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

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Chapter 1

General Introduction

1.1. Intertidal seagrass species

Seagrasses are flowering plants that grow fully submerged and are rooted in the estuarine and marine environment (Den Hartog, 1984). They are not true grasses. Although they are monocotyledons, they do not have one evolutionary origin but are a polyphyletic group, defined by a particular ecological niche they inhabit: the sea. These habitats serve as nurseries and feeding grounds for numerous marine species, including commercially important fish and invertebrates, while also contributing to sediment stabilization and water clarity (Unsworth et al., 2019). Seagrasses are also increasingly recognized for their significant role in carbon sequestration, acting as effective blue carbon sinks that mitigate the impacts of climate change (Fourqurean et al., 2012). Despite their ecological importance, seagrass ecosystems are facing global declines due to anthropogenic pressures such as coastal development, pollution, and climate change (Orth et al., 2023).

Typically, seagrasses grow in areas dominated by soft substrates such as sand or mud, but some species can be found growing on more rocky substrates (e.g. *Phyllospadix sp*]. Seagrasses require high levels of light, more than other marine plants, because of their complex below-ground structures which include considerable amounts of non-photosynthetic tissues. Thus, although they have been recorded up to 70 m deep in clear waters, they are more common in shallow coastal waters due to the rapid attenuation of light with depth (Lipkin, 1979; Green and Short, 2003).

Fig 1.1. Intertidal seagrass bed in Balikpapan Bay

Coastal seagrass habitats, being shallow intertidal to subtidal environments, are highly accessible by man either on foot or with simple snorkeling or diving equipment. As such, they are under pressure as a result of visits by fishermen, tourists and researchers, but also by physical stress like sedimentation and (oil) pollution (Aragones and Marsh, 2000). This may affect seagrass growth and quality. Several studies have been done to investigate factors affecting seagrass growth and quality resulting in changes in the aquatic environment and on seagrass survival, and plant-herbivore interactions (Duarte, 2002; Short and Escheveria, 2009; Murphy et al., 2019: Serrano et al., 2020).

Most studies have been conducted on seagrass growing in subtidal areas (some have interactions with estuaries and coral reefs) (Ooi et al., 2011). Seagrasses living in intertidal areas are unique in their adaptation to the phenomenon of desiccation at low tide and exposure to high air - and water temperature, changes in osmosis pressure, and high sunlight intensity. Survival strategies of seagrass have been rarely studied, especially in relation to the interaction with mega-herbivores (such as dugong and green turtle) and human activity (De Iongh et al., 1998).

Intertidal species zonation patterns and the mechanisms behind zonation have been the focus of research by marine ecologists and botanists for more than a century (Davison and Pearson, 1996). On non-rocky shores, the lower limits of intertidal species distributions are thought to be controlled more by biotic factors such as predation and competition (e.g. Schonbeck and Norton, 1980), whereas the upper limits are more determined by physiological tolerances to exposure, temperature and desiccation (Zaneveld, 1969 and Sconbeck and Norton, 1978). This is reflected in the zonation patterns of seagrasses:

The tropical intertidal zone is characterized by pioneer seagrass species including *Halodule uninervis, Halodule wrightii, Halophila ovalis, Cymodocea rotundata, Thalassia hemprichii* and *Enhalus acoroides* (Den Hartog, 1970; De Iongh et al., 1995; Jupp et al., 1996; Bjork et al., 1999; Tanaka and Nakaoka, 2004; Shafer et al., 2007). These species are known as seagrass "pioneer" species because they can adapt to disturbance and extreme physical stress. Aragones & Marsh (2000) reported that growth rates of *H. ovalis* and *H. uninervis* are faster and the turnover time shorter than that for other species. Preen (1992) argues that *H. ovalis* and *H. uninervis* are adapted to disturbance because of their opportunistic life history strategies.

