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Flow in seagrass canopies: The influence of patch width

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Abstract

Seagrass beds and the communities they form are well known for their ability to alter their local hydrodynamic environment, reducing current velocities and altering turbulent structure in and around the canopy. Much of the quantitative information that has been published on the interaction of seagrass canopies with flowing water has been derived from laboratory flume studies. The few studies that have been conducted all point to similar patterns of flow alteration around the seagrass canopy. Differences among the results of the study are likely primarily due to different experimental configurations. Some studies have used seagrass beds much narrower than the width of the flume while others have used seagrass beds extending the full width of the flume. The validity of the latter design has often been called into question because of scaling issues. In this study, artificial seagrass was used to examine the effects of bed width in a laboratory flume on the spatial pattern of water velocity and turbulence intensity within the bed. As seagrass bed width was increased, blocking more of the cross-sectional area of the flume, the seagrass became less effective at reducing within-canopy current velocities while over-canopy flow was increased. Narrow patches (0.3 m in a flume, 1.0 m wide) were significantly more effective at reducing current velocity within the canopy than were wider patches, but experienced higher turbulence intensity. Using laboratory findings from experiments to predict field flow conditions when patch geometry differs substantially from that of a flume may either over- or under-estimate flow reduction and turbulence intensity. This is particularly the case within the first meter of horizontal distance as flow enters the canopy. Therefore, flume conditions where the bed width equals the flume width may be more appropriate for mimicking flow interaction with broad and shallow seagrass beds. Use of bed widths narrower than the flume width are likely more accurate for modeling small, developmentally arrested patches, or recently established patches such as those arising from restoration projects.

Keywords: seagrass; currents; patch size; flume; flow

1. Introduction

Some of the important ecological functions of seagrass beds (see reviews by Zieman, 1982; Phillips, 1984; Thayer et al., 1984; Hemminga and Duarte, 2000) are the indirect result of seagrasses altering the near-field hydrodynamic environment above the sediment–water interface. Water velocity decreases with distance downstream into a seagrass canopy and with vertical distance below the canopy surface (Fonseca et al., 1982, 1983; Fonseca and Fisher, 1986; Eckman, 1987; Gambi et al., 1990). These reductions in velocity (along with concomitant reductions in bulk flow and sediment movement through the canopy, but increased turbulence intensity within the canopy) have important ecological consequences. Water-borne fauna and suspended sediment can be entrained and settle, while locomotion costs for benthic fauna can be reduced. Increased turbulence intensity may reduce the diffusion boundary layer thickness around the blades of the seagrasses, potentially enhancing primary production and photosynthesis (Koch, 1994). Thus, these changes in flow characteristics mediate ecological processes that help to define the unique roles of seagrasses in the coastal environment.

One useful way to understand the interaction of seagrass plant canopies with ambient water flow is to isolate and control various aspects of the hydrodynamic environment. This means that experiments are sometimes conducted in laboratory flumes, which should be scaled to provide hydrodynamic

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conditions comparable to those observed in the field (Nowell and Jumars, 1987). But which conditions?

One of the primary factors in setting up experimental seagrass beds in a flume is scaling the size and shape of the test bed to the flow apparatus. Nowell and Jumars (1987) concluded that in flume studies, care must be taken to not constrain the flow by forcing it to go through the seagrass bed, because flow might diverge around a patch in the field. The implicit purpose in allowing flow to diverge around the patch is to isolate the influence of the seagrass canopy on the flow field, which means interference of other structures, particularly the walls of the flume, must be eliminated.

The extant work on seagrass–flow interactions is limited, and has not always followed Nowell and Jumars' (1987) guidance. Studies have been conducted where the canopy extended across the full width of the flume and still water canopy height was nearly equivalent to water depth (Fonseca et al., 1982; Fonseca and Fisher, 1986). However, other studies have conformed to Nowell and Jumars' (1987) guidance (Gambi et al., 1990), where the canopy only occupied ~8% of the flume width and plants were shorter (<1/2 water depth). However, in general, these flume-based studies of flow through seagrass beds all produced very similar results: the seagrass canopy was compressed with increasing current velocity, water flux (velocity × cross-sectional area) decreased through the canopy, flow was deflected over the canopy with an increase in velocity compared to upstream conditions, and turbulence intensity within the canopy was increased. Even studies using comparatively rigid plant mimics to simulate the plant canopy (Eckman, 1983; Nepf et al., 1997) found similar results in that boundary shear stress and fluid transport through the canopy were significantly reduced. However, the studies using rigid plant mimics found strong density-dependent effects on flow; whereas, studies using live (and highly flexible) seagrass shoots did not (Fonseca et al., 1982; Gambi et al., 1990).

