al., 2007; Zimmerman and Alberte, 1996). However, the role of below ground biomass in the recovery of seagrasses after aboveground mortality is as yet unknown. Carbon reserves are important both for seagrass under prolonged stress (Chapman & Craigie, 1978, Dunton, 1990, Buwalda, 1991, Alcoverro et al., 1999), and as a major food source for dugongs, which increases the feeding frequency on rhizomes when carbohydrate contents in the rhizomes are highest (De Iongh et al., 1998). Therefore, understanding the allocation of carbon resources to growth, maintenance and regeneration of carbon reserves is critical for an understanding of the whole-plant responses to environmental stress and to production dynamics and the consequences for dugong survival.

Fig 6.3. Moderate oil-covered intertidal seagrass meadows in Balikpapan Bay

In Balikpapan Bay, a major oil spill was caused by a pipeline leak accident, because the anchor of a cargo ship broke the pipeline in March 2018 (Fig 6.3). The oil spill spread across the entire bay area to the Makassar Strait. During weeks after the oil spill, we visited the seagrass meadows and compared the condition of the seagrass meadows with the dataset on the same seagrass meadows a year before the oil spill. The oil contamination that occurred at the end of March 2018 appears to have had quite a short term impact on the intertidal seagrass and on dugong grazing frequency in the bay.

Dugongs did not graze the seagrass in the bay for more than 12 months after the oil spill, except for one location which had not been affected by the oil spill. However, the oil contamination in the Balikpapan Bay seagrass seemed to only exert a moderate effect on the seagrass condition itself. Over the period of 12 months following the oil spill, the seagrass biomass remained low but slowly recovered. This partial recovery did not synchronize with a return of dugong grazing. Also, this partial recovery and the fact that the seagrass never fully disappeared may suggest that the below ground reserves of the seagrass were sufficient to create a high resilience. High resilience may also have been facilitated by the upstream position of the seagrass meadows. The longer absence of dugong grazing may be explained by the fact that dugongs may be sensitive to the chemical contamination in the bay or by the possibility that they found other feeding meadows outside Balikpapan Bay. Given the location of the source of the oil contamination, the dynamics of the waters in the bay, and the condition of the bay currents, I suspect that only a small fraction of the oil contamination reached the upstream part of the bay.

During the oil spill, no one reported the presence of dugongs, while sightings by e.g., fishermen were relatively common before the oil spill. During the same period, we did not find any dugong grazing tracks in the entire area during April to September 2018. Only a year after the oil spill incident, we discovered new dugong grazing tracks in the same location as before (the Tempadung site). This observation suggests that seagrass meadows especially in the Tempadung site fully recovered from oil pollution, and that the dugongs came back to graze in this area. In combination, our results show that the intertidal seagrass in Balikpapan Bay shows a resilience to the oil contamination, while mega-herbivores such as dugong need more time to return for grazing in meadows that had been exposed to oil.

6.4. The effects of sedimentation on *Halodule pinifolia* in intertidal flats and in tidal pools in Balikpapan Bay, Indonesia

Living in a coastal environment, seagrass will have to deal with rapid changes in the landscape. These changes affect the quality of the aquatic environment. In intertidal areas, seagrasses face many environmental pressures (Björk et al., 1999; Shafer et al., 2007; Al-Bader et al., 2014; Suykerbuyk et al., 2018). The development of settlements, ports, and other constructions may cause a high load of sediments in the waters. Also, backfilling activities that are done in an effort to strengthen the structure of coastal buildings may result in additional sediment loads. Seagrass meadows composed of densely growing, long-leaved species help secure the sediment and preserve the structure of the seabed, playing an important role in protecting coastlines. However, this function is increasingly compromised by heavy grazing from large herbivores, which weakens sediment stability, and by invasive species that can be easily uprooted during storms, leaving the seabed more prone to erosion (James et al, 2020).

However, various factors can influence seagrass ecosystems, including the exchange of nutrients between the sediment and water, the accumulation of organic matter, erosion from waves or tidal currents, and grazing by marine animals—all of which can alter the structure and function of seagrass meadows, potentially leading to habitat degradation, reduced biodiversity, and a decline in vital ecosystem services such as coastal protection and carbon storage (Adhitya, 2016). In addition to sedimentation, desiccation is usually a limiting factor controlling the upper limit of seagrass growth on the intertidal flat (Van der Heide et al., 2010; Suykerbuyk, et al., 2018). Also, very turbid water may limit intertidal seagrass productivity during the hours of high tide (Suykerbuyk, et al., 2018). To better understand the impacts of these stressors and their interactive effects on seagrass performance, for which little was known, we examined the physiological ability of seagrass to withstand sedimentation and desiccation as a combination of stressors that are common due to human development activities in coastal areas (Chapter 4).