Kaewsrikhaw et al. (2016) reported that intertidal seagrass meadows such as composed of *H. ovalis* had 2– 3 times higher daily production in the lower intertidal zone than in other zones; this finding suggests that the best conditions for their growth are in the lower intertidal zone, which is likely related to light retention and nutrient availability. On the other hand, in the upper intertidal zone, seagrass faces stress from very high light intensity, high temperatures, and desiccation during the low tide periods; this generally leads to a smaller plant size with a higher sprout density to mitigate exposure to those stressors (Kaewsrikhaw et al., 2016). Intertidal seagrass species developed various adaptation mechanisms to deal with these adverse conditions. Kaewsrikhaw and Prathep (2014) reported that *H. ovalis* populations in exposed and tidal pool habitats on the upper shore limit produce much greater amounts of anthocyanins when they were exposed directly to the air. Anthocyanin accumulation is known to serve as UV irradiance protection (Trocine et al., 1981; Holton and Cornish, 1995; Close and Beadle, 2003). There is experimental evidence showing that long term exposure to higher light intensities can induce photo-protective responses in *H. ovalis* (Ralph and Burchett, 1995).

Seagrass degradation is principally related to three broad factors: poor water quality, physical disturbance, and degradation of food webs. Most studies are concerned with the effects of such factors on the prevalence and functioning of subtidal seagrasses. However, given that intertidal seagrasses may respond differently due to their adaptation mechanisms to adverse conditions and given the lack of studies on intertidal seagrasses and its interaction with mega-herbivores such as dugong and green turtle, more information is needed on the ability of intertidal seagrass to adapt to the environment and to threats from physical changes in waters and anthropogenic activities and its impact on mega-herbivores.

1.2. The importance of seagrass ecosystems

Worldwide in coastal areas, seagrass meadows cover large surface areas. These seagrass meadows provide important habitats, meaning they have a major functional role in helping various stages within the life cycles of different marine and coastal organisms. For instance, they provide crucial habitat for many fish species, including juveniles of sardines and anchovy, and for mega-herbivores like a green turtles and dugongs (Duffy, 2006; Bell et al., 2001).

Because of their important ecological role for many marine and coastal species, seagrasses are often described as "foundation species", comparable to reef-constructing organisms (Hughes et al., 2009). Seagrass meadows additionally produce large quantities of organic carbon, giving them a vital additional role in the food web (Mazarassa et al., 2018). They also stabilize sediments, which protects them from coastal erosion. Seagrasses are generally known as ecosystem engineers, as they reduce flow velocities in their canopies (Carr et al., 2016).

Annual intertidal eelgrass (*Zostera marina*) beds significantly contribute to the immobilization of sediment during the growing season with its magnitude depending on canopy density (Bos et al., 2007*)*. Garcia and Duarte (2001) reported that the effect of *Possedonia oceanica* in increasing primary deposition at an annual scale was modest. However, *P. oceanica* significantly buffered sediment resuspension, which was reduced more than threefold compared to the un-vegetated bottom. Rapid deposition by a high sedimentation rate can bury seagrass leaves and cause high mortality. The strong hurricane Gilbert, hitting the Mexican Caribbean in September 1988 (Fenner, 1991; Merino and Otero, 1991), moved large sand waves around Bahia de Mujeres (Aguayo et al., 1980). This caused a high mortality and burial of the surviving seagrass shoots, which still had a third of the length of their leaves buried below the sediment surface (C. Palillo, unpublished results, 1988; Marba et al., 1994). Marba et al. (1994) reported that *Thalassia testudinum* showed an enhanced growth response and survival with enhanced vertical growth and increased leaf production after the burial by Hurricane Gilbert in 1988. This regrowth strongly facilitated the stabilization of sediments after the hurricane.

To manage the ecosystem services of intertidal seagrass meadows, we must know how they are affected by human activities and how they can recover. In addition, we should study the impact on - and interactions with - mega-herbivores like dugong and green turtles and other marine species depending on seagrass.