Here we consider the circumstances under which it is appropriate to avoid constraining the water flow to pass through the seagrass canopy in a flume versus those for which wall-to-wall (sea) grass beds in a flume should be used. Even under the essentially borderless flow conditions in the field, very wide natural stands of seagrass (10s to 100s of meters, author's pers. obs.) presumably provide local blockage of the incoming flow. Flow blockage may be particularly influential when tides are low and seagrass plants occupy much of the water column (Fonseca and Fisher, 1986; Powell and Schaffner, 1991). Although extreme conditions such as the hydraulic jump created over a *Zostera marina* test bed by Fonseca et al. (1982) in a flume study may never occur in nature, broad seagrass stands regularly occupy shallow settings and much of the height of the water column (Bulthuis et al., 1984; Powell and Schaffner, 1991; author's pers. obs.). Therefore, having seagrass extending the entire width of a flow tank seems appropriate to examine the relative influence of natural seagrass stands of wide horizontal extent on water flow as it passes through and over those stands; in such situations there is likely limited lateral deflection of flow around the patch or intrusion of flow from edges of the stand. Conversely, allowing flow to pass around as well as over a seagrass canopy in a flume may instead better simulate small patches of seagrass.

Therefore, the purpose of this study was to measure and compare the effects on flow above and through flexible canopies when they spanned the width of a flume versus when they were narrower than the flume. Although plastic strips have been generally considered to be appropriate mimics for flexible vegetation in flume studies (Kouwen and Li, 1980), comparisons are made between other studies that have used live seagrass and the results obtained here with artificial seagrass (plastic ribbon).

2. Materials and methods

The study was conducted during 1995 in a seawater flume/wavetank (hereafter "flume") system located at the NOAA laboratory in Beaufort, North Carolina. The flume was 8 m long × 1 m wide × 0.75 m deep and was modeled after a design by Vogel (1981). The upstream end of the flume was fitted with 1.0 m long × 0.1 m diameter tubes for flow smoothing the current velocity over the test section (2 m downstream from the tubes). Velocity could be adjusted between 0.02 m s^{-1} and 0.7 m s^{-1}. Unidirectional currents were generated by a 2 HP DC motor fitted with a 5:1 reduction gear, driving two tandem, three-blade, stainless steel propellers (16 inches diameter × 12 inches pitch). Current velocity was controlled by regulating voltage to the drive motor.

Artificial seagrass was used to simulate seagrass shoots to isolate the effect of patch width from any sources of variation among plants due to epiphytes, plant flexural stiffness or plant size. Artificial seagrass patches were constructed to resemble natural *Zostera marina* beds based on the average blade length, width and ramet (shoot) density surveyed in estuarine habitats representing a wide range of environmental conditions in the Beaufort, NC area during 1993–1995 (refer to Fonseca and Bell, 1998; Townsend and Fonseca, 1998 for descriptions of the sampled habitats). Pieces of polypropylene ribbon 0.003 m wide and 0.50 m in length were folded in half forming shoots with two equal length blades, 0.25 m long; these dimensions compare favorably with local eelgrass (Table 1), although sometimes either several more senescent leaves or a very small, younger leaf are present in nature. Shoots were haphazardly glued to precut plastic Vexar® mats that had a mesh size of 5 mm. There was no mimic of the sheath structure found in live *Z. marina*. Shoot density of the artificial seagrass patches was equivalent to 1000 shoots m^{-2} (versus mean maximum densities of 724 shoots m^{-2} [standard deviation = 315.78]; Fonseca and Bell, 1998). The ribbon was positively buoyant

Table 1
Summary statistics of local *Zostera marina* shoot morphology. Values in [ ] are one standard deviation, $N = 20$

Plant component	Length (m)	Width (m)	2-D surface area (m^2)
Whole plant	0.21 [0.056]		0.002 [0.0008]
Blades	0.15 [0.044]	0.003 [0.0005]	
Sheathes	0.05 [0.013]	0.003 [0.0005]	

and had lower flexural stiffness than that of live *Z. marina* blades (author's unpublished data; Fonseca, 1998),

$$EI\ [\text{flexural stiffness}:\ \mathrm{N\,m^2}] = \left(FL^3\right)/d$$

where E = modulus of elasticity (a measure of the stiffness of the ribbon material), I = second moment of rectangular cross-sectional area, F = force (N), L = length of ribbon between attached end and position of force application, and d = lateral deflection distance (Niklas, 1992).

