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Hydrodynamic consequences of gaps in seagrass meadows: dependence on gap size, meadow density, shoot length and water depth

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Adhitya[1,2]*, A.M. Folkard[3], M. Van Katwijk[2], H. H. De Iong[4,5], P.M.J. Herman[1], T.J. Bouma[1]

Abstract

Most natural seagrass meadows contain unvegetated areas (gaps), but to date, only a few studies have investigated their hydrodynamics. Here, we investigate the hydrodynamics of these gaps via a laboratory flume experiment using an artificial seagrass meadow. We used a fixed flow speed of 200 mm s^{-1} and a novel circular gap design, creating gaps within the meadows with diameters of 100 to 1000 mm, and varied shoot density (480 and 1100 shoots m^{-2}), water depth (200 and 400 mm) and leaf length (50, 100 and 200 mm) between runs. Velocity profiles were measured at several along-stream locations and processed to provide values of turbulent kinetic energy and discharge per unit cross-sectional area. Canopy heights upstream and downstream of the gap were also measured, and the ratio of the former to the gap length was defined as the gap aspect ratio (GAR). We identify a clear distinction between cases where GAR < 0.3, in which within-gap turbulence levels are relatively low, intrusion of overflow into the gap

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[1]Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 140, 4400AC Yerseke, The Netherlands

[2] Departement of Enviromental Science, Institute for Wetland and Water Research, Radboud University Nijmegen, Faculty of Science, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands

[3]lancaster Environment Centre, University of Lancaster, Lancaster LA1 4YQ, United Kingdom

[4]Institute of Enviromental Sciences, CML/Conservation Biology, Van Steenis gebouw, Einsteinweg, P.O. BOX 22333 CC Leiden, The Netherlands

[5]Department Evolutionary Biology, Groenenbergerlaan 17, 2020, Antwerpen Belgium

is relatively high (but not dominant) and pronation of the downstream canopy is relatively strong, and cases where GAR > 0.3, where the opposite tendencies prevail. This suggests that the former gaps are relatively easily seeded from outside of the meadow, whereas the latter are more likely to be filled by clonal extension of the plants at the patch's periphery. Our results also suggest that shorter-leaved downstream canopies are facilitated by gaps' hydrodynamic effects because they receive increased throughflow.

Introduction

Seagrass meadows provide many important ecosystem services, such as provision of nursery and sanctuary habitats for a broad range of marine species, which enhance faunal abundance and species diversity (Duarte, 1989; Tanner, 2003; Hovel & Regan, 2008; Mills & Berkenbusch, 2008), and attenuation of hydrodynamic energy from waves and currents (Gambi *et al.*, 1990, Nepf & Vivoni, 2000; Bouma *et al.*, 2005; Luhar *et al.*, 2008), which increases sediment stability (Gacia & Duarte, 2001; De Falco*et al.*, 2000). Therefore, obtaining a fundamental understanding of factors contributing to the decline of seagrass meadows is of crucial importance. Previous studies of these globally significant ecosystems have focused on their large-scale stressors such as turbidity (Townsend & Fonseca, 1998; Carr *et al.*, 2010), eutrophication (Cardoso *et al.*, 2004) and hydrodynamically-induced mechanical stresses (Infantes *et al.*, 2012). Relative few studies have focused on the role of unvegetated areas (gaps) for the decline of seagrass meadows, even though a recent study suggests that gap creation may initiate a catastrophic collapse (Christianen *et al.*, 2014).

Most seagrass meadows in nature contain gaps of different shapes and sizes (Luhar, 2008). Gaps can be caused by human activities such as propeller scarring, vessel grounding and digging for benthic animals (Townsend & Fonseca, 1998; Hovel & Regan, 2007), bioturbation due to faunal burrowing (e.g. Valentine *et al.*, 1994; Townsend & Fonseca, 2008), or grazing by meso- or mega-fauna as diverse as, for example, the echinoids *Lytechinus variegates* in the northern Gulf of Mexico (Valentine & Heck, 1991) and *Diadema antillarum* in the Caribbean Sea (Ogden, 1973), or the Green Turtle (*Chelonia mydas*) in East Kalimantan, Indonesia (Christianen *et al.*, 2014). Hydrodynamic forces from currents and waves may also cause or exacerbate gaps in seagrasses, often creating crescent-shaped features known as "blowouts" (Patriquin, 1975; Fonseca & Bell, 1998).

Most studies of gaps in seagrass meadows have focused on seagrass-grazer interactions (e.g. Eggleston *et al.*, 1998; Irlandi *et al.*, 1999; Healey & Hovel, 2004; Almela *et al.*, 2008). However, hydrodynamic interactions are arguably as important as biotic interactions in determining seagrass meadow functioning (Gambi *et al.*, 1990; Nepf & Vivoni, 2000; Adhitya *et al.*, 2014). To date, most studies of seagrass hydrodynamics have focused on homogeneous meadows (e.g. Fonseca, 1982; Gambi *et al.*, 1990; Abdelrhman, 2007), but the relatively small number of studies on the hydrodynamic influence of heterogeneous meadows (e.g. Folkard 2005, 2011; Maltese *et al.*, 2007) have found it to be important. For example, heterogeneity in shoot density can cause heterogeneity in nutrient uptake by seagrasses (Morris *et al.*, 2008), and may enhance growth in lower-density patches (Adhitya *et al.*, 2014). Gaps may also entrap seeds and pollen via hydrodynamic processes, and thereby affect meadows' growth and gap colonization.

