1

Introduction

With this thesis, I aim to contribute to a better conservation and restoration of seagrass systems worldwide, by improving our understanding of key processes in seagrass ecosystem dynamics. As an introduction, I will present seagrass as highly specialized elements in coastal and estuarine ecosystems, highlight their role as keystone species in these systems, discuss their present conservation status and identify some major knowledge gaps in their dynamics. This will constitute the background for a presentation of the outline of this thesis and a summary of the underlying research questions and hypotheses.

1.1 What is seagrass?

Seagrass species are highly specialized marine flowering plants with unique characteristics that allow them to live (exclusively) in estuarine or marine environments. These characteristics are: (1) underwater pollination with specialized pollen; (2) underwater production of seeds which can be dispersed by biotic and abiotic agents; (3) specialized leaves with a very reduced cuticle and an epidermis which lacks stomata and is the main photosynthetic tissue; (4) a rhizome or underground stem which is important in anchoring; (5) roots that can live in anoxic environments and are dependent on oxygen transport from the leaves and rhizome (Larkum *et al.*, 2006). As all other flowering plants, seagrass have above and below ground parts. Above ground tissues are organized as shoots, in which several leaves surround (and protect) the apical meristem. The leaves are the site of primary production through photosynthesis. The below-ground tissues are composed of rhizomes and roots. They provide anchoring for mechanical support, are responsible for (part of) the nutrient uptake, and constitute reserve tissues, especially in annual species in temperate climates which survive winter based on these reserves. Global distribution and abundance of seagrasses have changed over evolutionary time in response to sea-level change and physical modification of coastlines during nearly 100 million years, with the first Hydrocharitaceae occurring 90 million years ago, the first Cymodoceae occurring 80 million years ago, and the first Zosteraceae occurring 30 million years ago (Orth *et al.*, 2006). This evolutionary process is reflected in different morphological

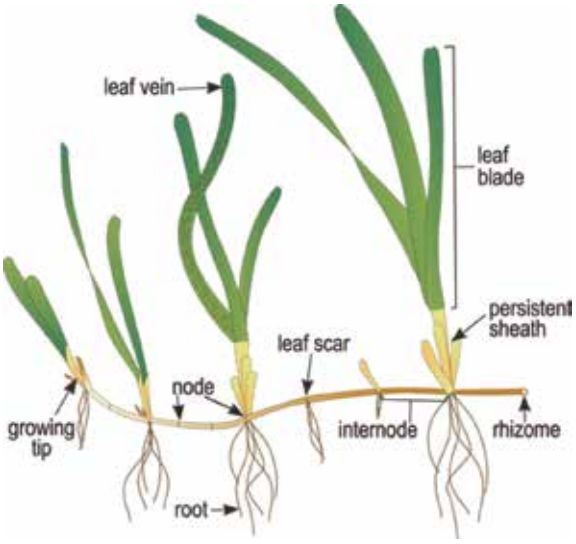

Figure 1.1
Illustration of the morphology of *Zostera carpensis* (Marine Eelgrass), showing different part of seagrass above and below ground (pictures taken from ian. Umces.edu)

adaptations to the environment, e.g. in leaves and roots, but also in reproductive organs (Figure 1.1). The high diversity of the latter suggests that seagrass did not evolve from a common ancestor and that parallel evolution lines have taken place in different geological periods (Les *et al.*, 1997; Waycott *et al.*, 2006)

1.2 Seagrass ecosystem services and functions

Seagrasses are distributed across the globe, but unlike other taxonomic groups with worldwide distribution, they exhibit low taxonomic diversity (approximately 60 species worldwide, compared with approximately 250,000 terrestrial angiosperms; Den Hartog, 1970).