Plants were detached from their rhizome at the first discernible root node and dissected into blades and sheathes. A force transducer was held vertically, attached to a motorized micromanipulator arm (Oriel Model "Encoder Mike") that moved the force transducer at a constant speed of 250 μm s^{-1}. A horizontally held section of the second oldest leaf from each replicate plant was then deflected less than 10% of L. The plastic ribbon had an EI of $\sim 4.7 \times 10^{-10}$; whereas, live blades had an EI of $\sim 8.0 \times 10^{-8}$ and sheathes of live plants had an EI of $\sim 1.7 \times 10^{-7}$.

Three different patch widths were compared: 1.0 m, 0.6 m, and 0.3 m. Patches of all three widths were the same length parallel to direction of water flow (1.0 m). Prior to the start of each run, the test patch was placed on the centerline of the tank and stapled flush with the flume floor. Water current velocity was recorded using a Marsh–McBirney bi-directional electromagnetic current meter (model 523), with a time constant set to the highest resolution (0.20 s). The head of the velocity probe was 0.0254 m in diameter. The probe was mounted in a bracket that was raised or lowered to the preset elevations above the bottom. Current velocity was recorded at 50 Hz for 30 s at each of the eight elevations above the bottom and at each of the four down-current (or horizontal) positions using LabTech® software run on a laptop computer [i.e., profiles were recorded at each of 4 horizontal positions × 2 flow velocities (low flow and higher flow) × 3 patch widths]. A systematic survey of the flume under all flow combinations was conducted without plant mimics present to ensure that the centerline flow measurements were not influenced by wall effects; all velocities stabilized in the test section within $\sim$0.15 m of the wall, allowing direct comparison of all velocity profile data taken under our procedures. Data were downloaded as ASCII files and processed using SAS (1989). Current velocity measurements at the four horizontal positions and eight elevations at each position were repeated for each of three replicate patches of each width.

Three replicate patches of each width were subjected to two upstream velocities of 0.123 m s^{-1} (low flow; SE = 0.007) and 0.209 m s^{-1} (high flow; SE = 0.003). Velocity profiles were recorded at four positions down the centerline of the flume: 0.25 m upstream of edge of the test patch (−0.25 m), 0.05 m into the upstream edge of the patch, 0.50 m into the patch and 0.95 m into the patch. Each velocity profile consisted of eight measurement elevations starting at 0.02 m above the bed and continuing in 0.03 m intervals up to 0.23 m (within 2 cm of the water surface). Water velocity was averaged for each elevation at the position 0.25 m upstream of the patch, and then averaged among elevations (grand mean profile velocity) to yield upstream velocity. Current velocities in seagrass beds near Beaufort have been reported to range from 0.07 to 0.36 m s^{-1} (Townsend and Fonseca, 1998). Total water depth was 0.25 m which was equal to the length of the artificial seagrass (and was the same as used by Gambi et al., 1990), but the still water height of the artificial seagrass was approximately half the water depth due to arbitrary orientations of the blades. A high percent of water column occupation by the canopy under still water conditions ($\sim$50%) was chosen for this study to ensure friction drag by the plants would be high (i.e., strong influence of the canopy on flow, Fonseca and Fisher, 1986). Water was drawn from the estuary through the Laboratory seawater system and was a constant 22.5 °C and salinity was $\sim$34 ppt.

Turbulence intensity (u_{rms}) was computed at each horizontal position and at each of the eight elevations above the bottom for each replicate patch following Gambi et al. (1990),

$$u_{\mathrm{rms}} = \left(\mathrm{rms}\,U'/\hat{u}(z)\right)100$$

where rms = root mean square, U' = observed velocity, $\hat{u}(z)$ = mean velocity at elevation (z).

However, because of the time constant limitation, the measurement of turbulence intensity did not include fluctuations in current velocity at frequencies greater than 5 Hz. Turbulence intensity (u_{rms}) was computed for each elevation in a velocity profile. A grand mean u_{rms} was computed for each position and flow treatment as was current velocity, but only using data from those elevations within the deflected canopy.