Studies to date of gap hydrodynamics in seagrass meadows have provided some understanding, but have left many questions unanswered, and raised many others. For example, Folkard (2011) proposed a flow regime diagram (Figure 11 in Folkard 2011), which indicated that the speed of the incident flow, the canopy height and the length of a gap were the factors that governed whether the flow within the gap came primarily from within the upstream canopy, or from above it via flow separation and recirculation. However, this study did not consider the effects of the shoot density of the surrounding meadow or the ratio of the canopy height to the water depth. In the present study, we consider the effects of these factors, in combination with leaf length/canopy height and gap length, via a laboratory flume experiment. We hypothesize that a low density seagrass canopy upstream of the gap may limit the formation of a recirculation cell in the gap, by allowing flow to pass through the canopy and thereby reducing velocity shear at the top of the canopy. In these cases, therefore, we predict flow within the gap to be dominated by throughflow that has arrived from within the upstream canopy. We further 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.

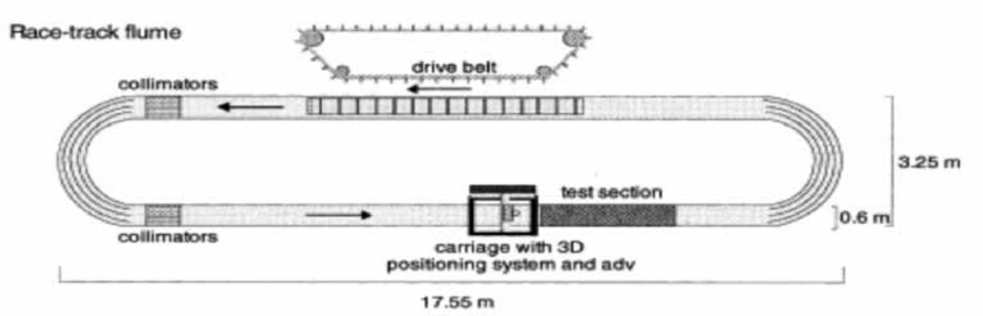
Materials and methods

Experimental Setup

The experiment was carried out in the race track flume at the Royal Netherlands Institute for Sea Research (NIOZ) Yerseke (Figure 3.1a; details in Bouma *et al.*, 2005; Jonsson *et al.*, 2006). Seagrass was simulated using artificial plant mimics made of polyethylene, which is a widely-accepted approach in flume experiments used to investigate interactions between aquatic vegetation and hydrodynamics (e.g. Nepf & Vivoni, 2000; Bouma *et al.*, 2005; Folkard, 2005; Peralta *et al.*, 2008). In the present study, the mimic morphology was based on *Thalassia testudinum* (turtle grass), a tropical species of seagrass, and each simulated shoot was made up of three leaves of equal length, which were attached to a 100 mm long sheath. The shoots were secured in the flume by inserting the sheath into a layer of sand on flume bed such that it was entirely buried, leaving only the leaves above the sand surface.

Seagrass meadows of two shoot densities were created in a 2m-long test section within the flume, filling its whole 600 mm width: the first had 480 shoots m^{-2}, and is referred to herein as the low density (LD) case; the second had 1000 shoots m^{-2}, and is referred to as the high density (HD) case. Between them, these are representative of shoot densities found in *Thalassia testudinum* meadows in nature (Whitfield *et al.*, 2004; Perez, 2006; Martinez-Daranas *et al.*, 2009). Two different water depths (H, mm) were used: 200 mm and 400 mm. In the 400 mm water depth cases, leaf lengths (h, mm) of 50, 100 and 200 mm (at both low and high shoot densities) were used, and in the 200 mm water depth cases, a leaf

A Race Track Flume



B Gap size set up along the flume

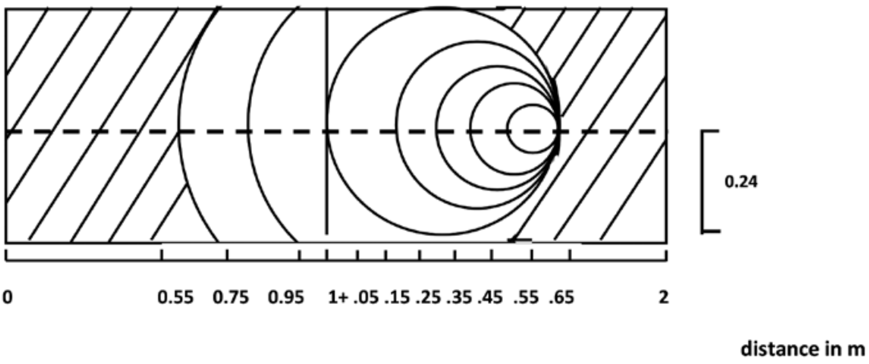


Figure 3.1
Schematic diagram of (a) the racetrack flume tank at NIOZ, Yerseke (b) the different gap sizes created within the simulated seagrass meadow. The circular gaps had diameters of 100, 200, 300, 400, 600, 800 and 1000 mm. The dashed line in the middle of the flume (Y = 240 mm) indicates the locus of velocity measurement positions.

length of 100 mm was used (again, at both shoot densities). By removing areas of seagrass mimics, circular gaps were made within the meadows with diameters of 100, 200, 300, 400, 600, 800 and 1000 mm (Figure 3.1b). This is a departure from previous studies, which have tended to use rectilinear, two-dimensional configurations. This novel approach was taken because circular gaps are closer in shape to many gaps found in nature caused, for example, by bioturbation and grazing (Heck & Valentine, 2005).

Throughout the experiment, the flow speed was set at 200 mm s^{-1} to simulate typical natural tidal conditions (Bouma *et al.*, 2005b). Velocity was measured using a Vectrino Acoustic Doppler Velocimeter (ADV, Nortek AS, Rud, Norway) located midway between the flume's sidewalls (Y = 240 mm from each wall) to minimize wall effects, at along-flume (X-direction) positions 550, 750, 950, 1050, 1150, 1250, 1350, 1450, 1550, and 1650 mm from the upstream end of the seagrass meadow (see Figure 3.1b for where these are in relation to the gaps). At each of these X-positions, measurements were made at 10 different vertical locations (Z-positions), the lowest at 5 mm above the bed and the highest at 310 mm above the bed. At each point, velocity was measured for 90 seconds at a frequency of 10Hz. For each case, the canopy height was measured immediately upstream of the gap, and at the closest point downstream from the gap where the canopy had reached an equilibrium height (i.e. approximately one leaf length downstream from the end of the gap).

