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Comparison of the influence of patch scale and meadow scale characteristics on flow within seagrass meadows: a flume study

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Abstract

Hydrodynamic processes are known to be an important agent of stress and facilitation in seagrass meadows, but little is known about the effects of the common phenomenon of heterogeneity of seagrass meadows on their interactions with hydrodynamic processes. To address this gap in knowledge, four heterogeneous configurations of *Posidonia oceanica* mimics were analyzed in a laboratory flume. The four configurations were created by placing four boards of mimics – two with high shoot density (~ 1100 shoots m^{-2}) and two with low shoot density (~ 400 m^{-2}) in different patterns (“checkerboard”, “parallel”, “dense-sparse” and “sparse-dense”). Our results show that volumetric flow rate through each canopy, which is an indicator of the rate of supply of resources transported by the flow, tended to be greater in the low density patches, regardless of the configuration. It was also found that the Reynolds Stress component $-\rho \overline{u'w'}$ was positive in the lower density patches – indicating horizontal momentum was being transferred into the patch – and negative in the high density patches – indicating horizon-

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tal momentum was being transferred upwards out of the patch. Our results suggest that, in resource limited environments, hydrodynamic processes favor the growth of lower density patches in heterogeneous seagrass meadows, thereby causing meadows to become more homogenous over time.

Keywords: seagrass, hydrodynamics, heterogeneity, patches, shoot density

Introduction

Seagrass meadows provide important ecosystem services in many coastal zone environments, such as sustaining biodiversity (Duarte, 1989; Tanner, 2003; Borg *et al.*, 2005; Mills & Berkenbusch, 2008), and contributing to coastal protection (Pergent-Martini *et al.*, 2006; Koch *et al.*, 2009), carbon sequestration (Suzuki *et al.*, 2003; Apostolaki *et al.*, 2011; Fourqurean *et al.*, 2012) and nutrient accumulation (Gacia *et al.*, 2002; Apostolaki *et al.*, 2012). In part, these services are provided, either directly or indirectly, via the interaction of the meadows with the hydrodynamics of the ambient water. For example, seagrasses contribute to coastal protection directly by attenuating wave and tidal current energy (Nepf & Vivoni, 2000; Bouma *et al.*, 2005; Koch *et al.*, 2006). This also has the indirect effect of decreasing sediment erosion and increasing sediment deposition (Hendriks *et al.*, 2008), which will reduce turbidity, enhance light availability and thus enable further seagrass growth (Van der Heide *et al.*, 2007, Carr *et al.*, 2010). The direct results of these interactions (which are purely physical), and their indirect consequences (which may be physical, chemical, ecological or physiological), depend on three things: the nature of the incident flow, the substrate topography, and the physical characteristics of the seagrass meadow. Since little is known about the effects of the common phenomenon of heterogeneity of seagrass meadows on their interactions with hydrodynamic processes, our intention is to focus on the last of these, so hereinafter we disregard the first two.

The relevant physical characteristics comprise seagrass meadows' mechanical and morphological properties (Bouma *et al.*, 2005; Peralta *et al.*, 2008), and shoot density (shoots per unit area of bed surface), all of which may be measured locally, but which are also likely to have variability over larger spatial scales. In this study, we focus on the effects of shoot density, which influences mean flow speed and turbulence distributions (Gambi *et al.*, 1990; Fonseca & Koehl 2005; Luhar *et al.*, 2008) and related parameters such as canopy throughflow and bed shear stress (Nepf & Vivoni, 2000; Luhar *et al.*, 2008), which in turn are likely to have a wide range of indirect effects, for example altering nutrient uptake rates (Thomas *et al.*, 2000; Morris *et al.*, 2008), sediment dynamics (Marba & Duarte

2001; Hendriks *et al.* 2008) and seagrass growth (Van der Heide *et al.*, 2007, Carr *et al.*, 2010).

Larger-scale spatial variability of seagrass meadow physical properties, which is the norm in natural settings (Den Hartog, 1972; Koch *et al.*, 2006), has also been found to have a strong influence on hydrodynamics (Townsend & Fonseca, 1998; Gacia *et al.*, 2003; Fonseca & Koehl, 2006; Maltese *et al.*, 2007; Folkard, 2011), which in turn is likely to affect, for example, the transport and fate of sediment, seeds, pollen and dissolved nutrients (Koch *et al.*, 2006). Spatial heterogeneity may also cause flow acceleration around seagrass patches, producing local erosion (Bouma *et al.*, 2009; Van der Heide *et al.*, 2010), and can influence sediment deposition and re-suspension rates (Gacia & Duarte, 2001; Temmerman *et al.*, 2007). However, most studies of flow-seagrass interactions have assumed meadows to be homogeneous, and our understanding of how heterogeneous seagrass distributions interact with hydrodynamics remains limited.

In this work, we focus on 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). Specifically, we test the null hypothesis (H_0) 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. To assess the relative importance of patch and meadow-scale characteristics for the hydrodynamics, we 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. Ecological consequences of patch versus meadow scale effects on hydrodynamic resource supply to seagrasses are discussed.