This study shows that intertidal seagrasses are relatively resilient to burial by sediment when the burial is moderate (< 4 cm). We found that at increased desiccation and sediment burial, the survival of seagrass is seriously negatively affected. This is particularly problematic in locations where the performance of intertidal seagrasses is already challenged, and additional stress leads to additional negative impacts on seagrass biomass and growth. For lower rates of sedimentation, our study offers proof that below ground carbon storage, which itself appears to be related to species strategies on leaf length and morphology, has a vital impact on seagrass survival and resilience. We conclude that below-ground carbon storage is a crucial trait in moderating the reaction of seagrasses to sediment burial in combination with desiccation. The presence of carbohydrates in the rhizomes helps seagrass to cope with high-stress environments. Since carbohydrates in the below-ground biomass carbon are also a very important food source for dugongs, the negative impact of a combination of burial and desiccation may have a large potential impact on dugong seagrass interactions and the availability of food (De Iongh et al., 1998). Although our experiment was done in a mono-specific meadow, we suggest that strategies related to below ground carbon storage may also be an endogenously driving force of species assemblage shifts in multi-specific meadows. In combination, our study provides important insights into the functioning of intertidal seagrass systems in response to multiple stressors and the direct impacts of stressors like desiccation and sedimentation thereon and the possible consequences for dugong survival.

6.5 Clonality: A potential survival strategy in changing environments

Coastal ecosystems are experiencing rapid transformations due to global environmental change. Understanding how ecological shifts affect species persistence is critical to modern management strategies. In the intertidal areas, emergence of seagrass above the water due to tidal regimes may affect seagrass growth (Azevedo et al., 2017). While the effects of desiccation (due to emergence) are well studied, little is known about the importance of sharing resources through clonality by shared rhizomes in the seagrass system (while clonality is known to help survival and growth upon stress in terrestrial grasslands (Vermaat et al., 2009)).

We tested seagrass clonality through shared rhizomes as one of the strategies to survive in intertidal and estuary environmental conditions. We found that clonal integration with rhizome connections between seagrass shoots might help intertidal seagrass to have enough resources to face stress imposed by emergence due to tidal actions and other stressors, such as sedimentation. When combined, these stressors show antagonistic effects on seagrass growth and survival. This study shows that intertidal seagrasses are vulnerable to such a combination. The fact that dugongs for their food mainly depends on below ground biomass of intertidal seagrass meadows confirms the importance of the rhizome biomass also for dugong survival (De Iongh et al., 1998)

6.6 Implications for conservation

The knowledge gained in this thesis can be used to improve our knowledge to investigate and mitigate the environmental impacts of oil spills, to improve national awareness in Indonesia and elsewhere, and to improve the enforcement of community-based conservation and management of dugongs and their associated seagrass habitat. The protection of intertidal fast-growing seagrass meadows in coastal bays may be an essential conservation action to protect critical habitats for dugong populations and also for fisheries. Our study shows that seagrass has the ability to tolerate environmental changes, but this ability is highly dependent on the level, composition, and intensity of environmental pressures. Land use conversion (deforestation) in coastal and inland areas causes high loading of nutrients and materials into coastal waters, which will greatly interfere with the growth of seagrass in coastal areas (Orth et al., 2006). It has been suggested that during the past decades there has been a large loss of seagrass meadows in most parts of Indonesia (De Iongh et al., 2007; Green and Short, 2010; Kuriandewa et al., 2003). This thesis provides quantitative evidence for the suggestions that development in coastal areas, eutrophication, and high dissolved solids are causing these declines.

We suggest that action should be taken, for example, to reduce untreated waste and sediment inputs into coastal waters to reduce turbidity (Graham et al., 2019). Development planning that involves various stakeholders is needed, primarily in conducting land use planning and land use of land and coastal areas. Planning and licensing of coastal development and coastal land use should be preceded by an environmental impact study of the estimated impacts, especially on watersheds and waters. Development in areas with important coastal ecosystems needs to make strict considerations of the impacts that may be inflicted on these ecosystems.