Data Processing

The ADV provided time series of quasi-instantaneous measurements of the along-flume, across-flume and vertical velocity components, U, V and W (mm s^{-1}) respectively. From these, and the measurements of the canopy height, we derived the following parameters:

Values of turbulent kinetic energy (TKE) were determined by calculating the turbulent components of velocity (u_i', v_i', w_i', mm s^{-1}) as the differences between the individual, quasi-instantaneous, measured velocity components (U_i, V_i, W_i) and their respective mean values ($\overline{U}, \overline{V}, \overline{W}$), and then taking their root mean square values

$$(u', v', w') = \left(\overline{u_i'^2}^{1/2}, \overline{v_i'^2}^{1/2}, \overline{w_i'^2}^{1/2}\right)$$

TKE was then calculated, following Morris et al. (2008):

$$\mathrm{TKE} = \frac{1}{2}\left(u^2 + v^2 + w^2\right) \qquad (1)$$

The gap aspect ratio (GAR) was calculated, following Folkard (2011), as the ratio of the (pronated) canopy height (h_c, mm) to the gap diameter (D, mm):

$$\mathrm{GAR} = \frac{h_c}{D} \qquad (2)$$

The unit discharge (q, mm^2 s^{-1}) was calculated as the rate of flow per unit cross-sectional width, following Morris et al. (2008):

$$q = \sum_{z=0}^{z=z_{max}} q_i \qquad (3)$$

where $q_i = (z_{mi} - z_{mi-1})u_i$, z_{mi} is the mid-height (mm) between the measurement heights for velocities u_i (mm s^{-1}) and u_{i+1} (mm s^{-1}) and z_{max} (mm) is the full water depth. This was calculated for the vertical sections of the flow above the canopy height (q_a) and below it (q_b). Mean values of each of these were calculated from all of the measured flow profile data from the region upstream of the gap ($q_{a-,up}$, $q_{b,up}$), within the gap ($q_{a,gap}$, $q_{b,gap}$) and downstream of the gap ($q_{a,down}$, $q_{b,down}$). From these, the proportion of the flow passing through the canopy, as opposed to over it were calculated as, for example, $q_{a,up}/(q_{a,up} + q_{b,up})$. The way in which this proportion changed as the flow passed over the gap and into the downstream canopy was quantified using the ratios of these proportions $R_{gap\text{-}up}$ and $R_{down\text{-}up}$ as shown in Figure 3.2.

The gap Reynolds number (Re_{gap}, dimensionless) was calculated, following Folkard (2011) as

$$\mathrm{Re} = \frac{\bar{U}h_{c1}}{} \qquad (4)$$

where $\bar{U} = q_c/z_{max}$ (mm s^{-1}) is the mean along-flume flow speed, h_{c1} (mm) is the canopy height immediately upstream of the gap and ν (mm^2 s^{-1}) is the kinematic viscosity of water (taken here as 1 mm^2 s^{-1}). The canopy height difference (Δh_c, mm) was calculated as the canopy height immediately downstream of the gap (h_{c2}, mm) subtracted from h_{c1}.

$$\Delta h_c = h_{c1} - h_{c2} \qquad (5)$$

Results

Flow regime within the gap

Calculation of GAR and Re_{gap} enable comparison of our results with the regime diagram proposed by Folkard (Figure 11 in Folkard 2011). All of the experimental runs carried out in the present study have $Re_{gap} < 40{,}000$ and thus fall into the "throughflow" region identified in that diagram. Analysis of the flow profile data obtained from the upstream end of the gap shows that Folkard's throughflow

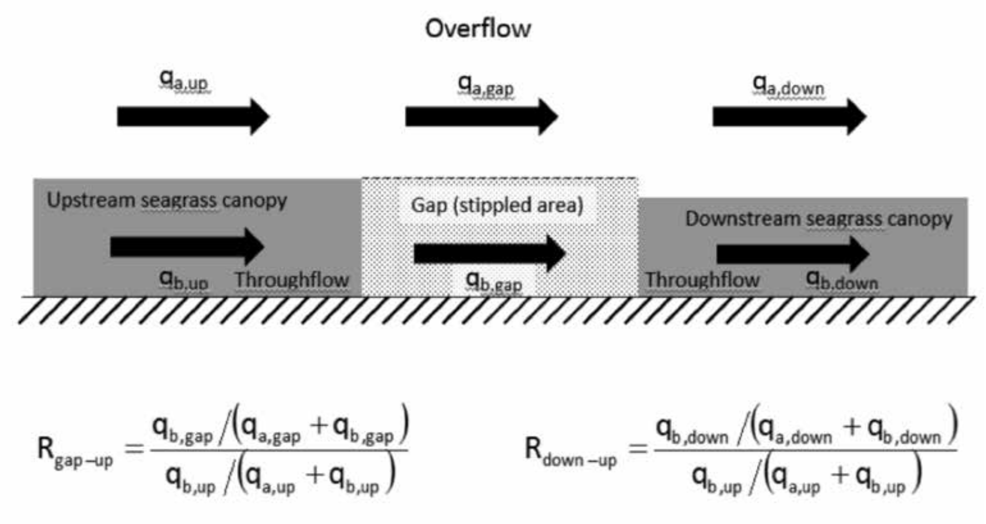


Figure 3.2
Illustrative figure showing how the unit discharge ratios were calculated. The q's indicate unit discharge ratios below (b) and above seagrass patches (a) the canopy and upstream (up), downstream (down) and within the gap (gap).

criterion (that the along-flume flow speed at 10 mm above the bed in the most upstream profile in the gap is greater than 5% of the overall mean flow speed) is satisfied in 36 out of our 42 runs. In the other six, although this criterion is failed strictly speaking, closer inspection shows that this is due to local anomalies in the flow measurements, and there is evidence of significant throughflow emerging into the gap, and no evidence of flow recirculation cells being formed here. Neither are any of the criteria for the other overflow-dominated forms of flow considered by Folkard (2011) satisfied in any of them. Therefore, we can assume that the categorization, *sensu* Folkard (2011), of all of the present results as throughflow cases is appropriate.