Materials and methods

The experiment was carried out in a race track flume at the Royal Netherlands Institute for Sea Research (NIOZ), Yerseke, the Netherlands measuring 17.55 m long, 0.6 m wide and holding water of depth 0.4 m (Figure 2.1; further details in Bouma *et al.* 2005). The free-stream velocity was set at 100 mm s⁻¹. This velocity was used to represent hydrodynamic conditions that apply to many seagrass meadows, although lower and higher velocities can occur (Fonseca & Koehl, 2006; Bradley & Houser, 2009). Comparing different velocities was however not feasible within the scope of the present study. Before starting measurements, the

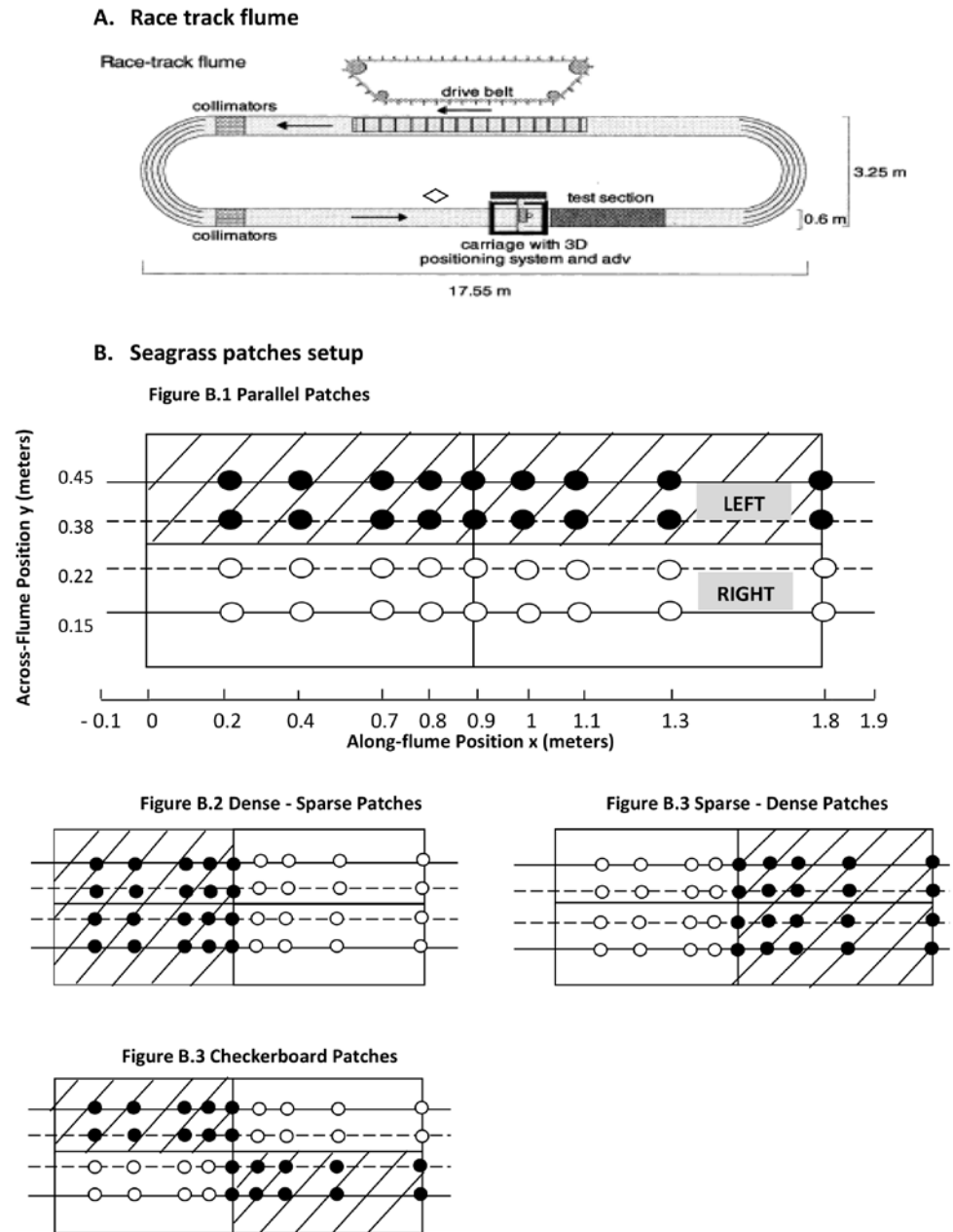


Figure 2.1

Schematic diagram of (A) racetrack flume tank at NIOZ, Yerseke and (B) top views of the four spatial configurations of seagrass mimic boards. The horizontal axis indicates along-flume position; the vertical axis indicates across-flume position. Here and in all subsequent figures, hatching indicates the HD patches, non-hatching the LD patches. Locations of ADV profile measurements are shown as black circles for HD patches and white circles for LD patches.

flume was allowed to run for 7 to 10 minutes to develop stable flow conditions, following previous testing and experiments on this facility. For practical reasons, we used fresh water in this experiment. The small difference in density between fresh ($\rho = 1000 \text{ kg m}^{-3}$) and seawater ($\rho = 1030 \text{ kg m}^{-3}$) was not expected to give significantly different results. Where relevant for the calculations (e.g. of Reynolds Stress) we used the density of fresh water.