Seagrass provide important ecosystem services in the marine environment, such as: provision of physical structure enhancing and sustaining the biodiversity for other marine species, as well as the provision of nursery functions for fish (Suchanek *et al.*, 1985; Tanner, 2003; Borg *et al.*, 2005; Mills and Berkenbusch 2009), contribution to coastal protection (Pergent-Martini *et al.*, 2006; Koch *et al.*, 2009; Christianen *et al.*, 2013), accumulation of nutrients (Gacia *et al.*, 2002; Apostolaki *et al.*, 2012) and sequestration of carbon (Suzuki *et al.*, 2003; Duarte *et al.*, 2005; Apostolaki *et al.*, 2011; Fourqurean *et al.*, 2012). Seagrasses are known to produce large quantities of organic carbon (De Iongh *et al.*, 1995) and are an important food source for mega herbivores such as dugongs (*Dugong dugon)*, green turtles (*Chelonia mydas*) and manatees (*Trichecus manatus*) (Orth *et al.*, 2006).

Seagrasses require some of the highest light levels of any aquatic and marine plant group, in order to provide oxygen to their roots and rhizomes (since they often grow in highly reducing sediments with toxic sulfide levels), and to support large amounts of nonphotosynthetic tissue (Terrados *et al.*, 1999). These high light requirements imply that seagrasses mainly occur in very clear water and at places with high solar fluxes; further away from the equator they must live in more shallow water, thus exposing them more to frost, which is a source of stress. In spite of their low species diversity and their particular physiological properties, seagrasses have been very successful in dispersing widely during their evolution in all but the most polar seas (Figure 1.2). Some seagrasses thrive in temperate climates and survive severe winters (Orth *et al.*, 2006) by shedding their leaves in autumn and surviving as below-ground tissue or by annual regeneration from seeds.

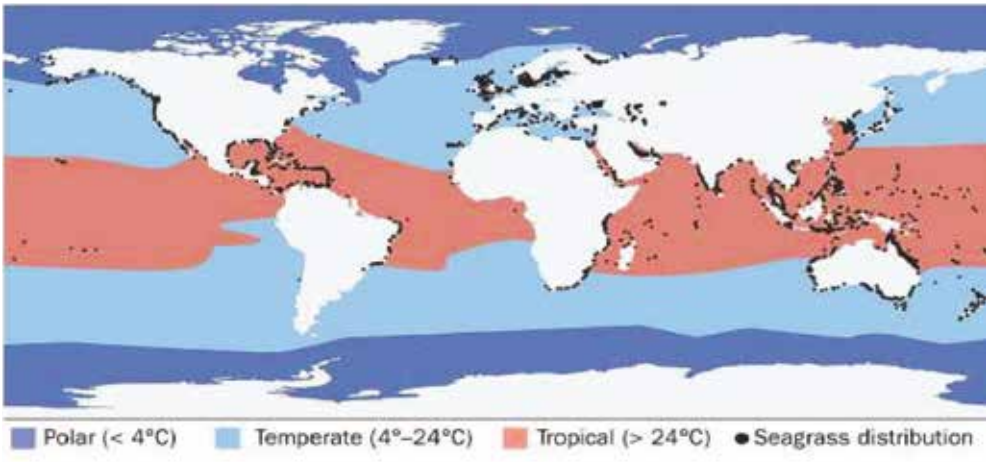

Figure 1.2
Distribution of seagrass projected on a map of mean ocean temperature; polar (< 4 degree Celcius [°C]), temperate (4°C- 24°C), and tropical (>24°C) climate (Green and Short, 2003)

The Indo-Pacific region is the centre of seagrass diversity. Primary productivity of seagrass is found to be highest in the Indo-Pacific including the Indonesian coastal zone (Hemminga & Duarte, 2000). Within this area, seagrass beds provide a high economic value. In East Bintan, Riau, Indonesia, seagrass has contributed to a net income of USD 3,5 million (or USD 2,287 ha^{-1}) per year by 2010, this comes from use values (fisheries, aquarium trade, bioprospecting, biological support, coastal protection and oxygen production) and non-use values of seagrass meadows (biodiversity, species richness), higher than tourism and fisheries in the same location that contributed USD 2,4 million per year (Dirhamsyah, 2007). The Total Economic Value (TEV) estimates made under a "deforestation" scenario over 30 years (from 2000-2030), prepared for the TEV of Indonesian coasts and oceans, by using a dynamic simulation model, indicated that seagrass meadows had a potential TEV of USD 7 billion (Van Beukering, Cesar & Janssen, 2003).