Turbulence and mean flow within the gap

In order to investigate the within-gap level of turbulence, we calculated the spatially averaged value of TKE (TKE_{mean}) in the region defined as the gap in Figure 3.2 (i.e. the region below the upstream canopy height). Our results show that, for each combination of water depth (H) and leaf length (h) values, TKE_{mean} was minimum at smallest GAR values (i.e. for the longest, shallowest gaps), where the gaps were long enough to allow the turbulent wake of the upstream canopy to decay and a new boundary layer flow structure to develop. In most cases, TKE_{mean} peaked at an intermediate GAR value and then had a fairly constant value for larger GAR values (Figure 3.3). For the shortest leaves (h = 50 mm), the maximum TKE_{mean} occurred at a larger value of GAR (≈0.5) than for the h = 100 mm

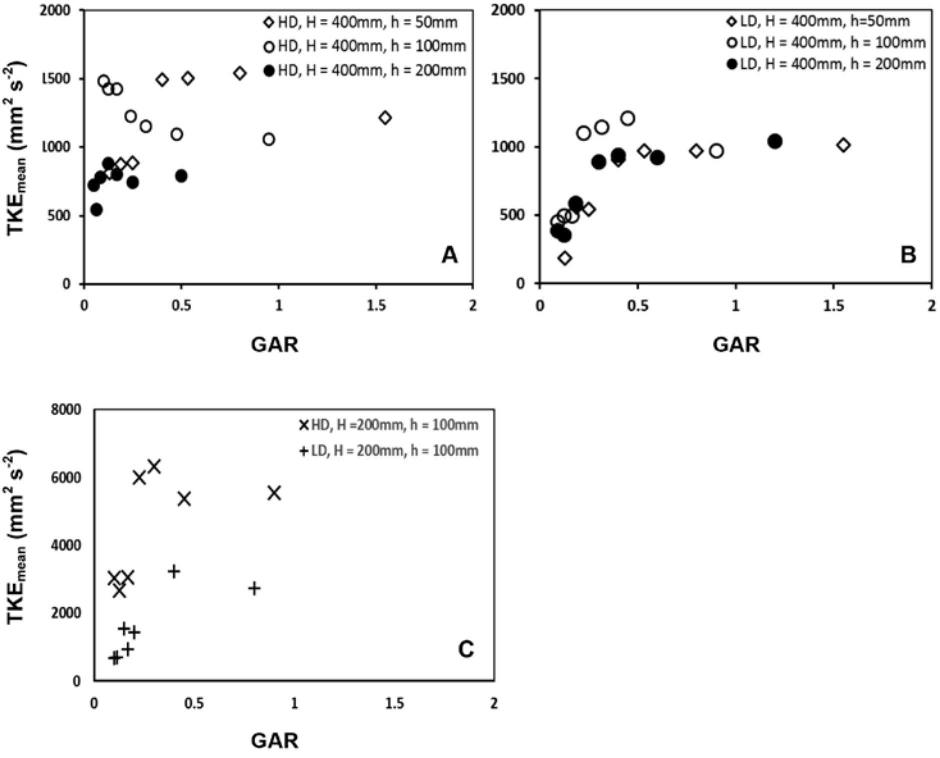


Figure 3.3
The mean turbulent kinetic energy with the gap, TKE$_{mean}$, plotted against the gap aspect ratio, GAR, for runs with (A) high density (HD) canopies, water height H = 400 mm and seagrass leaf lengths of h = 50, 100 and 200 mm; (B) low density (LD) canopies, water height H = 400 mm and seagrass leaf lengths of h = 50, 100 and 200 mm; and (c) HD or LD canopies, water height H = 200 mm and seagrass leaf length h = 100 mm.

and h = 200 mm leaves, where the TKE$_{mean}$ peak occurred at GAR = 0.1 – 0.4. These patterns were less clear in the LD canopy cases (Fig. 3b), where the peak value was not apparent; instead, TKE$_{mean}$ increased from a minimum at the lowest GAR values to a steady value for GAR > 0.3.

To investigate the nature of the mean flow within the gap, we considered how the ratio R$_{gap\text{-}up}$ (as defined in Figure 3.2) varies with GAR and changes in H and h (Figure 3.4). This parameter may be interpreted as follows: if R$_{gap\text{-}up}$ = 1, then the proportion of the flow through a given cross-section of the flume that takes place within the seagrass canopy (as opposed to above it) in the upstream canopy region, is the same as the mean value of that proportion within the gap. In other words, there is no instrusion of the upstream overflow into the gap, nor any intrusion into the overflow of the throughflow that emerges from the upstream canopy into the gap. If R$_{gap\text{-}up}$ > 1, then there is intrusion of the overflow into the gap in