1.3. Seagrass--mega-herbivore interactions

Seagrass meadows are considered to be very productive ecosystems (Vermaat et al., 1995; Orth et al., 2006) and are a main food source for mega-herbivores like the dugong (*Dugong dugong*, (Müller 1776)) and green turtle (*Chelonia mydas,* (Linneaus 1758)). It is suggested that early Sirenians (including dugongs and manatees) and especially the early dugongids co-evolved with seagrasses and that their dispersion very much depended on seagrass availability (Domning and Ray, 1985).

Sirenians have been herbivores ever since they first evolved, dependent upon seagrasses and aquatic angiosperms (flowering plants) for food (Hemminga and Duarte, 1999). Domning (2001) and De Iongh et al. (1995) concluded that, in tropical and subtropical areas, marine Sirenians are obligate seagrass feeders; they feed both on seagrass rhizomes and seagrass leaves. Dugongs are known to be very efficient rhizome feeders when leaf biomass is very low or absent (De Iongh et al., 1995; De Iongh et al., 2007). Seagrass is known to have a relatively high fiber content, surpassing that of terrestrial grasses, and dugongs may reduce the neutral detergent fiber (NDF) content to enhance digestibility (Thayer et al., 1984).

Fig 1.2 A dugong calf stranded in Teluk Sumbang, Berau, Indonesia.

Recent studies have provided valuable insights into the seagrass species favored by dugongs in tropical intertidal ecosystems. Species such as *Halophila ovalis* and *Halodule uninervis* are particularly preferred due to their high nitrogen content and digestibility. For instance, research indicates that dugongs exhibit a preference for these species, likely because of their greater nitrogen content and lower fiber concentrations (De Iongh et al., 2007; Marsh et al., 2011). Additionally, feeding trails have been predominantly observed in meadows dominated by these species, highlighting their significance in dugong foraging behavior

(Fourqurean et al., 2012). This pattern is consistent with findings from various regions, including studies in Thailand, where dugong feeding trails were primarily found in *Halophila ovalis* and *Halodule uninervis* meadows that dominate the intertidal zone (Loneragan et al., 2017). These observations underscore the ecological importance of *Halophila ovalis* and *Halodule uninervis* in supporting dugong populations in tropical seagrass habitats.

De Iongh et al (1998) also reported the existence of grazing lawns of pioneer species *Halodule spp* and *Haplohila spp* in intertidal areas in the Moluccas, maintained by dugongs through rotational grazing. Grazing lawns are important foraging areas from where herbivores can maximize their rate of intake of high-quality forage (Verweij et al., 2006; Mayengo et al., 2020; Thapa et al., 2021; Fig 1.2). Grazing lawns contain short grasses that have a higher proportion of quality forage parts (higher levels of leaf-to-stem ratio), higher bulk density, and lower biomass compared to tall grasslands (Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984; Hudson, 1981; Anderson, 1998). Intertidal *H. uninervis* meadows contain high contents of soluble carbohydrates in the below-ground, which may explain why they are preferred as food sources ((De Iongh, 2007; Sheppard et al., 2010). Further, Sheppard et al. (2010) explained that nitrogen and organic carbon are the primary limiting nutrients for dugong populations and confirmed dugongs' preference for high-energy foods. However, Preen (1995b) showed that dugongs in sub-tropical Moretón Bay may have significant quantities (in 69% of the samples) of ascidians (a source of animal protein) in their stomach. Anderson (1989) reported the dietary preference of a captive held dugong in Surabaya zoo. Moreover, dugongs were observed to deliberately forage on the thin shelled burrowing mussel (*Botula vagina*) and on seapens (*Virgularía* sp.) in sub-tropical Shark Bay (West Australia). Preen (1995b) postulated that this omnivory by the dugongs in Moretón Bay is a response to seasonal nutritional stress combined with the physiological and energetic stresses caused by cold water temperatures at the edge of the species range.