1.3 Global seagrass current condition

Despite their important ecosystem services, seagrass systems have undergone significant losses over the last 20 years. Seagrass has become a priority subject for conservation efforts in international (e.g. Rio Convention, EU's Habitats Directive) and national frameworks (Green & Short, 2003). It is estimated that seagrass loss from direct and indirect anthropological impacts amounts to 33,000

km^2 or 18% of the documented seagrass area (Duarte *et al.*, 2004). Data from UMCES (2009) indicate that 58% of the world seagrass population is currently decreasing In quantity and quality. Several factors contribute to seagrass decline. An important factor is extensive nutrient input in coastal ecosystems, which induces eutrophication (Van Katwijk *et al.*, 2007; Koch & Erskine 2001; Van der Heide *et al.*, 2008), significant animal disturbance (Valentine & Heck, 1991; De Iongh *et al.*, 1998; Preen & Marsh, 1995; Christianen *et al.*, 2012), and light attenuation due to increased turbidity by suspended sediments (Orth *et al.*, 2006; Van der Heide *et al.*, 2007).

Seagrass losses occur globally. Examples can be found in Adelaide metropolitan coastline, South Australia (Westphalen *et al.*, 2004), Florida Bay, United States (Hall *et al.*, 1999), Japan (Nakamura, 2009), Bermuda Island (Murdoch *et al.*, 2007), Thailand and Vietnam Region (UNEP, 2004). Based on UNEP (2004), seagrass loss in Indonesia is estimated at 30-40% over a period of 10 years. Banten Bay, Jakarta has lost about 26% of its seagrass meadows, caused by human interventions through the development of port and industrial estates. Seagrass has also significantly declined in the Derawan archipelago, East Kalimantan, caused directly or indirectly by human interventions. This leads to secondary negative effects on meso and macro grazers (De Iongh *et al.*, 1995; Supriadi & Kuriandewa, 2008; Christianen *et al.*, 2012).

Seagrass loss has been used as a biological indicator to detect changes in the marine environment. For example, large seagrass losses in Cockburn Sound, Australia in the 1990s were used as an indicator of increasing nutrient inputs. Due to sustained nutrient inputs, seagrass biomass has remained low in that area today (Walker *et al.*, 2006). Large seagrass losses in Chesapeake Bay, United States, have been used as an indicator for water quality in relation to extensive nutrient and sediment inputs (Orth *et al.*, 2002).

1.4 Seagrass interactions

Seagrasses form the keystone species of complex ecosystems with multiple interactions. For the seagrass itself, both bottom-up regulation by nutrients, and top-down regulation by herbivory, are the most important biotic interactions. In addition, important interactions exist with abiotic factors, notably hydrodynamics and nutrient dynamic (Figure 1.3).

1.4.1 Interaction with herbivores

Herbivores form one of the dominant biotic factors which have a significant impact on seagrass (Hemminga & Duarte, 2000: De Iongh *et al.*, 1995). In its inter-

action with herbivores, seagrass provides food and shelter to marine organisms and thus contributes directly to the marine food web. Vice versa, herbivores also influence seagrass, in the first place by grazing (removal of biomass) but also indirectly by burrowing and digging. Green Turtles (*Chelonia mydas*) in East Kalimantan, Indonesia (Christianen *et al.*, 2012) and dugongs (*Dugong dugon)* in tropical seagrass beds in the Moluccas or East Kalimantan, Indonesia (Thayer, 1984; De Iongh *et al.*, 1998) created patches in seagrass meadows that were expected to change interactions between hydrodynamics and seagrass (see below). In addition, dugongs are known to dig holes (and create gaps) in seagrass beds in search of macro invertebrates (Anderson, 1986).