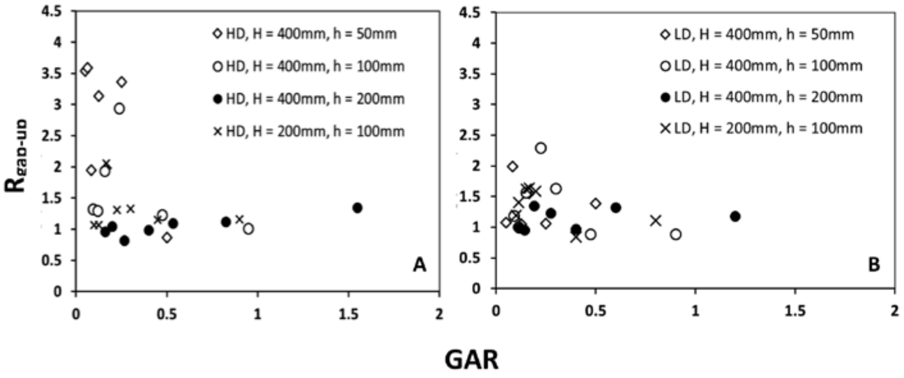


Figure 3.4
The ratio R_{gap-up} in in-canopy unit discharge proportion between the upstream canopy and the gap (as defined in Figure 2), plotted against the gap aspect ratio GAR, for (A) high density (HD) and (B) low density (LD) canopy cases, and various values of water depth (H) and seagrass leaf length (h), as indicated.

the canopy. If $R_{gap-up} < 1$, then there is removal of throughflow from the gap into the overflow. In both the HD (Figure 3.4a) and LD (Figure 3.4b) cases, but more clearly in the former, there is a distinction between lower and higher GAR cases, the transition occurring at GAR ≈ 0.3. In many of the lower GAR cases, $R_{gap-up} > 1$, reaching its highest values of 3-4 for the shortest-leaved (h = 50 mm), high density canopy. This indicates that the overflow intrudes significantly into the gap in these cases, and the gaps can thus be thought of as "overflow-influenced". Typical values for the ratios $q_a/(q_a+q_b)$ in these cases are 10% for the upstream canopy (i.e. 10% of the flow passes through the canopy, and the other 90% passes above it), and 35% (3.5 times higher) in the gap. So, even these highest values do not indicate that the gaps become dominated by the overflow, and throughflow is still dominant in the gap in these cases. For the higher GAR cases, and for several lower GAR cases, notably those with the longest-leaved canopy (h = 200 mm), $R_{gap-up} \approx 1$, indicating little or no exchange between the gap and the overflow, implying that these are cases where the flow in the gap is almost all deriving from the throughflow in the upstream canopy.

Influence of gap hydrodynamics on downstream seagrass canopy

One way in which the presence of a gap and its influence on the hydrodynamics of the flow may affect the downstream seagrass canopy is by causing the canopy to become more or less pronated (i.e. mechanically stressed) than the upstream canopy. In the absence of the gap, given that the upstream canopy height has reached equilibrium with the flow and is constant for some distance upstream, one can assume that the downstream canopy would also have this canopy height. Any differences in height between the canopies upstream and downstream of the

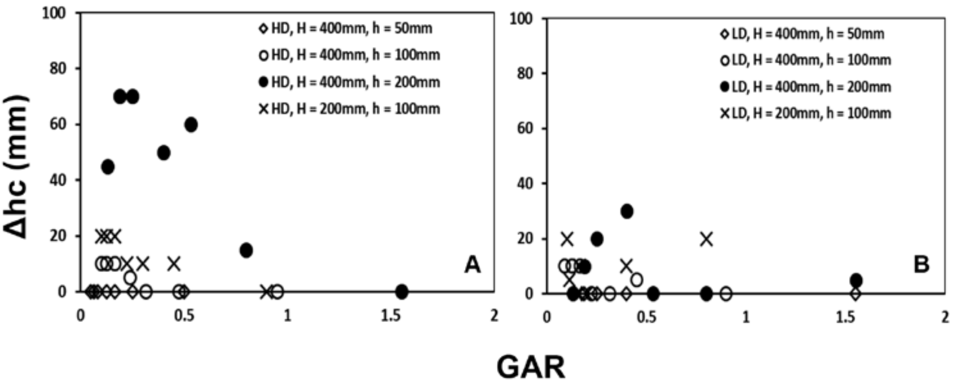


Figure 3.5
The canopy height difference (Δhc, mm) plotted against the gap aspect ratio GAR, for (A) high density (HD) and (B) low density (LD) canopy cases, and various values of water depth (H) and seagrass leaf length (h), as indicated.

gap can therefore be assumed to be due to the influence of gap hydrodynamics on the downstream canopy. Figure 3.5 shows how this difference Δh_c varies with GAR for all of the experimental runs reported here. In every case, the downstream canopy is at either the same height or lower than the upstream canopy, i.e. it is either equally or more mechanically stressed. Although there is significant scatter in the data, it is clear that Δh_c increases with increasing plant density, water depth and seagrass leaf length, and with decreasing GAR, and is zero for all runs with the shortest leaf length (50 mm).

A second way in which the gap's hydrodynamic influence can affect the downstream canopy is by altering the rate of flow (and therefore the rate of supply of dissolved nutrients and gases necessary for seagrass productivity) through it. This is quantified and investigated via the ratio $R_{down-up}$, as defined in Figure 3.2. The meaning of this ratio is similar to that given above for R_{gap-up}: when $R_{down-up} = 1$, the downstream canopy received the same rate of through flow as the upstream canopy (i.e. no gap influence); when $R_{down-up} < 1$, the downstream canopy receives less throughflow than the upstream canopy (i.e. stressing effect of gap), and when $R_{down-up} > 1$, the downstream canopy receives more throughflow than the upstream canopy (i.e. facilitating effect of gap). $R_{down-up}$ is plotted again GAR for the different flow depth, leaf length and plant density cases measured in Figure 3.6. As for R_{gap-up}, there is a clear distinction between cases either side of GAR ≈ 0.3. For the smaller GAR cases, and especially for the shortest-leaved (h = 50 mm), high density canopy, $R_{down-up} > 1$, indicating increase flow in the downstream canopy, whereas for the larger GAR cases, $R_{down-up} \leq 1$. In the longest-leaved (h = 200 mm), high density canopy in particular, there is a clear reduction in the downstream canopy throughflow compared to that in the upstream