Fig 1.3. Dugong tracks in intertidal seagrass meadows in Balikpapan Bay, Indonesia

The only native mega-herbivore that may compete with contemporary dugongs and manatees is the green turtle *Chelonia mydas* (Hemminga & Duarte, 2000; Andre et al., 2005). Although both green turtles and dugongs have been reported to graze in similar seagrass meadows, it is clear that dugongs feed on both leaves and rhizomes, while green turtles exclusively feed on leaves (Bjorndal, 1980). Bjorndal also suggested that green turtles maximize the intake of total nitrogen and not of carbon (energy), which would imply a completely different feeding strategy than dugongs, which maximize energy (carbohydrates in the rhizomes) (De Iongh et al, 1995). De Iongh et al. (1998) suggested that dugongs can completely uproot pioneer seagrass meadows to maximize their energy intake, thereby leaving no seagrass for other mega-herbivores like green turtles. As a consequence, dugongs may easily outcompete green turtles in seagrass meadows by grazing to a level that limits the availability of leaves for turtles.

Grazing by herbivores is not only beneficial to the herbivores but may also benefit the primary producers. A substantial information base exists on herbivore plant interactions in terrestrial and algal-based marine systems (e.g., Mattson and Addy, 1975; Ogden and Lobe, 1978; McNaughton, 1979; Hay, 1981; Gaines and Lubchenco, 1982; Vadas et al., 1982; Hay et al., 1983). Herbivores have been shown to alter plant productivity, distribution, community structure, nutrient relations and tissue nutrient contents. With respect to seagrass, Aragones and Marsh (2000) reported that mega-herbivores grazing improves the structure and dynamics of tropical seagrass communities by altering their biomass, the volume of detritus, net above-ground biomass productivity, and species composition.

Mega-herbivores may also play a role as secondary seagrass seed dispersers. Seagrass propagules are produced in two basic forms: positively buoyant (floating) fruit, rhipidia, and viviparous seedlings, and neutrally or negatively buoyant seeds and viviparous seedlings. Seeds of seagrasses are generally neutrally or negatively buoyant because they must settle on the substrate at considerable depth. Kendrick et al. (2012) showed that the longest measured dispersal distances (300–400 km) have been recorded for those seagrass genera with floating fruit and rhipidia (e.g., *Enhalus* and *Thalassia*) and for negatively buoyant propagules, for which the potential scale of dispersal is determined by hydrodynamic processes occurring within the bottom boundary layer. There is the potential for secondary dispersal as sediments containing seeds are re-suspended and transported under high-energy storm conditions. Secondary dispersal may also occur through transport by herbivores like turtles, dugongs, manatees, ducks, and geese. In May 2009, Tulipani and Lipcius (2013) discovered eelgrass (*Zostera marina*) seeds in fecal samples of wild-caught northern diamondback terrapins (*Malaclemys terrapin*). This was the first field evidence of eelgrass seed ingestion in this species. Furthermore, Tulipani and Lipcius (2014) reported that 26 – 39 % of the ingested seeds were deemed viable.

As described above, mega-herbivores are highly dependent on the presence of seagrass. The impact of hurricanes on seagrass meadows may have large indirect impacts on dugong populations by the destruction of their main food source (Preen, 1995a). At the same time, not all seagrass meadows are visited by mega-herbivores. Do they minimize interactions with humans, or might other ecological factors influence these considerations? Thus, within this research, ample efforts will be dedicated to grazing by mega-herbivores such as dugongs to better understand their functional role in maintaining productivity and the distribution of intertidal seagrass meadows and the driving factors that influence the dugongs in choosing their foraging area.

1.4. Anthropogenic disturbance of seagrass ecosystems

Seagrass meadows are especially vulnerable to damage and degradation by human activities because of their location in the shallow coastal seas where the activities of humans are greatest (Duarte, 2002; Short and Escheveria, 2009; Murphy et al., 2019; Serrano et al., 2020). The potential for damage is higher in seagrass meadows inside the coastal zone, such as near harbors, inside estuaries, and inside lagoons and areas close to shipping lanes.

