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Synthesis

6.1 General background

My PhD research was based on experiments using seagrass mimics simulating *Possidonia oceanica* and *Thallasia testudinum* in controlled environments, which were conducted in a race track flume at the Nederlands Instituut voor Onderzoek ter Zee (NIOZ), in Yerseke, The Netherlands. The experiments explored the effects of a variety of different seagrass properties (patch and gap size, leaf length, number of leaves and density of shoots) and hydrodynamic forcings (currents and waves) that determined the values of important hydrodynamic parameters (flow speed, turbulence intensity, turbulent kinetic energy, Reynolds stresses), and provided new understanding of mechanisms of biophysical feedback that

affect the stability of seagrass beds upon fragmentation. The fundamental aim of this work was to contribute to understanding of the biophysical mechanisms that drive seagrass meadows to become increasingly fragmented and eventually disappear or to re-homogenize and recover after fragmentation.

The experiments simulated heterogeneous patches (**chapter 2**), seagrass meadows interrupted by the presence of circular gap (unvegetated area) (**chapter 3**) and homogeneous patches (**chapters 4 and 5**). These different forms of fragmented seagrass distributions were exposed to different hydrodynamic conditions (currents of different speeds, and waves) (**chapters 2, 3, 4 and 5**). Through analyses of these experiments, my thesis offers new insights into interactions between hydrodynamics and fragmented seagrass meadows. Two major effects are investigated in particular: i) hydrodynamic development within and around fragmented seagrass (**chapter 2 and 3**) ii) advective solute exchange from the water column to porewater or vice versa (**chapter 4 and 5**).

6.2 What are the effects of fragmentation on seagrass?

6.2.1 Fragmented seagrass-hydrodynamic interaction

Most of the seagrass meadows are fragmented under natural conditions as a result of seagrass-hydrodynamic interactions (Fonseca & Fisher, 1986) such as strong wave action or strong tidal currents (Fonseca & Bell, 1998; Bell et al., 2006), bioturbation due to faunal burrowing (Valentine *et al.*, 1994), grazing by different fauna echinoids *Lytechinus variegates* (Valentine & Heck, 1991), grazing by *Diadema antillarum* (Ogden, 1973) or by mega herbivores such as the Green turtle *Chelonia mydas* (Christianen *et al.*, 2012) and the dugong *Dugong dugon* (De Iongh *et al.*, 1998). Fragmentation can also be caused by human interventions such as propeller scarring, vessel grounding and digging for benthic animals (Townsend & Fonseca, 1998; Hovel & Regan, 2007). The importance of a better understanding of the hydrodynamic interaction of fragmented seagrass beds because it can be used as parameter to detect and predict local erosion that may occur around seagrass beds (Bouma *et al.*, 2009) and thereby by early detection possibly prevent damage to roots and rhizomes (negative impacts) of seagrass. However, it is suggested that seagrass fragmentation is also expected to increase turbulent intensity and may also result in an increase of the exchange of nutrients and dissolved gas which is required for seagrass photosynthesis process (positive impacts).

However, there is limited information about how fragmented seagrass will behave under different hydrodynamic conditions. To address this gap in knowledge, I started a race track Flume experiment in the Nederlands Instituut voor

Onderzoek ter Zee (NIOZ), in Yerseke- in which I simulated three different seagrass patches: i) heterogeneous patches, large seagrass patches consisting of four smaller patches with different densities (**chapter2**); ii) fragmented seagrass, with the presence of circular gaps, within the seagrass meadow (**chapter 3**); iii) homogeneous patches, consisting of no smaller patches, set up with 2 different densities (**chapter 4 and 5**).