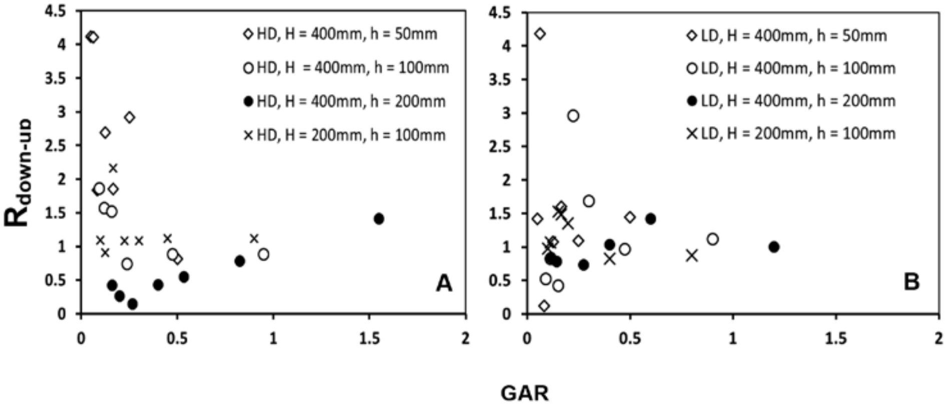


Figure 3.6
The ratio $R_{down-up}$ in in-canopy unit discharge proportion between the upstream and downstream canopies (as defined in Figure 2), plotted against the gap aspect ratio GAR, for (A) high density (HD) and (B) low density (LD) canopy cases, and various values of water depth (H) and seagrass leaf length (h), as indicated.

canopy. This is strongest at GAR ≈ 0.3, and becomes weaker as GAR increases, being replaced by a slight increase in downstream canopy throughflow at the largest GAR value used (1.6).

Discussion

Our results confirm the implication of the regime diagram proposed by Folkard (2011), that throughflow from the upstream canopy is the dominant source of flow in all of the cases in the present study. We hypothesized that this throughflow would be more dominant in the LD cases than the HD cases, because we expected the lower density canopy to allow more flow to pass through it, but this expectation is not borne out by our results (compare Figures 3.4a and 3.4b). The amount of turbulence generated within the gaps was also expected *a priori* to be greater in the HD cases than in the corresponding LD cases, because we expected stronger shear at the top of the HD canopy, but this is also found to be only marginally the case, if at all (compare Figures 3.3a and 3.3b). Instead, the clearest differences in the in-gap hydrodynamics provide two insights. Firstly, they indicate that reduced water depth creates more shear stress at the top of the canopy and thus increases the level of turbulence inside the gap (compare Figure 3.3c to Figures 3.3a and 3.3b). Secondly, they indicate that longer, shallower gaps with low GAR values (less than ≈0.3), especially those where the seagrass leaf length is short, are significantly more affected by intrusion of overflow than shorter, deeper gaps in canopies with longer leaves, where the within-gap flow is almost purely derived from throughflow in the upstream canopy (Figure 3.4).

The occurrence of a peak level of $\mathrm{TKE}_{\mathrm{mean}}$ in gaps with intermediate values of GAR (i.e. of intermediate length) in the HD cases reflects the structure of the wake of the upstream canopy (Folkard 2005), in which the turbulence maximum is a short distance downstream from the canopy edge. Thus, at for the shortest gaps (largest GAR values), the wake turbulence does not have the space to develop to its maximum extent within the gap, whereas for the longest gaps (smallest GAR values), the wake has time to both develop to its maximum extent and then decay. So the GAR values at which $\mathrm{TKE}_{\mathrm{mean}}$ is maximum is that where the wake's turbulence maximum just fits into the gap length. The lack of such a maximum in the LD cases indicates that the wake turbulence is weaker in these cases (because the upstream canopy is less dense, so the shear forces that generate the wake turbulence are weaker), so no significant turbulence maximum is generated.

The results showing the influence of gap hydrodynamics on the downstream canopy show that it is most strongly pronated (relative to the upstream canopy) when it has a high density of long leaves and the gap has a low GAR value (Figure 3.5). The greater length of the leaves makes them more easily pronated, and the low GAR value (greater length) of the gap implies that the flow has had space to develop a more established boundary layer flow structure, and thus us able to more strongly pronate the canopy. The greater difference between the upstream and downstream canopy heights in the HD cases compared to the LD cases (compare Figure 3.5a to Figure 3.5b) may be due to the lower density of plants in the upstream canopy in the LD case meaning that it is more easily pronated to its maximum extent, meaning that any increase in pronation of the downstream canopy is more limited.

The difference in the ratio $R_{\text{down-up}}$ between the longer and shorter leaved cases (Figure 3.6) indicates that shorter-leaved canopies downstream of a gap receive enhanced throughflow compared to those upstream of the gap, whereas the opposite is the case for longer-leaved canopies, especially for long, shallow gaps (low GAR values). Thus, there is a clear, qualitative difference in the relationship between the seagrass canopy and the gap-induced hydrodynamics that is dependent on seagrass canopy structure (shoot density) and morphology (leaf length).

Overall, our results show a clear distinction between cases where GAR is less than ≈0.3, in which within-gap turbulence levels are relatively low, intrusion of overflow into the gap is relatively high (but not dominant) and increased pronation of the downstream canopy is relatively strong, and cases where GAR is greater than this threshold value, where the opposite tendencies prevail.