In the test section of the flume, we arranged boards of *Posidonia oceanica*-like mimics, fabricated following Folkard (2005). Such mimics have been found by several authors to offer a suitable approach to studying the biophysical interactions between seagrasses and hydrodynamics (e.g. Nepf & Vivoni, 2000; Bouma *et al.*, 2005; Peralta *et al.*, 2008). Each mimic shoot had three leaf pairs with lengths of 0.5 m, 0.25 m and 0.15 m respectively. The mimic leaves were made of polyethylene sheeting (Decco Ltd., Glasgow UK) with thickness $\sim 2 \times 10^{-4} \text{ m}$, density $\rho = 9 \times 10^{-7} \pm 2 \times 10^{-8} \text{ kg m}^{-3}$, modulus of elasticity $E = 5.4 \pm 0.1 \times 10^8 \text{ N m}^{-2}$, and coefficient of kinetic friction $\mu = 0.47 \pm 0.03$, all of which are comparable to average values of natural *P. oceanica* (Folkard, 2005).

Seagrass Patches Setup

In each experimental run, we used four boards (each 0.9 m long and 0.3 m wide). Two were divided into $0.03 \text{ m} \times 0.03 \text{ m}$ squares, in which we attached one mimic shoot per square to obtain a relatively high density (HD) of $\sim 1100 \text{ shoots m}^{-2}$. The other two boards were divided into $0.05 \text{ m} \times 0.05 \text{ m}$ squares, in which we again attached one mimic shoot per square to obtain a relatively low density (LD) of $\sim 400 \text{ shoots m}^{-2}$. Herein, we use “density” to refer always to shoot density. Where we refer to HD-patches or LD-patches, we mean patches with high or low shoot density, respectively. In this experiment, the densities used are in the range of *Posidonia oceanica* density values found in nature (Buia *et al.*, 2004; Scardi *et al.*, 2006). The four boards were arranged in the four possible different spatial configurations over the course of the experiment, which we refer to as parallel, checkerboard, dense-sparse and sparse-dense (Figure 2.1). Each pattern aimed to represent an element of natural seagrass heterogeneity. Thus, the checkerboard configuration simulated a fragmented pattern due, for example, to turtle grazing (Christianen, 2012) or the effect of a hydrodynamic energy gradient from high energy – producing patchy seagrass – to low energy – producing a continuous seagrass bed (Fonseca *et al.*, 2002). Because of the idealized nature of the configurations, we completed a single experimental run for each configuration, following previous work of this type (e.g., see Newel & Koch, 2004; Folkard, 2005).

Flume measurements

Vertical profiles of the flow velocity components in three orthogonal directions (along-flume, across-flume and vertical, denoted u , v and w respectively) were measured at a set of horizontal locations inside and outside the patches for 30 s per point, at a frequency of 10 Hz, using an Acoustic Doppler Velocimeter (ADV, Nortek field version). Reference velocity profiles over the bare flume bed were measured 0.1 m upstream of the patches (i.e. at $x = -0.1$ m, where x is the along-flume coordinate and the leading edge of the patches is at $x = 0$; Figure 2.1). Velocity profiles within the patches were measured at $x = 0.2, 0.4, 0.7, 0.8, 0.9, 1, 1.1, 1.3$ and 1.8 m. A final set of profiles was measured at $x = 1.9$ m, 0.1 m downstream of the end of the seagrass. At each along-flume location, we measured profiles at four across-flume positions: $y = 0.15, 0.22, 0.38$ and 0.45 m (where y is the across-flume coordinate, measured from right to left when looking in the along-flume direction, and the right hand wall of the flume is at $y = 0$; Figure 2.1).

Each vertical profile consisted of 12 measurement points, which were distributed as follows. For each run, we first measured the height of the top of the deflected canopy (z_{top}) in each patch. We then took measurements at six locations around the top of the canopy, at 0.02, 0.04 and 0.06 m above and below z_{top} . Three measurements were then made at locations evenly distributed between top of seagrass board ($z = 0.05$ m) and $z_{\text{top}} - 0.06$ m. Finally, three measurements were made at locations evenly distributed between the water surface ($z = 0.31$ m) and $z_{\text{top}} + 0.06$ m. Here, z is the vertical coordinate, and the base of seagrass board, which is level with the overall flume bed, is at $z = 0$.

Hydrodynamic parameters

We measured or calculated the following hydrodynamic parameters:

- 1 Mean flow speed (mm s^{-1}) in the along-flume ($\bar{U}$), across-flume ($\bar{V}$) and vertical ($\bar{W}$) directions, was measured at each point in each profile, to provide insight into how canopy spatial structure modifies current velocity and may create coherent flow patterns;
- 2 Volumetric flow rate ($Q, \text{mm}^3 \text{s}^{-1}$) was calculated, following Morris et al. (2008) as

$$Q = \sum_{i=1}^n \left(\frac{\bar{U}_i + \bar{U}_{i-1}}{2} \right) (z_i - z_{i-1}) w \quad (1)$$

where $\bar{U}$ and z are defined above, w (mm) is the width of each patch board, and the subscripts refer to the vertical positions at which each velocity meas-

urement was taken. Q was calculated for each of the four patches and the regions of clear water above them, giving eight values for each configuration.