Another ecological process having an impact on seagrass meadows is bioturbation of the substrate, due to burrowing or grazing by other (macro) fauna (Maire *et al.*, 2008; Sandwell *et al.*, 2009). Bioturbation is caused by a.o. echinoids (*Lytechinus variegates*) in the northern Gulf of Mexico (Valentine & Heck, 1991) and by *Diadema antillarum* in the Caribbean Sea (Ogden, 1973). Bioturbation can increase the diffusional and advective exchange of nutrients between the porewater and the overlying water column (Wild *et al.*, 2005; Volkenborn *et al.*, 2007).

1.4.2 Interaction with hydrodynamic

Abiotic factors like the hydrodynamics of currents and waves, can increase sediment and nutrient fluxes within seagrass meadows (Koch, 1999; Hendriks, 2008; Vonk, 2008). These same factors can also severely disturb seagrass meadows by creating gaps or widening existing gaps or even swiping away entire seagrass beds under strong wave and current action (Marsh *et al.*, 1984). Seagrass does not only passively undergo hydrodynamic forcing, but by its presence also influences the spatial pattern of flows and wave intensity. This can be expressed as an increase in bottom roughness. The resulting increase in Turbulent Kinetic Energy (TKE) will reduce the thickness of the Diffusive Boundary Layer (DBL) and hence intensify the supply of dissolved gasses which may result in an increase of the photosynthesis process (Fonseca & Kenworthy, 1987) and/or may also alter the nutrient uptake rates (Thomas *et al.*, 2000; Morris *et al.*, 2008). However, in its interaction with hydrodynamic processes, seagrass meadows also reduce the mean flow speed and flow discharge within the vegetation (Gambi *et al.*, 1990; Velasco *et al.*, 2003; Fonseca & Koehl, 2006), leading to a reduced renewal of the water in the canopy and, potentially, an increase in limitation by nutrients and gasses.

During its interaction with hydrodynamics, referring to one of the seagrass ecosystem functions, seagrass also requires to provide sediment stability through entrapment of sediment and it reduces erosion compared to unvegetated sea-

grass (De Falco, 2000; Hendriks *et al.*, 2007; Christiansen *et al.*, 2013). This ecosystem function of seagrass is related to the seagrass ability to reduce hydrodynamic energy caused by waves and currents as explained earlier. Direct impact of this seagrass function is increasing light availability and reduced turbidity (Van der Heide *et al.*, 2007).

1.4.3 Interaction with nutrient

Nutrients are important for seagrass to maintain high productivity (Erftemeijer & Herman, 1994; Stapel *et al.*, 1996). Nutrient input into a seagrass meadow can be obtained from nutrient fixation, trapping and mineralization of senescing leaves and other particulate organic matter (McRoy & Goering, 1974; Perez-Llorens *et al.*, 1993; Romero *et al.*, 2006). The water column and sediment porewater are other nutrient sources for seagrass meadows. Nutrient concentration in the water column is usually lower than in porewater inside the sediment (Romero *et al.*, 2006: Erftemeijer & Middelburg, 1995). This is especially the case in offshore subtidal tropical seagrass beds. Therefore, seagrass in these offshore meadows mainly depend on nutrient uptake by the root (Stapel *et al.*, 1996). Inshore intertidal seagrass meadows are often characterized by both high nutrient concentrations in the water column and in porewater, therefore nutrient uptake in these meadows may both take place through the roots and through the leaves (Stapel *et al.*, 1996).

Nutrient exchange between porewater inside the sediment and the water column or vice versa is an important mechanism for the nutrient balance of the porewater. Nutrient exchange can be dominated by diffusion processes, especially in fine sediments. However, in permeable sediments advective exchange between porewater and the overlying water column can prevail in importance over diffusional exchange. Advective porewater exchange can be driven by wave propagation that induces oscillatory pressure gradients at the sediment surface (Webb & Theodor, 1972; Shum, 1992; Prech & Huettel, 2004) or by bottom currents, including pressure gradients due to interactions with seabed topography (Huettel & Webster, 2001). According to Santos *et al.* (2002), there are at least twelve mechanisms that drive porewater exchange 1) terrestrial hydraulic gradients, 2) seasonal changes in the aquifer level on land moving the location of the subterranean estuary, 3) wave setup and tidal pumping, 4) water level differences, 5) flow induced pressure gradients, 6) wave pumping, 7) ripple and other bed form migration, 8) fluid shear, 9) convection induced by density, 10) bioirrigation, 11) gas bubble upwelling and 12) sediment compaction.