Mean velocity was computed at each of the eight elevations in every velocity profile. For positions within the artificial seagrass patch, profiles were then segregated into those elevations above the canopy versus those within the canopy. Canopy height was determined by measuring the height of the ribbons when the water was flowing. These measurements were made to the nearest 0.01 m with a ruler at each horizontal position within the canopy.

Bulk flow Reynolds number (Re_{b}; sensu Gambi et al., 1990) was computed using the mean velocity of all eight elevations per horizontal position (i.e., grand mean). Canopy Reynolds number (Re_{c}) was also computed using a grand mean of velocity, but only using elevations from within the deflected canopy (2, 5, 8 and 11 cm above the bottom for low flow treatments; 2, 5, and 8 cm for high flow treatments). Water depth was used, as the characteristic length in the Re_{b} number computation whereas deflected canopy height was the characteristic length for Re_{c}. Reynolds number was defined as:

$$Re = Lu/\nu$$

where L = characteristic length (m), u = average current speed (m s^{-1}), ν = kinematic viscosity of seawater (m^2 s^{-1}) (Vogel, 1981).

For each position within the test patch and for each flow treatment, the mean percent change in current velocity relative to upstream free-stream velocity was calculated using the grand mean of current velocity from elevations below the height of the deflected canopy:

$$\%\text{change}_{(\text{horizontal position } n)} = \left(U_{\text{gm (horizontal position } n)}/U_{\text{gm (horizontal position } -0.25\text{ m)}}\right)100$$

where U_{gm} = grand mean velocity at a given horizontal position. Horizontal position $n = 0.05$ m, 0.50 m or 0.95 m from the upstream edge of the patch.

Using these grand means for each of the three replicates of each bed width, turbulence intensity and mean water velocity through the canopy were compared using two-way ANOVA to test for the effects of downstream position and of bed width (means and variance computed from the three replicates of each patch width). Because of flow continuity, there can be no expectation of sample independence; this obviates the common psuedoreplication problem using ANOVA that would otherwise lead to potential misinterpretation of results freeing us to use this statistic to determine the change in velocities specifically as the result of non-independent factors.

3. Results

3.1. Reynolds number

In the low flow treatment, Re_b ranged from 20,000 for the narrowest bed to 46,000 for the widest bed. In the high flow treatment, Re_b ranged from 46,000 for the narrowest bed to 56,000 for the widest bed (mean = 49,996). In the low flow treatment, Re_c ranged from 10,000 for the narrowest bed to 18,000 for the widest bed (mean = 15,885). In the high flow treatment, Re_c ranged from 14,000 for the narrowest bed to 19,000 for the widest bed (mean = 16,061). All Re values tended to increase slightly with downstream distance as well.

3.2. Velocity over and through the canopy

In the low flow treatment, the artificial seagrass canopy was 0.125 m tall (25% of its height in still water), while in the high flow treatments, it was only 0.085 m tall (17% of its height in still water). All velocity profiles taken in the artificial seagrass displayed stratification into two distinct flow fields, one above and one below the canopy top. Velocities increased over the canopy and declined within the canopy for beds of all widths in both flow treatments (Fig. 1a–h).

The flow both within and above the canopy was faster in wide beds than in narrow beds (Table 2). This effect was more pronounced at positions that were further downstream from the leading edge of the bed (Table 2) and at elevations above 0.07 m (Fig. 1a–d). Specifically, at the 0.50-m and 0.95-m positions in the low flow treatment (Fig. 1c, d) and the 0.95-m position in the high flow treatment (Fig. 1h), increased bed width resulted in increased velocities within and above the canopy, likely because flow could no longer be deflected around the canopy. Thus overall, the effect of bed width was less pronounced in the high flow treatments (Fig. 1e–h).

Water velocities were slightly reduced by a few percent at the upstream edge (0.05 m) of the canopy, regardless of bed width (Table 1). In contrast, flow velocities were reduced substantially at positions further into the bed from the leading (upstream) edge (Table 3). For the 0.5-m and 0.95-m downstream positions within the canopy, the percent reduction in current velocity was greater in narrow beds than in wide beds; this effect was more pronounced in the low flow treatments, presumably the result of the canopy being less compressed and therefore more penetrable by the flow field (Table 3). Only the 1.0-m bed width treatment display a marked, increased current velocity over the canopy at all positions within the bed, including the 0.05-m distance. The narrower bed width treatments did not cause an obvious increase in current velocity over the canopy until the 0.5-m distance (Table 3). For both the flow treatments, there was no significant difference between the two downstream stations under the high flow treatment, but here both were significantly lower than the upstream (0.05 m) station (not shown). This means that at these high flow velocities, by 0.5 m into a bed the flow velocity profile had largely stabilized.