- 3 The mean solute flux per unit leaf area (N , $\text{g s}^{-1} \text{mm}^{-2}$) was calculated for each patch, assuming a uniform nutrient concentration in the incident flow, as

$$N = \frac{Q}{A_L} \quad (2)$$

where C (g mm^{-3}) is the concentration of nutrients in the incident flow, and A_L (mm^2) is the total leaf area within each patch. Because we used this parameter only in the form of ratios of its values between the LD and HD patches in each configuration, and the upstream nutrient concentration C is assumed constant, the value of C is not relevant (because it will always cancel out when ratios are calculated). Moreover, because constant shoot morphology is used throughout, the leaf area A_L can be substituted by the shoot density (D). Hence, we can calculate the ratio of solute flux per unit leaf area between the n^{th} LD patch and the m^{th} HD patch in each configuration as

$$\frac{N_{LD-n}}{N_{HD-m}} = \frac{Q_{LD-n} D_{HD-m}}{Q_{HD-m} D_{LD-n}} \quad (3)$$

Since we have two LD patches (i.e. $n = 1$ or 2) and two HD patches (i.e. $m = 1$ or 2) in each configuration, we have 4 values of this solute flux ratio for each configuration (N_{LD-1}/N_{HD-1} ; N_{LD-1}/N_{HD-2} ; N_{LD-2}/N_{HD-1} ; and N_{LD-2}/N_{HD-2}).

- 4 Turbulent kinetic energy (TKE, $\text{mm}^2 \text{s}^{-2}$), one of the hydrodynamic parameters that governs processes such as the exchange of dissolved nutrients (Morris *et al.* 2008) and gases (Gambi *et al.*, 1990) across leaf surfaces, and particle trapping and resuspension (Hendriks *et al.*, 2008). This was calculated, at each point in each profile, from the root mean square turbulent velocity components, of which the along-flume component was calculated as

$$\overline{u} = \left(\overline{u'(t)^2} \right)^{1/2}$$

where $u'(t) = u(t) - \overline{U}$ and $u(t)$ is the time series of quasi-instantaneous measurements of along-flume flow. The corresponding across-flume and vertical turbulent velocity components $\overline{v'}$ and $\overline{w'}$ were calculated in the same way, using the relevant mean and time series flow component values. TKE ($\text{mm}^2 \text{s}^{-2}$) was then calculated as

$$TKE = \frac{1}{2} \overline{u'^2} + \overline{v'^2} + \overline{w'^2} \quad (3);$$

- 5 The Reynolds Stress component $\tau_{Re} = (\text{Pa})$, where $\rho = 1000 \text{ kg m}^{-3}$ is the density of the water in the flume, was calculated at each point in each profile, in order to understand the distribution of vertical turbulent transfer within the patches. The sign of τ_{Re} indicates the direction of momentum transfer: positives values indicate net downwards transfer of along-flume momentum, negative values indicate net upwards transfer of along-flume momentum.

Results

Canopy height

The height of the seagrass patches depended strongly on both the patch-scale density and the meadow scale configuration. In general, the HD patches had greater canopy heights, because the same incident force of the water flow on their frontal area was balanced by the resistive forces due to the rigidity of a greater number of leaves, meaning that the resistive force required per leaf was lower (Fonseca *et al.*, 2008). However, the meadow scale configuration (Table 2.1A, B) influenced strongly the canopy heights to the extent that, for example, the LD patches in the dense-sparse configuration were higher than the HD patches in the sparse-dense configuration (Figure 2.2).

Volumetric flow rate through and over the canopy

The spatial configuration of the seagrass patches had a major influence on the volumetric flow rate through each patch. In those runs where, at the leading edge, an LD-patch was beside an HD-patch (i.e. the parallel & checkerboard configurations), 55-56% and 42-43% of the flow travelled over the LD and HD patches, respectively (Table 2.1B). In cases where there were two similar patches at the leading edge (i.e. the sparse-dense & dense-sparse configurations), between 45-48% of the flow travelled over the canopy, irrespective of the patch density (Table 2.1B). These proportions persist at roughly the same level over the downstream half of each configuration (i.e. what starts above the canopy largely remains above the canopy, regardless of patch configuration). Only in case of the checkerboard pattern do these percentages adjust in the downstream half of the configuration (Table 2.1B). Note, however, that there is a mis-match in the measured total volumetric flow rate between the upstream and downstream pairs of patches, of up to 7% ($154 \text{ mm}^3 \text{ s}^{-1}$, in the sparse-dense configuration). This is evidently due to variations in flow speed in regions where we did not directly measure the flow speed.