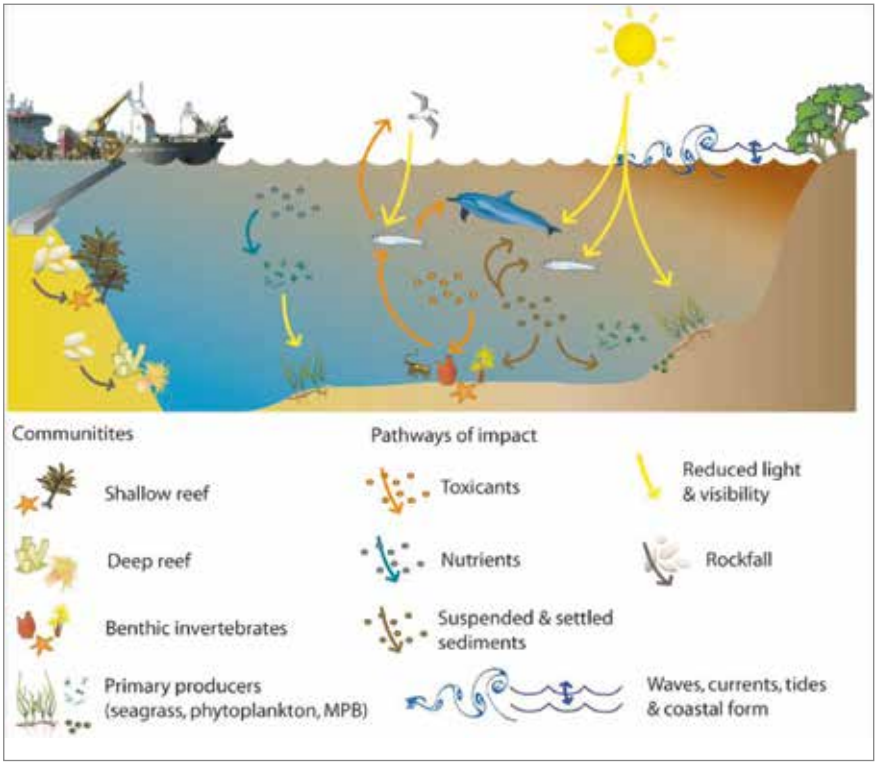

Figure 1.3
Illustration of seagrass interaction with biotic and abiotic factors. Seagrass interaction induces different impact (e. g.: sedimentation, nutrient exchange, turbulence) to seagrass ecosystem (picture taken from publicwiki.deltares.nl)

1.5 Gap dynamics

Seagrass directly interacts with biotic and abiotic factors and this can significantly impact seagrass growth. In particular, interaction caused by both biotic and abiotic effects, may disrupt the homogeneous structure of meadows and give rise to holes in the meadow, or in more extreme cases to a patchy structure of the meadow. Strong monsoon winds and waves are known to create gaps in intertidal seagrass meadows (De Iongh, 1996; Marsh *et al.*, 1984). In some locations, seagrass interactions with (mega- and meso-) herbivores in combination with wave action and currents can create a "halo" or an unvegetated area/gap within the seagrass meadow (De Iongh *et al.*, 1995; De Iongh *et al.*, 2007). This patchy structure is expected to have a different interaction with the hydrodynamics, because the influence of seagrass on flow and waves will vary spatially. Flow acceleration around patches may produce local erosion and cause stress for seagrass

growth (Bouma *et al.*, 2009, Van der Heide *et al.*, 2010), but may also affect the fate of seeds and pollen involved in seagrass spreading (Koch *et al.*, 2006). Mosaics of unvegetated 'halos' within a seagrass meadow may increase turbulence and reduce sediment and particulate nutrient deposition, thereby inhibiting clonal prolongation into the gaps (Randall, 1965; Ogden & Zieman, 1977; McAfee & Morgan, 1996).