The patterns in percent flow reduction (Table 3) within and above the canopy were generally verified by the results of the two-way ANOVAs (Tables 4 and 5). There were no significant interaction effects of horizontal position and bed width treatment either within or above the canopy (Tables 4 and 5). The mean current velocities for those elevations measured within the artificial canopy were significantly reduced with downstream distance (position) for both flow treatments. However, under the low flow treatment, there was a trend, albeit significant only at $p = 0.06$, for mean velocity within the canopy to increase with bed width (1.0 m > 0.6 m > 0.3 m bed widths). Under the high flow treatment, only position had a significant (negative) effect on current velocity within the canopy.

For elevations above the deflected canopy, the effect of both position and bed width on current velocity was significant (Table 5). In these instances, velocity decreased with downstream position within the bed but increased significantly at any given position as a function of increased bed width, with shoot density being constant.

3.3. Turbulence intensity

Turbulence within the canopy tended to be slightly higher under the lower flow treatment when the canopy was less deflected. Under the low flow treatment, u_{rms} increased rapidly and significantly with downstream position within the canopy and with distance down into the canopy (Fig. 2a–c). There was no significant interaction effect of downstream position and bed width on u_{rms} under the low flow treatment (Table 6). Turbulence intensity increased with downstream position but was somewhat (but not significantly) lower for the widest bed (Fig. 2). Bed width alone had no significant effect on u_{rms} in the low flow treatment.

Under high flow treatments, there was a significant interaction effect of position and bed width. Increased downstream position lead to significantly increased u_{rms}, but that effect was itself diminished significantly as bed width increased. Like the low flow treatment, turbulence intensity increased with downstream position under high flow but was lower for