The through-canopy volumetric flow rate is highest where there is a uniform LD canopy over the whole width of the section (Table 2.1A), and lowest in LD patches laterally-paired with HD patches (Table 2.1A). Here, the over-

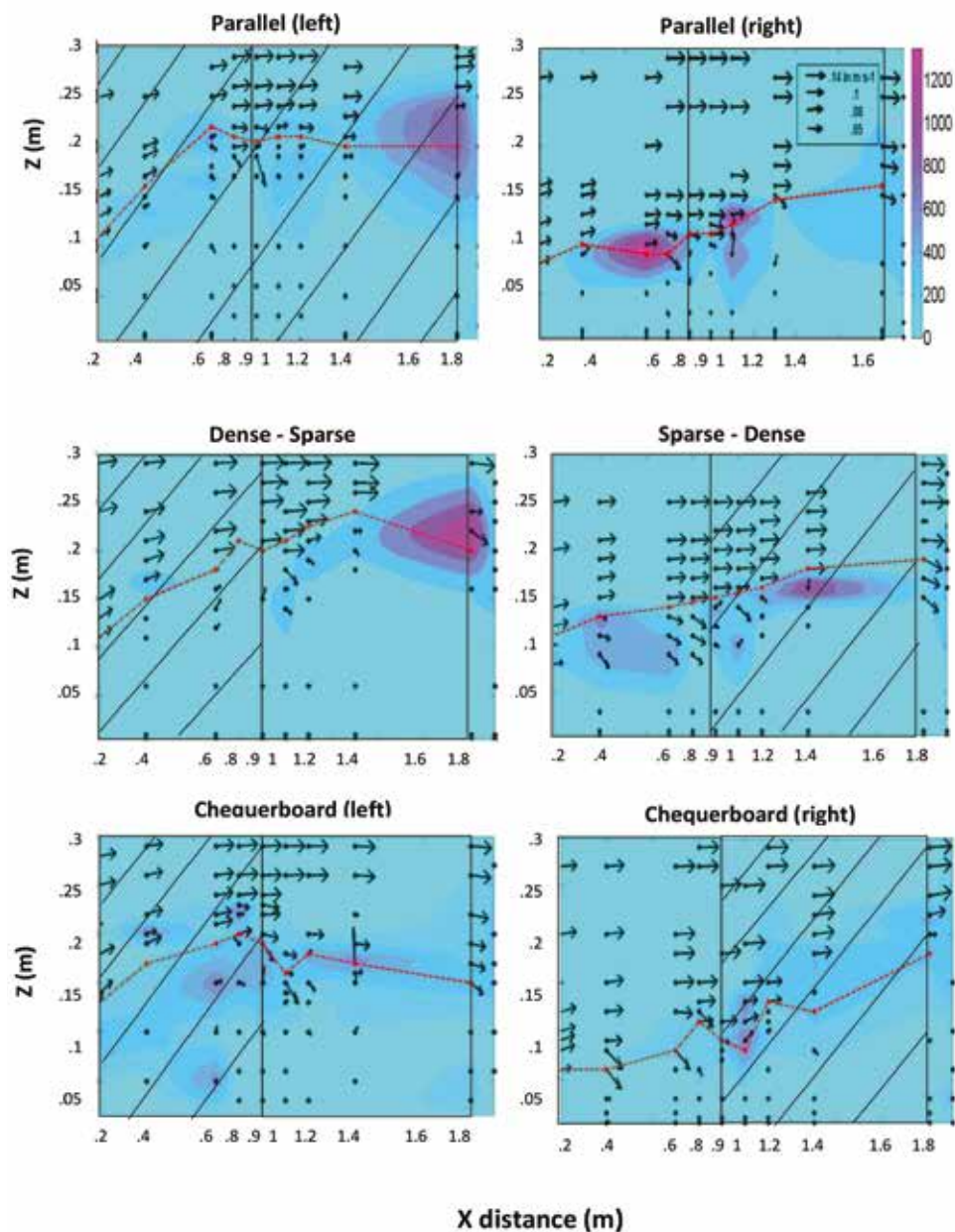


Figure 2.2

Flow velocity (arrows), canopy height (red dashed lines) and turbulent kinetic energy (colors, legend shows values in $\text{mm}^2 \text{s}^{-2}$) plotted in longitudinal section through the seagrass patches. Boxes with oblique lines indicate HD patches and without oblique lines indicate LD patches. Plotted values have been averaged across the flume.

2 Patch scale and meadow scale characteristics on flow within seagrass meadows

flow pre-dominantly follows the path of least resistance – the LD portion of the cross-section – resulting in a relatively strong flow which strongly pronates the LD canopy, reducing its volume and thus the volumetric flow rate through it (Figure 2.2B, F) compared to all other leading edge patches.

Table 2.1

Volumetric flow rate over and through canopies for the four meadow scale configurations (parallel, sparse – dense, dense – sparse and checkerboard), (A) in $\text{mm}^3 \text{s}^{-1}$ (B) as percentages of total volumetric flow rate.