In addition to questions about flow and sediment dynamics, gap dynamics give rise to questions about nutrient exchange in seagrass meadows. Diffusive and advective porewater exchange processes have rarely been studied in seagrass meadows. The available studies tend to focus on experiments without seagrass presence and with a single driving mechanism (Precht & Huettel, 2003; Miyajima *et al.*, 2007).

1.6 Outline of this thesis

Optimizing seagrass conservation requires solid scientific knowledge about the main processes determining seagrass health. The overall aim of my study is to explore and analyze the mechanisms of biophysical feedback that affect the stability of a seagrass bed upon fragmentation. In other words, if current, turbulence, sediment-water exchange, water-plant exchange (of CO_2 and nutrients) are all changed by the fragmentation, will this tend to promote filling of the gaps with vegetation (i.e. return to closed bed, a negative feedback), or will it give rise to a runaway reaction (further fragmentation of the bed, ultimately leading to disappearance – this is a positive feedback, a self-reinforcing reaction). My main research questions are developed to approach this overall theme from different angles: i) How do heterogeneous patches in the seagrass bed interact with the hydrodynamic force? ii) How do the different seagrass properties (density, leaf length) and gap sizes influence flow development inside the gap? iii) How is the advective porewater exchange influenced by the presence of seagrass? and iv) How do the different hydrodynamic factors (diffusion, flow, wave and flow induced by wave) influence porewater exchange from sediment to water column?
I addressed these research questions by focusing on the biophysical feedback loop between hydrodynamics and seagrasses, as this can have an overriding impact on seagrass functioning. This biophysical feedback loop is known to have a significant influence *both* on sediment trapping and on sediment stability within a meadow. For bare sediments, it may affect seston (here defined as phytodetritus and other particulate organic matter) and the exchange between the water column and sediment porewater (Erftemeijer & Middelburg, 1995). To obtain answers to the research questions of my study, I developed four experimental approaches to investigate the interaction of seagrass with different hydrodynamic

processes. Better knowledge of this interaction may be useful for environmental managers involved in the conservation and management of coastal ecosystems and seagrass meadows.

In ***chapter 2,*** I investigate how hydrodynamics (e.g. volumetric flow rate through and over the canopy, turbulence, Reynolds stresses and solute fluxes) within homogeneous patches of seagrass depend on both the nature of the patches themselves ('patch scale' characteristics) and the nature of variations in seagrass density in their immediate neighbourhood ('meadow-scale' characteristics). I compared the four different spatial configurations of a set of four homogeneous patches of plant mimics (two patches of a higher shoot density, and two of a lower shoot density). These spatial configurations represent, in a schematic way, vegetation heterogeneity as it may occur in natural seagrass meadows. We hypothesize that spatial patterns in shoot density at the meadow scale are no more or less important than shoot density values at the patch scale, in determining hydrodynamics within and above the canopy.

In ***chapter 3***, I suggest that most studies of seagrass hydrodynamics have focused on homogeneous meadows (e.g. Fonseca, 1982; Gambi *et al.*, 1990; Abdelrhman, 2007). Gaps are important as transitional zones between patches and within meadows for flow development. Alteration of hydrodynamically-mediated sediment and nutrient fluxes between the water column and substrate in gaps may affect nutrient uptake by roots and rhizomes and therefore seagrass growth which leads to gap closure. Gaps may also entrap seeds and pollen via hydrodynamic processes, and thereby further affect growth and gap colonization by seagrass. Therefore, studying the hydrodynamics of gaps within seagrass meadows is important. In this chapter I investigate what determines gap hydrodynamics, its structure and implications. Most importantly, the effect of the shoot density of the surrounding meadow, and the seagrass length-water height ratio on flow regimes within gaps has not been considered in previous work.