In addition, tropical archipelagic countries such as Indonesia have different development patterns and are unique in their ecological landscape, so there needs to be a conservation area in each sub-ecoregion (district) that really protects the authenticity of coastal ecosystems (seagrass, mangrove, and coral reef). Such identification of protected areas should be based on the ecological value and biodiversity of the area. Migratory species such as dugongs (Vulnerable on the global IUCN red list) strongly depend on local coastal seagrass meadows. I suggest that conservation programs should not only focus on the prevention of dugong hunting and accidental catches in fishing nets but also on the protection of local coastal seagrass meadows as their habitat. The protection of intertidal fast-growing seagrass meadows in coastal bays is an essential conservation action to protect critical habitats for dugong populations (De Iongh, 1996). We expect that dugong grazing in Balikpapan Bay is part of a seasonal cycle, where dugongs migrate into Balikpapan Bay, when intertidal seagrass quality is high or when the weather conditions in the coastal zone deteriorate (strong winds and high waves) due to the monsoon period at sea (De Iongh, 1996). Such sanctuaries therefore form a critical element for the dugong population that migrates alongside the coasts of East Kalimantan. The protection of intertidal seagrass habitats inside Balikpapan Bay may well be an important element for the survival of the entire dugong populations in the coastal area of East Kalimantan.

It is necessary to establish a special authoritative board in the province of East Kalimantan that is a contact point for various stakeholders in the coastal area. Such board should create awareness about the importance of seagrass ecosystems, not limited to the educational sector (elementary schools to universities) and to coastal communities, but should socialize with the government- and businesses sectors promoting the importance of seagrass ecosystems. Government research institutions need to accommodate communication between researchers across regions. This is needed to provide updates on seagrass conditions and provide suggestions for the protection and utilization of coastal ecosystems.

And finally, law enforcement and compensation for damage to the aquatic environment must be done properly. Many regulations and laws have been made, but the implementation is not followed by strict law enforcement.

6.7. Scientific implications

Seagrass resilience remains an important topic for future research. The ability of seagrass to tolerate environmental changes is important to know. This will later become the basis for making seagrass resilience models predicting the rapid changes in land use.

Intertidal seagrass meadows are great bio-indicators for predicting aquatic environmental conditions. The photosynthetic ability of intertidal seagrass both at emergence and underwater is not widely studied, especially in real conditions outside the laboratory. By looking at this ability, we will be able to estimate how much time seagrasses need to produce and store energy from photosynthesis.

6.8. Conclusions

Marine bays and coasts are not only important areas for human communities but are also areas of high biodiversity. Seagrass is one of the important ecosystems that support life in coastal and marine waters. Marine mega-herbivores such as green turtles and dugongs are highly dependent on the availability of good quality seagrass ecosystems, especially in coastal waters and bays. The availability of intertidal seagrass in sheltered bays makes it easier for dugongs to seek shelter during the monsoon period and raise their calves in these areas. The ability of seagrasses to survive is highly dependent on the magnitude of environmental stress and the energy reserves stored from optimal metabolism. Below ground carbon storage is a crucial trait in moderating the reaction of seagrasses to sediment burial and, in this way, helps them cope with high-stress environments. Based on my research, I conclude that in Balikpapan Bay, seagrass abundance and seagrass quality is still good and provide a suitable habitat for dugong. The availability of seagrass biomass and carbohydrates are essential factors for dugong grazing. In addition, dugongs need shelter and protection from the sea in bad seasons.

Rapid development, increasing water turbidity and nutrients, have resulted in a decline in water quality and light penetration in the water and increased sedimentation. We show that seagrass is well able to withstand single stresses, including oil exposure. Below ground carbon storage, which itself appears to be related to species strategies on leaf length and morphology, has a vital impact on dealing with these stresses. However, seagrasses are less able to deal with a combination of stresses. Moreover, we showed that even though seagrass can withstand oil exposure well, mega-herbivores such as dugong need more time to return to grazing in meadows exposed to oil. I conclude that in order to protect coastal intertidal seagrass meadows as a life support system for dugongs and other marine organisms, human stressors should be reduced as much as possible, while the creation of local protected areas for coastal seagrass fields with the support of local communities is crucial.

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