A – Volumetric flow rate over and through in $\text{mm}^3 \text{s}^{-1}$

No.	patch mosaic scale	over ($\text{mm}^3 \text{s}^{-1}$)				through ($\text{mm}^3 \text{s}^{-1}$)			
		left		Right		left		right	
		front	back	front	Back	front	back	front	back
1	Parallel	870	835	1132	1160	37	28	12	40
2	sparse – dense	996	955	1062	994	76	31	61	61
3	dense – sparse	985	946	978	905	42	65	32	79
4	checkerboard	900	925	1170	1027	20	33	11	9

B – Volumetric flow rate over and through in %

No.	patch mosaic scale	over (%)				through (%)			
		left		right		left		right	
		front	back	front	back	front	back	front	back
1	Parallel	42	41	55	56	2	1	1	2
2	sparse – dense	45	47	48	49	4	1	3	3
3	dense – sparse	48	48	48	45	2	3	2	4
4	checkerboard	43	46	55	51	1	2	1	1

Turbulent Kinetic Energy & Reynolds Stress

In all of the configurations (Figure 2.2), the maximum TKE values occurred near the top of the canopy, the region of greatest velocity shear (between the slow in-canopy flow and the fast overflow). There is a general tendency for the TKE to increase downstream (as the velocity shear increases at the top of the canopy) and to be higher over the HD patches than over the LD patches, but these are not consistent patterns.

The Reynolds stress component τ_{re} has a rather patchy distribution (Figure 2.3) but, like the TKE, is concentrated in the shear layer near the top of the canopy. There is a tendency for it to become positive towards the downstream end

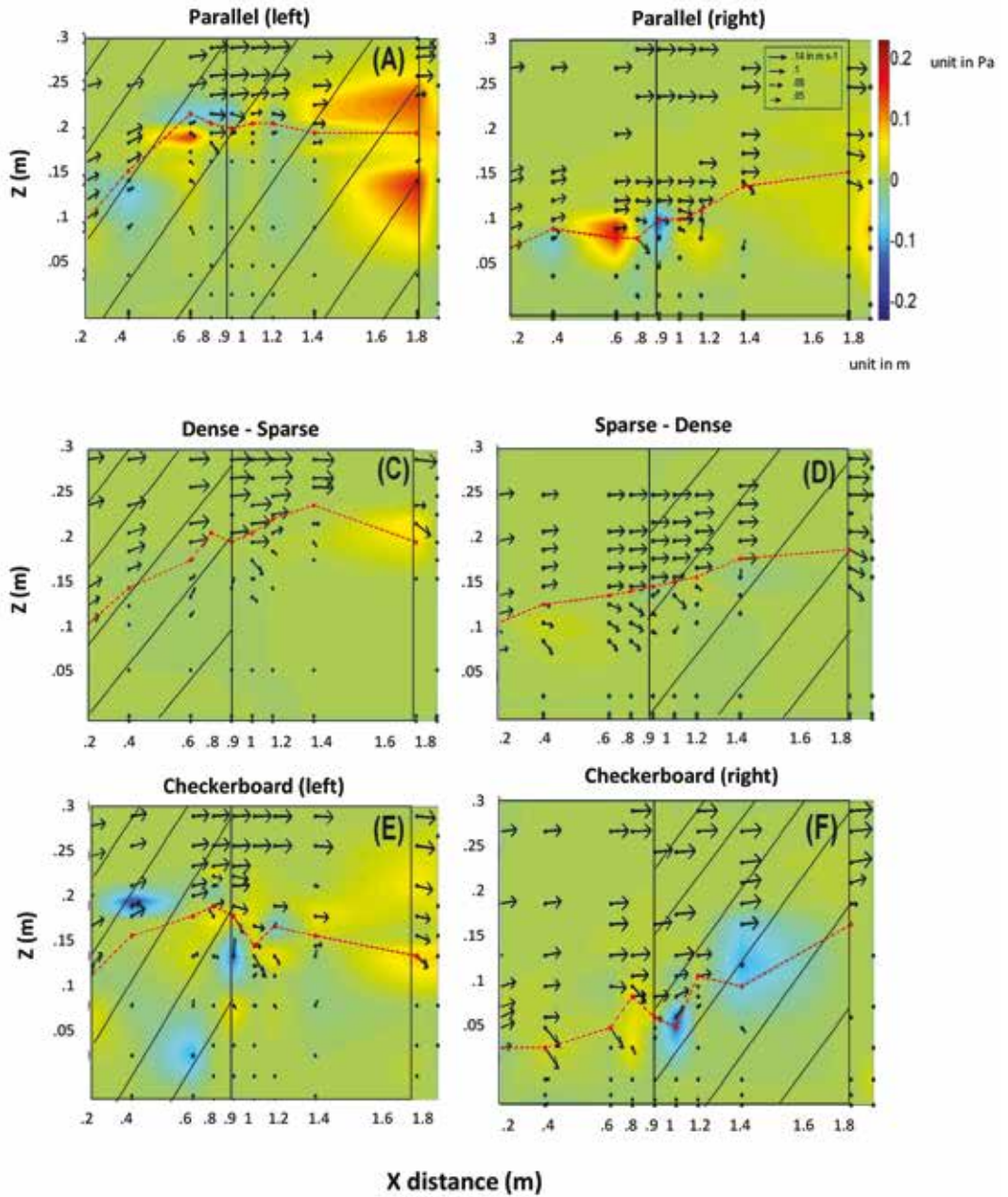


Figure 2.3

Reynolds Stress component τ_{re} (contoured colors, legend shows values in Pascals), flow velocities (arrows) and canopy height (red dashed lines) plotted along a longitudinal section through the seagrass patches. Boxes with oblique lines indicate HD patches and without oblique lines indicate LD patches. Plotted values have been averaged across the flume.

of the patches (Figure 2.3A, C, E) as would be expected: as the shear at the top of the canopy increases, turbulence becomes stronger (Figure 2.2) and will cause a net transfer of momentum downwards (positive τ_{Re}) from the rapid overflow into the canopy. In certain locations, mainly those where the height of the canopy is increasing downstream, τ_{Re} is negative, indicating that the flow through the canopy at these points is faster than that immediately above it.