In ***chapter 4,*** I explore models of flow adjustments at the upstream end of vegetation(-mimic) canopies (Folkard 2005; Tanino & Nepf, 2008; Chen *et al.*, 2013). The general pattern observed in these experiments is that, on encountering such a canopy, the flow adjusts to the canopy's presence such that a part of it is deflected upwards and travels at accelerated speeds over the top of the canopy, and another part travels at decelerated speeds through the canopy. However, there is also a third possible flow path – just as the flow can be deflected over the canopy, it can also be deflected beneath it, into the permeable substrate. This mechanism is analogous to the enhancement of infiltration by pressure gradients around seabed topography discussed by Huettel *et al.* (1998) and would cause changes in the pore water exchange rate: we would expect enhanced infiltration from the open water into the substrate while the in-canopy flow decelerates as a result of the presence of the canopy.

In ***chapter 5***, I explore nutrient exchange between sediment and water column. It was recently discovered that dissolved organic nitrogen is relatively abundant and not refractory in coastal waters, even in oligotrophic systems (Bronk *et al.*, 2007). Moreover, it was discovered that seagrasses can rapidly consume this dissolved organic nitrogen, particularly via their roots (van Engeland *et al.*, 2011, 2013), thus providing a competitive advantage over other primary producers (Vonk *et al.*, 2008). In permeable, sandy sediment, DON (Dissolved Organic Nitrogen) and POM (Particulate Organic Matter) could be transported due to pressure differences that induce porewater flow (Huettel & Webster, 2001). Surface gravity waves may also influence porewater exchange by causing oscillating flow near the seabed–water interface (Huettel & Webster, 2001). Studies of such porewater exchange have been carried out in unvegetated contexts. It would be useful to know under which hydrodynamic conditions such exchange processes may occur within seagrass meadows, and how this depends on meadow properties such as, for example, seagrass density.

Finally, in ***chapter 6***, I provide a synthesis, conclusions and recommendations, based on 4 experimental approaches carried out in a race track flume experiment at NIOZ, Yerseke.

This dissertation was designed to get more insight in the hydrodynamic interactions within fragmented seagrass meadows, simulating natural conditions. My research focus has been on the understanding of the consequences of gap formation in seagrass meadows. In the discussion, I address the question of stability of seagrass meadows subjected to gap forming processes. Since gap formation affects the biophysical interaction between seagrass and hydrodynamics, as well as vital functions such as the provision of nutrients, the effect of gaps on seagrass growth, and on the potential of meadows to recover from gap formation, is vital to predict the fate of seagrass meadows after disturbance. This knowledge should be taken into account when conserving and managing seagrass ecosystems.

The research questions and hypotheses of my research are summarized in Table 1.1. I will use this table to discuss the outcomes of the research in chapter 6.

Table 1.1
Overview of questions and hypotheses underlying the research in this thesis.

Questions	Hypothesis	Chapter
How do heterogeneous seagrass patches interact with hydrodynamic forces?	We hypothesize that spatial patterns in shoot density at the meadow scale are no more or less important than shoot density values at the patch scale, in determining hydrodynamics within and above the canopy.	2
How do the different seagrass properties (density, leaf length) and gap size influence hydrodynamic flow development inside gap?	We hypothesize that reducing the water depth relative to the canopy height will increase the overflow speed and thus shear at the top of the canopy, thereby encouraging the formation of a recirculation cell within the gap and enhancing the intrusion into the gap of the flow over the upstream canopy.	3
How does advective porewater exchange occur from the water column to sediment, influenced by the presence of seagrass?	We hypothesize that flow be deflected beneath seagrass, into the permeable substrate. This mechanism enhances infiltration by pressure gradients and causes changes in the pore water exchange rate, enhanced infiltration from the open water into the substrate while the in-canopy flow decelerates as a result of the presence of the canopy.	4
How do different hydrodynamic factors (diffusion, flow, wave and flow induced by wave) influence porewater exchange from the sediment to the water column?	We hypothesize that porewater exchange decreases with *i)* decreasing current velocity, *ii)* reducing wave energy and *iii)* increasing vegetation density.	5

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