The results of these studies show that, in controlled environments which exclude the effects of factors other than the hydrodynamic conditions, seagrass meadows have the ability to restore and re-homogenize themselves. A variety of hydrodynamic parameters, most prominently turbulent kinetic energy (TKE, $mm^2\ s^{-2}$), flow discharge (Q, $mm^3\ s^{-1}$) and unit discharge (q, $mm\ s^{-1}$) were analysed to see how the hydrodynamic fields developed in the presence of seagrass. The turbulence was found to be altered in the upstream part of seagrass patches (chapter 4) and in the downstream part of seagrass patches in heterogeneous arrangements (chapter 2). In both cases, it was found that different seagrass densities and leaf lengths were dominant factors in determining the level of flow intrusion into seagrass meadows and the level of turbulence in the flows around them. Lower seagrass density reduced seagrass resistance and produced less turbulence within the meadow. But this was not the case for fragmented seagrass meadows (chapter 5). In the presence of a gap within a meadow, the gap aspect ratio (GAR), i.e. the ratio of leaf length to horizontal gap extent, determined the hydrodynamic development. I found that reduced water depth creates more shear stress at the top of canopies and thus increases the level of turbulence inside the gaps. Moreover, the results indicated that longer, shallower gaps with low GAR values (less than ≈0.3, see chapter 3), were significantly more affected by intrusion of the overflow than shorter, deeper gaps in canopies, where the within-gap flow is almost purely derived from flow coming through the upstream canopy (Figure 6.1).

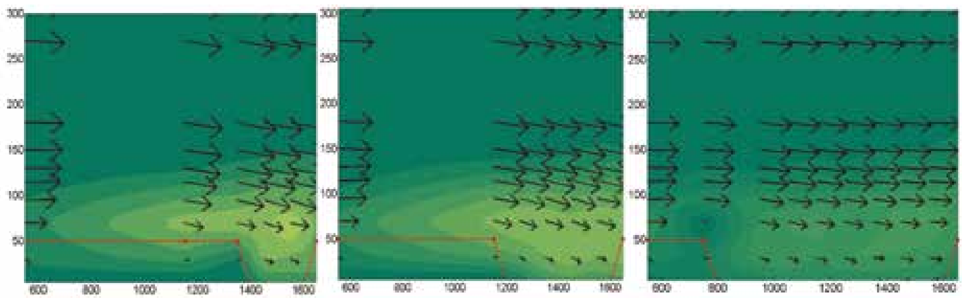

Figure 6.1
Flow development inside a gap within a simulated framented seagrass meadow. Turbulence reaches its maximum intensity within the gap, but decreases with increasing gap size (see chapter 3).

In homogeneous seagrass, unidirectional water flow is smoothly deflected over the top of the seagrass canopy as "skimming flow" (Nowell & Jumars, 1984; Fonseca & Kenworthy, 1987), effectively trapping a layer of water within the canopy (Koch & Gust, 1999), i.e. increasing the residence time. In contrast, a reduction in shoot density leads to increased flow intrusion and velocity within the canopy (Van Keulen, 1997) but in fragmented seagrass, uni-directional flow will be shifted based on spatial pattern arrangement within the seagrass meadow (chapter 2). When unvegetated seagrass is present within the meadow, unidirectional flow can accelerate the influx of water into the canopy (Granata *et al.*, 2001), replenishing nutrients, introducing spores and propagules, eroding sediment and increasing mixing in general. Understanding the interaction of fragmented seagrass-hydrodynamics provides insight in how nutrient and dissolved gas exchange from porewater and water column or vice versa.

6.2.2 Fragmented seagrass-porewater exchange interaction

Porewater exchange is an important mechanism to transfer nutrients or dissolved gas to seagrasses through roots, rhizomes or leaves to conduct photosynthesis. Porewater exchange can be driven by different physical forces, such as 1) wave setup and tidal pumping, 2) flow- and topography – induced pressure gradients, 3) wave pumping, 4) ripple and other bed form migration, 5) fluid shear, 6) bio-irrigation, 7) sediment compaction (Santos et al., 2012). These physical forces induce porewater exchange through the sediment-water interface. Seagrass meadows use porewater exchange to obtain nutrients for the uptake by roots, rhizomes and leaves (Erftemeijer, 1993; Stapel, 1997; Evrad *et al.*, 2005; Barron *et al.*, 2006; Vonk *et al.*, 2008). Stapel (1997) showed that the leaves of *Thalassia hemprichii* in a laboratory experiment showed a clear capacity for ammonium and phosphate uptake. Other studies have focused on porewater exchange in an unvegetated context (Shum, 1992; Huettel & Rusch, 2000; Huettel & Webster, 2001). Offshore subtidal seagrass meadows are often characterized by low nutrient levels in the water column and higher nutrient levels in sediment porewater, while inshore intertidal seagrass meadows are often characterized by both high nutrient concentrations in the water column and in sediment porewater, therefore nutrient uptake in these meadows may both take place through the roots and through the leaves (Stapel *et al.*, 1996).