Ratio of available solute flux per unit leaf area

The mean values of the four solute flux ratios defined above were calculated for each configuration (Figure 2.4). The dense-sparse configuration has a significantly higher value of this mean ratio than the parallel configuration, indicating that the LD patches in this configuration get significantly higher amounts of solute delivery per unit leaf area than in the parallel configuration. This is evidently because, in this case, the HD patches shelter the LD cases, allowing them to form a much less pronounced canopy than in the parallel configuration, and thus receive

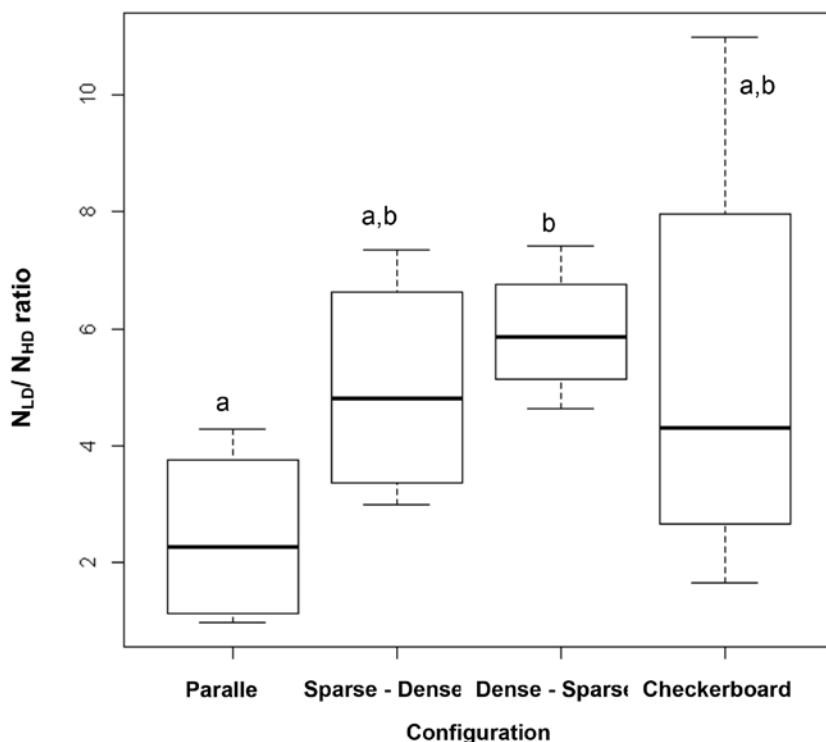


Figure 2.4

Box and whisker plot showing range of values of the ratio of solute flux per unit leaf area for LD patches to that for the HD patches in each spatial configuration. Statistically significant groupings are indicated by the letters a and b, as derived from pairwise Mann Whitney tests (confidence threshold $\alpha = 0.05$).

a greater volumetric flow rate. The lower mean ratio in the parallel configuration is evidently because of the strong overflow and pronation seen in the LD patches in this case, which results in a lower volumetric flow rate through them. The checkerboard pattern has the highest variability, indicating that this configuration generates the greatest difference in solute flux values between the two LD patches and between the two HD patches.

Discussion

The results presented here support the argument 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. This can be seen in our measurements of volumetric flow rate apportionment (Table 2.1A, B), flow speed (Figure 2.2), TKE (Figure 2.2) and Reynolds stress (Figure 2.3).

Our findings hold for cases with relatively low water depths, as used in our flume experiments. It should be noted that in cases with larger water depths, where the ratio of canopy height to water column height is less than 0.1, turbulence can more easily penetrate the canopy from the overlying water column (Nepf & Vivoni, 2000). Hence, in such situations, resource supply and hydraulic renewal within the canopy is determined by overlying TKE, as well as by the volumetric flow rate through the canopy (Nepf *et al.*, 2007).

Importance of patch scale vs. patch mosaic scale distribution

In general terms, the results presented here confirm earlier observations of how higher shoot density (Gambi *et al.*, 1990; Peralta *et al.*, 2008; Hendriks *et al.*, 2008) and spatial heterogeneity (Folkard, 2011) inhibit flow intrusion and cause flow deflection around patches. Flow deflection from patches of higher shoot density to those of lower shoot density increase the availability of resources such as dissolved nutrients and gases to the latter (Nepf *et al.*, 2007, Morris *et al.*, 2008). However, the present results also show that the pattern of canopy pronation within a heterogeneous seagrass meadow is complicated by its non-linear relationship with the spatial distribution of the flow. Because of this, canopy height is not only determined by patch scale shoot density but is also affected by the meadow scale distribution of patches (e.g. compare the LD patches in Figures 2.2B, D & E).