Ecological implications of gap hydrodynamics

In ecological terms, a distinction can be made between gaps that are relatively open to influences from the overflow, and those whose character is strongly determined by the throughflow from the upstream canopy. The former tend to be longer gaps in shorter-leaved canopies in shallower water, whereas the latter tend to be shorter, deeper gaps in longer-leaved canopies in deeper water. Often, gaps create competition for nutrient uptake between pioneer vegetation and existing vegetation (Picket & White, 1985), which can result in faster growing seagrass species like *Halodule wrightii* and *Syringodium filforme* colonizing gaps in meadows of another seagrass species (e.g. Den Hartog, 1971; Patriquin, 1973). This implies that their seeds must be delivered to the gaps from outside of the meadow, a process most likely to occur via the flow over the meadow canopy. Our results suggest that this process is more likely to happen in relatively long gaps, in shorter-leaved canopies, and in shallower water. Gaps that are relatively short, occur in longer-leaved canopies, and in deeper water are more dominated by flows from within the existing meadow, and hence will be less open to seed trapping, and thus may expected to be more likely to be filled by clonal extension of the plants at the patch's periphery (Williams, 1987; Rasheed, 1999).

Our results regarding the downstream canopy imply that shorter-leaved seagrass canopies downstream of gaps, especially where the gap is long, are facilitated by the hydrodynamic effects of the gap, because they receive increased throughflow of dissolved nutrients and gasses (which typically enhances uptake; cf. Morris *et al.*, 2008), and are not increasingly pronated (mechanically stressed). Longer-leaved downstream canopies, in contrast, are increasingly stressed, both by being more strongly pronated, and by receiving decreased amounts of throughflow. These expectations need however experimental testing by field studies in different vegetation types. Overall, a proper understanding of the hydrodynamics within gaps helps to obtain a better ecological understanding of the health, functioning and resilience of patchy seagrass meadows.

References

Abdelrhman, MA. (2007). Modeling coupling between eelgrass Zostera marina and water flow. Mar. Eco. Prog. Ser. Vol: 338: 81-96.

Adhitya, A., Bouma, T.J., Folkard, A.M., Van Katwijk, M.M., Callaghan, D., De Iongh, H.H. & Herman, P.M.J. (2014). Comparison of the influence of patch-scale and meadow-scale characteristics on flow within seagrass meadows: a flume study. Mar. Eco. Prog. Ser. Vol: 516: 49-59.

Almela, E.D., Marbā, N., Alvarez, A., Santiago, R. & Martinez, R. (2008). Patch dynamics of the Mediterranean seagrass *Posidonia oceanica* implication for recolonisation process. Aquat. Bot. 89: 397-403.

Beheshti, A.A. & Ataie-Ashtiani, B. (2008). Analysis of threshold and incipient conditions for sediment movement. Coastal engineering 55: 423-430.

Borg, J.A., Attrill, M.J., Rowden, A.A., Schembri, P.J. & Jones, M.B. (2005). Architectural characteristics of two bed types of the seagrass Posidonia oceanic over different spatial scales. Est. Coast. and Shelf. Sci. 62:667-678.

Bouma, T.J., De Vries, M.B., Low, E., Peralta G., Tanczos, I.C. & Van de Koppel, J. (2005). Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. Ecology 86(8): 2187-2199.

Cardoso, P.G., Pardal, M.A., Lillebø, A.I., Ferreira, S.M., Raffaelli, D. & Marques, J.C. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. Jour. Exp. Mar. Bio. Eco. 302: 233-248.

Carr, J., D'Odorico, P., McGlathery, K. & Wiberg, P. (2010). Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resuspension and light attenuation. Jour. Geophys. Res. – Biogeosciences. Vol: 115 h 115: G03011. doi:10.1029/ 2009JG001103.

Chen, S.N., Sanford, P.L., Koch, E.W., Shi, F. & North, E.W. (2007). A Nearshore model to investigate the effect of seagrass bed geometry on wave attenuation and suspended sediment transport. Est. Coast. Vol 30 2: 296 -310.

Christianen, M.J.A, Herman, P.M.J., Bouma, T.J., Lamers, L.P.M., Van Katwijk, M.M., Van der Heide, T., Mumby, P.J., Silliman, B.R., Engelhard, S.L., Van de Kerk, M., Kiswara, W. & Van de Koppel, J. (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. Proc. R. Soc. B 281: 20132890. http://dx.doi.org/10.1098/rspb.2013.2890.

Cornelisen, C.D. & Thomas, F.I.M. (2004). Ammonium and nitrate uptake by leaves of the seagrass Thalassia testudinum: impact of hydrodynamic regime and epiphyte cover on uptake rates. Jour. of Mar. Syst. 49: 177-194.

De Falco, G., Ferrari, S., Cancemi, G. & Baroli, M. (2000). Relationship between sediment distribution and Posidonia Oceanica seagrass. Geo Mar. Letters Vol 20 1: 50-57

Eggleston, D.B., Etherington, L.L. & Elis, W.E. (1998). Organism response to habitat patchiness: species and habitat-dependent recruitment of decapods crustaceans. Jour. of Exp. Mar. Bio. Eco. 223: 111-132.

Eklőf, J.S., Gullstrő, M., Bjőrk, M., Asplund, M.E., Hammar, L., Dahlgren, A. & Őhman, M.C. (2008). The importance of grazing intensity and frequency for physiological responses of the tropical seagrass *Thalassia hemprichiii*. Aquat. Bot. 89: 337-340.

Folkard, A.M. (2005). Hydrodynamics of model *Posidonia Oceanica* patches in shallow water. Limnol. Oceanogr. 50(5): 1592-1600.

Folkard, A.M. (2011). Flow regimes in gaps within stands of flexible vegetation: laboratory flume simulations. Environ. Fluid Mech. 11: 289-306.

Fonseca, M.S., Fisher, J.S., Zieman, J.C. & Thayer, G.W. (1982). Influence of The Seagrass, Zostera-Marina L, On Current Flow. Est. Coast. and Shelf Sci. Vol:15: 351-354.