Because of their unique mode of growth, seagrasses are susceptible to damage from stress or pollutants either in the water column or sediment. One of the most important sources of pollutants in marine environments are oil spills (Fonseca et al., 2017). Seagrass meadows located near refineries or oil depots or adjacent to major tanker lanes have a greater likelihood of coming into contact with petroleum products than those in other locations (Fonseca et al., 2017; Taylor et al., 2011; Thorhauch and Marcus, 1987).

Fig. 1.4. Kariangau Industrial estate establishes in Balikpapan Bay

Seagrasses are also impacted by increased turbidity. Water clarity may decrease due to increased sedimentation or eutrophication, which will impact seagrass quality and may cause a disruption of seagrass fitness and survival (Amri et al., 2011). The relatively high light requirements make seagrasses vulnerable to a decrease in light penetration of coastal waters

(Green and Short, 2003). In oligotrophic waters, increased total nutrient loads may initially lead to non-significant or small increases in water and sediment nutrient concentrations because the extra nutrients are rapidly incorporated into algae, seagrasses, and microorganisms (Bradley et al., 2002). However, water clarity is affected by higher nutrient loads. Lee et al. (2007) reported that seagrasses may exhibit several physiological and morphological responses to light reduction. The magnitude and time required to initiate a response may depend on species, light intensity and duration, and its interactions with environmental conditions (e.g. temperature and nutrient availabilities). Increased nutrient availability in the environment can also lead to an increase in plant nutritional quality (e.g., increase in nitrogen content, decrease in C/N). This may result in increased feeding pressure by mega-herbivores such as dugongs and green turtles as ecosystems dominated by plants with high nutritional quality suffer higher grazing rates, which may ultimately result in lower levels of carbon accumulation in the system (Cebrian et al., 2009; Tomas et al., 2015).

Seagrass resilience the ability of seagrass meadows to withstand and recover from disturbances—depends on a range of factors, both natural and human-influenced. High nutrient pollution, particularly excess nitrogen from coastal runoff, is one of the most pressing threats, as it can lead to eutrophication, promote algal overgrowth, and reduce light availability for seagrass photosynthesis. However, the impact of this nutrient enrichment is not uniform; studies show that meadows with higher seagrass biomass and a rich variety of bottom-dwelling animals (macrofauna) tend to be more resistant to such stressors, likely due to enhanced nutrient cycling and sediment oxygenation (Gladstone-Gallagher et al., 2018). This suggests that healthy, diverse ecosystems are better equipped to handle stress. Interestingly, even in areas that have experienced long-term human disturbances, some seagrass populations have adapted over time, showing strong resilience despite having lower genetic diversity, likely due to the selection of tolerant genotypes (Connolly et al., 2018). Environmental timing also plays a role, as Soissons et al. (2016) demonstrated that seagrass meadows in temperate regions exhibit varying recovery rates depending on the season when disturbances occur, with resilience being lowest during peak growth phases. In subtropical systems like Florida Bay, resilience is compromised by climate-induced stressors (e.g., hypersalinity, hypoxia), which can trigger sulfide toxicity and widespread die-offs, especially in dense stands of climax species like *Thalassia testudinum*. These findings collectively emphasize that maintaining seagrass resilience requires preserving biomass and biodiversity, managing nutrient inputs, and minimizing disturbances during vulnerable growth phases.

Due to these and other impacts of anthropogenic disturbances on seagrass fitness and survival, the feeding behavior of dugongs, as the largest mega-herbivore feeding on seagrass, may also be affected. However, this impact is still poorly understood. This dissertation will reveal how anthropogenic impacts will affect the feeding behavior of dugongs and this is summarized in Fig.1.3. Seagrass and dugongs are inextricably linked, with dugongs relying entirely on seagrass for their survival. Unfortunately, human activities have had a devastating impact on both seagrass and dugongs. Human activities most affecting seagrasses are those that alter water quality or turbidity: nutrient and sediment loading from runoff and sewage disposal, dredging and filling, pollution, upland development, and certain fishing practices. We tested the impact of several factors on seagrass growth and biomass, i.e. sedimentation, oil spill, and fishing activity, to better understand the anthropogenic impact on link human-seagrass and mega-herbivores.