Understanding canopy pronation is important, as the volumetric flow rate over and through the canopy is a function of both the canopy height (and width), and the flow speed. At shoot densities typically found in natural seagrass mead-

ows, volumetric flow rate through canopies is generally an order of magnitude slower than that over or around them (Gambi *et al.*, 1990; Koch *et al.*, 2006), a finding supported by our results (Table 2.1). Canopy height appeared to be the most important factor determining differences in through-canopy volumetric flow rate, as the flow velocity within the vegetation was almost constant between treatments (Figure 2.2), while, for example, the relatively high volumetric flow rate in the sparse-dense configuration is evidently due to the relatively high canopy in that case (Figure 2.2). In contrast, differences in volumetric flow rates over the canopies appeared to be determined more by a combination of the amount of cross-sectional area above the canopy and the overflow speed, as both these factors vary between and within configurations (Figure 2.2).

Comparing the different spatial patterns observed here reveals that parameters like canopy height and volumetric flow rate through and over the canopy are not only determined by local density but are also affected by the position of a patch within its local meadow scale arrangement (e.g. compare the LD patches in Table 2.1). In general, most flow will be deflected over or around higher density patches towards areas with less flow resistance, although some flow will always penetrate even the densest of patches. Understanding these flow-shoot density relationships is important for understanding the functioning of a seagrass meadow in terms of the uptake of limiting resources from the water column (Gambi 1990; Folkard 2005; Morris *et al* 2008).

It is also interesting to note a specific observation in the dense-sparse patch configuration case. The HD patches at the leading edge act as a barrier that shields the downstream LD patches. Nevertheless, the highest TKE values are observed at the downstream end of the LD patches rather than in the HD patches. This may be caused by the flow being forced over the HD patches, leading to a relatively rapid, “skimming” overflow (Gambi *et al.*, 1990; Koch *et al.*, 2006), which builds up a strong shear layer between itself and the very weak through-flow also caused by the uniformly high density seagrass in the upstream portion of the seagrass configuration.

Ecological consequences of hydrodynamic interactions with meadow scale heterogeneity in seagrass meadow shoot density

Heterogeneity in shoot density at the meadow scale, as schematized in our idealized experiment, may be regarded as an inherent characteristic of natural seagrass meadows (Koch *et al.*, 2006). It may be caused by a wide variety of environmental factors, such as sedimentary processes, nutrient availability and patterns of colonization and disturbance (Balestri *et al.*, 2003, Ruiz & Romero, 2003). Such meadow scale heterogeneity in vegetation density is known to have important consequences for the functioning of both the seagrass and the communities it supports. For example, it can affect faunal abundance and species richness

(Irlandi, 1997; Hovel, 2003; Tanner, 2003). It can also cause increased turbulence or flow acceleration, and thereby locally reduce the growth of organisms on seagrass leaves that, by their presence, hamper seagrass growth (Gambi *et al.*, 1990). However, such increased turbulence or flow acceleration can also damage leaves and thereby cause a reduction in photosynthesis (Koch *et al.*, 2006). These opposing effects demonstrate that interpreting the ecological consequences of altered hydrodynamics at a specific location is extremely complicated.

The importance of local (patch-scale) shoot density on hydrodynamics conditions within seagrass meadows has been well established (e.g. Peterson *et al.*, 2004). The present work clearly demonstrates the importance of meadow scale heterogeneity in vegetation density in addition to this. The delivery of resources to the seagrass and the organisms it supports is reliant on hydrodynamics. Our results indicate that in heterogeneous meadows, the solute flux rate per unit leaf area tends to be greater in lower density patches than in higher density patches. The implication of this is that lower density patches would have greater access to hydrodynamically-delivered, limiting resources (Gambi, 1990; Folkard, 2005; Morris *et al.*, 2008).

Assuming that hydrodynamic supply of resources affects growth rates, our results suggest that growing conditions are more favorable in lower density patches than in neighboring high density patches, because the lower density patches have higher solute flux rates per unit leaf area. This would imply that the adjustment of hydrodynamic flows to meadow scale heterogeneity is a factor that favors heterogeneous seagrass meadows becoming more homogenous. Of course, there are a very wide range of other factors that contribute to determining whether heterogeneous meadows become more or less homogeneous, such as: nutrient cycling from sediment into the water column or vice versa, deposition or erosion, or animal grazing, and all of these would need to be taken into account in predicting their development.

Apart from meadow scale heterogeneity within a single species, the present results are also relevant to meadows made up of species differing in vegetation density, e.g., *Caulerpa racemosa* & *Posidonia oceanica* or *Spartina anglica* & *Zostera marina* (Dumay *et al.*, 2002; Peralta *et al.*, 2008). As species interactions are typically highly complex, involving many processes, we refrain from speculating the ecological consequences of hydrodynamic effects following from meadow scale heterogeneity caused by species mixtures, and only note that this is an interesting field for future studies.

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