Fonseca, M.S. & Kenworthy, W.J. (1987). Effects of current on photosynthesis and distribution seagrass. Aquat. Bot. 27: 59-78.

Fonseca, M.S. & Bell, S.S. (1998). Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Eco. Prog. Ser. 171: 109-121.

Gacia, E. & Duarte, C.M. (2001). Sediment retention by Mediterranean Posidonia oceanic Meadow: The balance between deposition and resuspension. Est. Coast. Shelf Sci. 52: 505-514.

Gacia, E., Duarte, C.M., Marba, N., Terrados, J., Kennedy, H., Fortes, M.D. & Tri, N.H. (2003). Sediment deposition and production in SE – Asia seagrass meadows. Est. Coast. Shelf Sci. 56: 909-919.

Gambi, M.C., Nowell, A.R.M. & Jumars, P.A. (1990). Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. Mar. Eco. Prog. Ser 61: 159-169.

Healey, D. & Hovel, K.A. (2004). Seagrass bed patchiness: effects on epifaunal communities in San Diego bay, USA. Jour. Of Exp. Mar. Bio and Eco. 313: 155-174.

Heck Jr., K.L. & Valentine, J.F. (2006). Plant-herbivore interactions in seagrass meadows. Jour. of Exp. Mar. Bio. Eco. 330: 420-436.

Hovel, K.A. & Regan, H.M. (2008). Using an individual – based model to examine the roles of habitat fragmentation and behavior on predator-prey relationships in seagrass landscapes. Lands. Eco. 23: 75-89.

Infantes, E ., Orfila, A., Simarro, G., Terrados, J., Luhar, M. & Nepf, H. (2012). Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. Mar. Eco. Prog. Ser. 456: 63-72.

Irlandi, E.A., Orlando, B.A. & Ambrose Jr., W.G. (1999). Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradiant concentricus* (Say). Jour. of Exp. Mar. Bio and Eco. 235: 21-43.

Jonsson, P.R. *et al.* (2006). Making water flow: a comparison of the hydrodynamic characteristics of 12 different benthic biological flumes. Aquatic Ecology 40 (4): 409-438.

Koch, E.W., Ackerman, J.D., Verduin, J. & Van Keulen, M. (2001). Fluid Dynamics in Seagrass Ecology-from Molecules to Ecosystems. Seagrass: Bio. Eco. Conserv.: 193-225.

Luhar, M., Rominger, J. & Nepf, H. (2008). Interaction between flow, transport and vegetation spatial structure. Environ. Fluid Mech. 8 : 423-439.

Marjolijn, J.A.C., Govers , L.L., Bouma, T.J., Kiswara, Roelofs, W.J.G.M., Lamers, L.P.M. & Van Katwijk, M.M. (2012). Jour. Of Eco. 100: 546-560.

Martínez-Daranas, B., Cabrera, R. & Pina-Amargós, F. (2009). Spatial and Seasonal Variability of Thallassia Testudinum in Nuevitas Bay, Cuba. Rev. Mar. y Cost. ISSN 1659-455X. Vol. 1. 9-27, December 2009.

Maltese, A., Cox, E., Folkard, A.M., Ciraolo, G., La Loggia, G. & Lombardo, G. (2007). Laboratory measurements of flow and turbulence in discontinuous distributions of ligulate seagrass. Jour. Hydraulic Eng-ASCE 133: 750-760.

Mills, V.S. & Berkenbusch K. (2009). Seagrass (*Zostera muelleri*) patch size and spatial location influence infaunal macroinvertebrate assemblages. Est. Coast and Shelf Sci. 81: 123-129.

Morris, E.P. & Peralta, G., E.P., Brun, F.G., Van Duren, L.A., Bouma, T.J. & Perez-Llorens, J.L. (2008). Interaction between hydrodynamics and seagrass canopy structure: Spatially explicit effects on ammonium uptake rates. Limnol. Oceanogr 53(4):1531-1539.

Nepf, H.M. & Vivoni, E.R. (2000). Flow structure in depth limited, vegetated flow. Jour. Geophysic. Res 105: 28,547-28,557.

Patriquin, D.G. (1975). “Migration” of blowouts in seagrass beds at Barbados and Caricou, West Indies, and its ecological and geological implication. Aquat. Bot. 1:163-189.

Pérez, D., Guevara, M. & Bone, D. (2006). Temporal variation of biomass and productivity of Thalassia testudinum (Hydrocharitaceae) in Venezuela, Southern Caribbean. J. Trop. Bio. Vol 54 (2): 329-339.

Tanner, J.E. (2003). Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities. Oikos 100: 517-524.

Townsend, E.C. & Fonseca, M.S. (1998). Bioturbation as potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. Mar. Eco. Prog. Ser. 169: 123-132.

Valentine, J.F. & Heck, K.L. (1991). The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. Jour. of Exp. Mar. Bio and Eco. 154: 215-230.

Valentine, J.F., Heck, K.L., Harper, P. & Beck, M. (1994). Effects of bioturbation in controlling turtlegrass (*Thalassia testudinum* Banks ex Konig) abundance: evidence from field enclosures and observations in the northern Gulf of mexico. Jour. of Exp. Mar. Bio. Eco. 178: 181-192.

Whitfield, P.E., Kenworthy, W.J., Durako, M.J, Hammerstrom, K.K., Merello, M.F. (2004). Recruitment of Thalassia testudinum seedlings into physically disturbed seagrass beds. Mar. Ecol. Prog. Ser. 267: 121-131.

Valentine, J.F., Heck Jr., K.L. & Busby, J. (1997). Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112: 193-200.

Valentine, J.F. & Heck Jr., K.L. (1999). Seagrass herbivory: evidence for continues grazing of marine grasses. Mar. Eco. Prog. Ser. 176: 291-302.