The work reported here simulated porewater exchange in the presence of a fragmented seagrass meadow. As explained earlier, fragmented seagrass affects the hydrodynamics of the flow around it in a way that is different to that due to homogeneous seagrass. The most relevant effect is the pressure gradient created by flow deceleration at canopy/gap edges (chapter 4). Here, the flow hits the upstream end of a section of seagrass and a horizontal gradient in vertical pressure is set up due to the flow deceleration caused by the seagrass canopy, which forces solute-bearing water into the substrate (Figure 6.2). In my study, this effect persisted over a horizontal distance of ~0.5-1 m into the canopy. This finding has important ecological implications, as it implies favorable nutrient conditions for clonal expansion at the edges of seagrass patches, which can increase the seagrass growth rate and thus facilitate patch and meadow expansion.

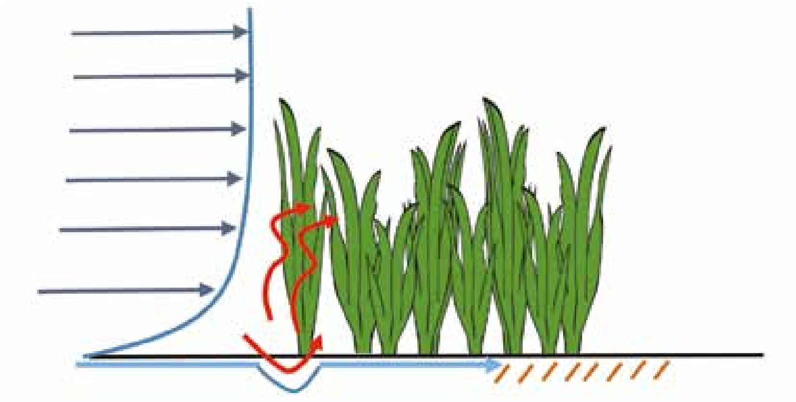

Figure 6.2
Porewater exchange caused by the pressure gradient created by flow deceleration at the upstream end of a seagrass patch. The leading edge of the meadow is the location of maximum solute intrusion into the sediment (see chapter 4).

6.3 Battle of the millennium: seagrass vs carbondioxide

Carbondioxide (CO2) in our atmosphere may reach the level of 450 parts per million and threatens our global ecosystem and associated (human) life (UN IPCC, 2014). Increasing CO2 may increase the risk of climate variability, extreme drought, frequency of typhoons, and as a result may enhance famine and worldwide species extinctions, if the average annual temperature will rise with two degrees celcius (Macreadie, 2014). Seagrass ecosystems can sequestrate carbon 35 times faster compared to tropical rainforest ecosystems (Macreadie, 2014) and therefore seagrass ecosystems can play an important role in this "battle of millennium".

This recognition has led to large-scale attention on mitigation strategies to reduce the impact of increasing concentrations of carbon dioxide. As ~30% of the CO2 emissions are absorbed into the world's marine waters, one such strategy is Carbon Capture and Storage (CCS) (Russell *et al.*, 2013) in oceans, although productivity in marine ecosystems also faces pressures from global warming, oxygen loss and concomitant ocean acidification (Connell & Russell, 2010; Rodolfo-Metalpa *et al.*, 2011). Recent research has highlighted the valuable role that coastal and marine ecosystems play in sequestering carbon dioxide as seagrass meadows rank amongst the most productive ecosystems on earth (Duarte *et al.*, 2010; Duarte *et al.*, 2013).