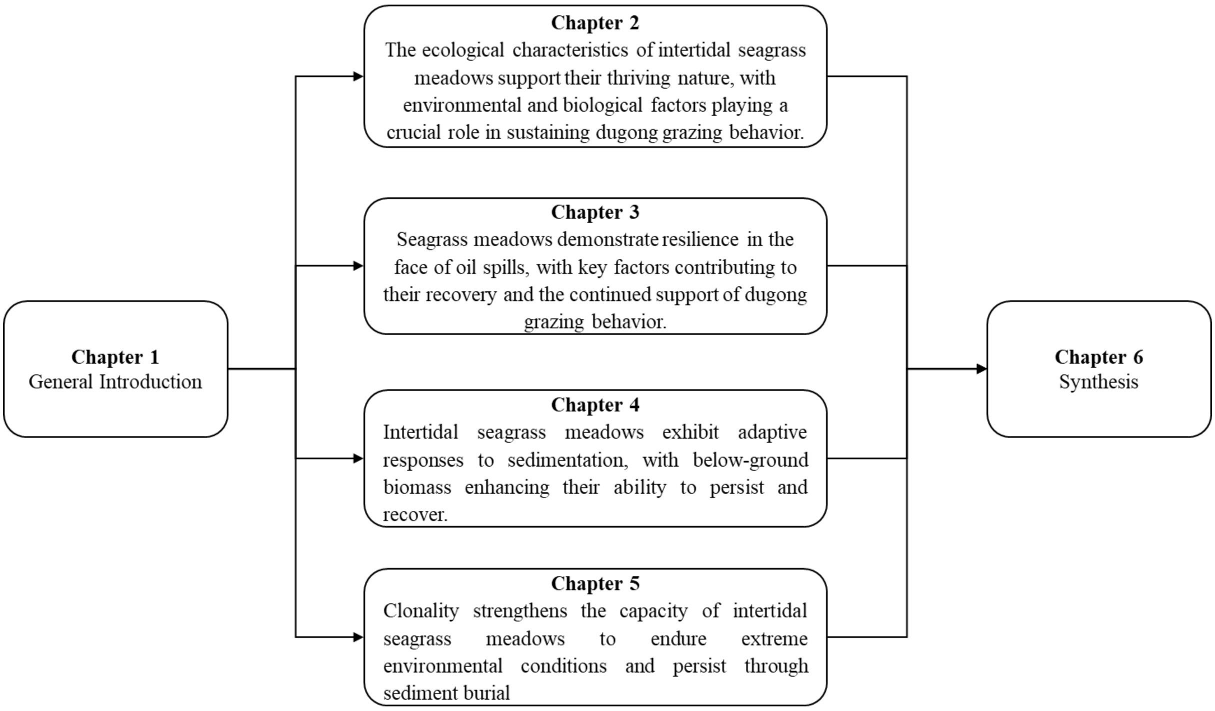

Fig 1.5. Model of interactions among anthropogenic disturbance and other factors in seagrass herbivore ecosystems

1.5 Research Aims and research questions

Research Aims

The main aims of the proposed research are i) to investigate which factors influence the dugong feeding frequency in space and time in intertidal seagrass meadows, ii) to analyze the impact of anthropogenic disturbances (oil pollution and sedimentation) on tropical intertidal seagrass meadows grazed by dugongs, iii) to analyze the resilience of tropical intertidal seagrass meadows that are grazed by dugongs after these impacts, and iv) to study the contribution of clonality as a strategy of intertidal seagrass meadows to cope with anthropogenic pressure (See Fig. 1.3 for a conceptual overview of the relationships among these aims).

Fig 1.4.
Map of the 7 selected field in Balikpapan bay with the specific seagrass (adapted according to De Bruijn, 2002)

Research questions

Based on the various knowledge gaps identified in this chapter, I defined the following research questions:

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)

1.6. Study area and site selection

The Bay of Balikpapan is situated on the East coast of Kalimantan, Indonesia (Fig. 1.4). Balikpapan Bay covers a surface of 16,000 ha which drains a watershed of approximately 195,000 ha, bordering a large rural/business region (De Iongh et al., 2007). The bay has several industrial ports with a massive oil refinery and excessive tanker site visitors. The upper water layers in Balikpapan Bay are saline (> 20 ‰), although it varies seasonally, and soft corals and some hard corals can be discovered deep in the bay (De Iongh et al., 2007). The sediment composition of Balikpapan Bay is known (De Bruijn, 2002). Most of the bay shores are covered by mud or a combination of mud and sand. Some parts consist of stones or coral. The seagrass meadows were assumed to be intertidal if the low tide was equal to or lower than 50 cm above ELWS (Extreme Low Water Spring Tide) of Balikpapan. Along the bay, there is a stretch of mangroves, which is linked to intertidal inshore seagrass meadows. Around 22 seagrass meadows have been discovered alongside the coastal line of Balikpapan Bay, mostly dominated by *Halodule pinifolia*, but also *Halophila ovalis, Halophila minor, Thalassia hemprichii ,* and *Enhalus acoroides* have been shown to occur (De Iongh 2005, 2006).

Based on a review of earlier studies/surveys on seagrass and dugong interactions, i.e. De Bruijn (2002); Cruz & van Esch (2005); Moraal and Souffreau. (2006); Bree (2008); Kreb (2008), seven seagrass meadows were investigated in Balikpapan Bay: Jenebora Kariangau, Pulau Kuangan, Pulau Balang, Petrosea, Beranga, and Tempadung. The position of these seven selected seagrass fields is shown in Fig 1.4.

An interesting coincidence is that the location of the study (Balikpapan Bay) is one of Indonesia's largest refineries and oil depots. During the study, there was an oil spill accident involving a tanker anchor that severed an undersea oil pipeline. This provided an ideal opportunity to study how seagrasses, particularly in intertidal areas, cope with this issue and survive the impacts of oil spills.

The studies in this thesis were therefore conducted in 2 stages. The first stage was conducted to collect data for the current ecological conditions (seagrass meadow surface, species composition, productivity, reproduction, strategy, sedimentation rate, and water quality) in intertidal seagrass meadows in Balikpapan Bay. The results of this study are presented in Chapter 2. In the second stage of this research, the impacts of anthropogenic disturbances (sedimentation and oil spills) on seagrass functioning and dugong grazing were evaluated (Chapters 3-5).

1.7. Thesis outline

This thesis describes the anthropogenic factors that might have an impact on seagrass-mega-herbivores interactions. The thesis is comprised of six chapters. **The present chapter** gives a general overview of the topic and presents the research aims methods, and steps used in the study. **Chapter 2** determines the factors (natural and anthropogenic activity) that influence the decision of mega-herbivoress to choose certain seagrass meadows to browse. In addition, this chapter also describes the food preferences of dugongs, the estimated population and ecological function of seagrass in the bay for Dugong. **Chapter 3** presents the resilience and recovery rate of seagrass meadows after exposure to oil spills. This chapter also shows the alleged extent and magnitude of oil spill concentrations and their effects on seagrass meadows. **Chapter 4** describes experiments on the effect of sedimentation on seagrass survival. This chapter describes the strategy of intertidal seagrass, in addition to adapting to extreme environments (desiccation, etc.), also facing burial levels and turbidity of waters. In **Chapter 5**, the potential of clonality as part of the survival strategy of intertidal seagrass is presented. This chapter also explains the factors that make it possible for seagrass to survive, including the possibility of energy transfer from one shoot to another in a clonal series. **Chapter 6** is the synthesis of the findings, and discusses appropriate strategies for seagrass-dugong conservation and management.

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