The carbon (C) sequestered in vegetated coastal ecosystems, specifically mangrove forests, seagrass beds, and salt marshes, has been termed "blue carbon" (McLeod *et al.*, 2011). Seagrass beds also strongly support carbon sequestration through their capacity to trap particles from the water column and enhance sediment deposition and retention leading to high rates of carbon burial in seagrass sediments (Duarte *et al.*, 2013). Recent synthesis of available results evaluates the capacity of seagrass to capture CO2 through metabolic processes and by stripping suspended particles off the flow at an average of 586–681 g CO2 m-2 year-1 (Duarte *et al.*, 2010; Duarte *et al.*, 2013). Seagrass ecosystems, through the process of photosynthesis, simply capture and store carbon, this process is called biosequestration. Seagrass ecosystems reduce the CO2 levels in the atmosphere, by biosequestration. This process is economically viable since it has been estimated that globally seagrass can capture CO2 worth USD 45 billion with the current carbon price of USD 23 per tonne. Seagrasses can no longer be seen as humble plants that only decorate the marine ecosystem but should be considered to be an important global vegetation that contributes to mitigate the impact of climate change. These results show that seagrasses have a major potential for future "blue carbon" storage and can contribute to the efficacy of other CCS strategies. This potential may, however, be constrained by anthropogenic stressors resulting in seagrass fragmentation. My research has contributed to a better understanding of the impact of fragmentation and gap dynamics of a seagrass bed on the biophysical feedback that affects the stability of a seagrass bed upon fragmentation.

6.4 Conclusions

I draw the following conclusions from my PhD research:

- Seagrass meadows with heterogeneous spatial densities have the tendency to become more homogenous because flow deflection from the higher density parts of the meadow carry dissolved nutrients and gases to the lower density parts. However, a wide range of other factors may also play a role in determining whether heterogeneous patches become more or less homogeneous, such as nutrient cycling from sediment into the water column or vice versa, deposition of organic matter, erosion by waves or tidal currents, or animal grazing.

- There is a transitional zone between unvegetated areas and seagrass meadows that provides a space for turbulent development and increased mixing intensity.
- Exchange from the water column to the sediment porewater or vice versa in the presence of fragmented seagrass is governed mostly by pressure gradients due to the deceleration and acceleration caused by hydrodynamic interactions with the seagrass meadow.

Table 6.1
Overview of questions and answers underlying the research in this thesis.

Questions	Answers	Chapter
How do heterogeneous seagrass patches interact with hydrodynamics?	We found that at least for the specific patch properties and meadow-scale patch arrangements studied in these experiments, spatial distribution of shoot density at the meadow-scale is more important in determining hydrodynamic interactions within seagrass patches than the patch-scale shoot density.	**2**
How do the different seagrass properties (density, leaf length) and gap size influence hydrodynamic flow development inside the gap?	We found that Gap Aspect Ratio (GAR) value determine a threshold value for the intrusion of overflow into the gap. Intrusion occurred when within-gap turbulence levels are relatively low and intrusion is enhanced by increased pronation of the downstream canopy when GAR is greater than the threshold value, where the opposite tendencies prevail.	**3**
How does advective porewater exchange occur from the water column to the sediment, influenced by the presence of seagrass?	We found that the pressure gradient caused by flow deceleration at the patch edge was the main factor affecting this exchange process – as well as the ambient nutrient concentration.	**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 found that hydrodynamic forcing was the main factor affecting this exchange process, while vegetation density (including the absence of vegetation) had little effect. Hence, porewater exchange may be equally important in seagrass meadows as previously shown for bare sediments.	**5**

6.5 Recommendations

This PhD thesis presents findings that elucidate the fundamental processes of seagrass–hydrodynamic interactions, which impact ecological processes such as patch and gap dynamics and advective porewater exchange. These processes are important in order to create and implement strategies of restoration of disturbed seagrass meadows. The global decline of seagrass meadows must be mitigated so that seagrass functions that are important for marine ecosystems may be maintained and enhanced. The neglect of seagrass conservation and restoration will lead to widespread impacts, such as increased coastal erosion, greater impacts of storms on coastal environments and communities and disturbed marine food chains. Seagrass meadows not only have environmental functions but also have economic potential. Seagrass must be seen as one of the most important marine commodities, and one that needs sustainable management in order to optimize its economic value. Further research is required to investigate causes of global seagrass decline and to establish a strategy for the restoration and conservation of seagrass ecosystems.

In terms of improving the value of future laboratory flume experiments simulating seagrass-hydrodynamics interactions such as those studied here, my main recommendation is that roots and rhizomes are more fully simulated. This is likely to be particularly important in experiments investigating interactions between seagrasses and their substrate, in particular the porewater, which is an area that has very little thorough biophysical research to date.

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