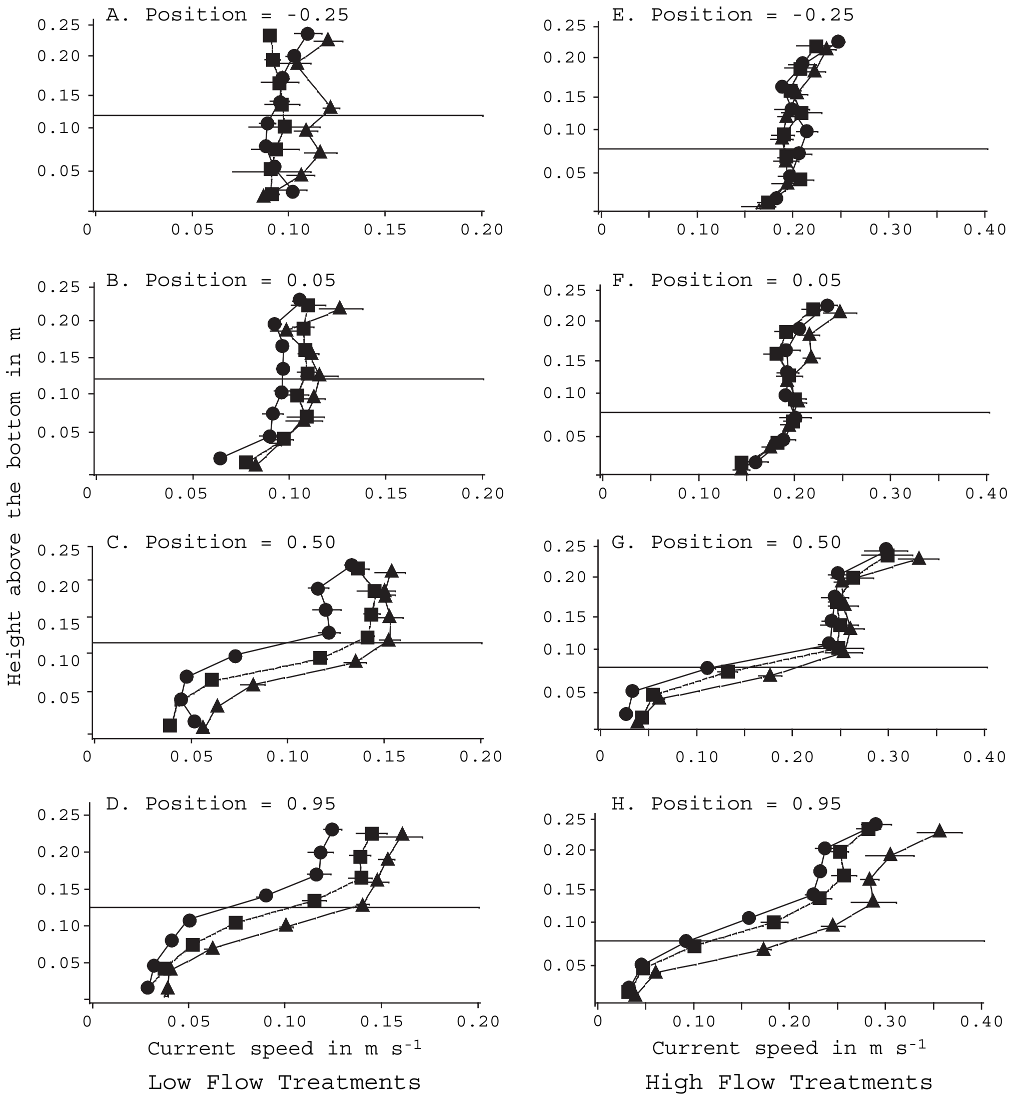

Fig. 1. Velocity profiles for each position (0.25 m upstream of the test bed, and within the test bed at different distances from its upstream edge [0.05 m, 0.50 m, 0.95 m]), at each of two flow treatments (0.123 [low] and 0.209 m s^{-1} [high]), and three test bed widths (circles = 0.3, squares = 0.6, triangles = 1.0 m). Note different velocity axes for each of the two flow treatments. Horizontal line is the deflected canopy height. Error bars are one standard error of the mean; if not visible then they are less than the size of the symbol.

the widest bed near the bottom. Under both velocity trials, the beds that were 0.3 m and 0.6 m wide tended to have mutually similar patterns of u_{rms} while the widest bed (1.0 m) tended to have lower u_{rms} within the canopy. This occurred as more flow was directed over the canopy with increased bed width.

4. Discussion

4.1. Comparison of artificial canopies with natural seagrass canopies

Although the artificial seagrass canopy used in this study bent over more, moving the blades closer together than live seagrasses used in previous flume studies (Fonseca and Fisher, 1986; Fonseca and Kenworthy, 1987; Gambi et al., 1990), the previously observed pattern of velocity reduction with downstream distance within the canopy was upheld (Table 1). Specifically, the artificial seagrass blades were deflected more (by a factor of 1.8; deflection being the horizontal displacement of the blade tips) than had been previously described for live *Zostera marina* of similar length (e.g., 0.25-m-long shoot mimics used here as compared to 0.185-m live plants used by Fonseca and Kenworthy, 1987). This deflection difference appeared to result primarily from lower flexural stiffness of the plastic mimics, despite their positive buoyancy. This difference between the artificial shoots and live *Z. marina* meant that the higher deflection of the artificial shoots at any given velocity made for a higher density of obstructions to the flow near the bottom of the flume than would be expected with live plants.

Compressing the canopy into a dense mass near the bottom of the flume likely deflected water over and around the canopy to a greater degree than was experienced in previous studies that used live seagrass (e.g., Fonseca et al., 1982). For

Table 2
Grand means of turbulence intensity and current velocity WITHIN and ABOVE the artificial seagrass canopy by downstream distance (position) and bed width. U = profile averaged current velocity 0.25 m upstream from edge of canopy

	Flow regime							
	$U = 0.209$ ($m\,s^{-1}$)		$U = 0.123$ ($m\,s^{-1}$)		$U = 0.209$ ($m\,s^{-1}$)		$U = 0.123$ ($m\,s^{-1}$)	
	Turbulence intensity				Mean velocity			
	In	Above	In	Above	In	Above	In	Above
Position (m)								
0	57.5	57.6	58.5	59.4	18.9	20.8	8.9	10.1
0.5	58.6	57.4	68.2	59.6	7.4	18.5	4.6	10.3
1.0	62.9	59.4	65.4	60.8	6.4	14.8	3.2	7.6
Bed width (m)								
0.3	60.9	59.4	65.4	60.2	10.2	16.5	4.5	7.2
0.6	59.8	57.7	62.2	60.9	10.6	17.5	5.6	9.7
1.0	58.4	57.3	64.5	58.6	11.9	20.0	6.7	11.1

example, shoot densities and free-stream velocities here were comparable to those of Gambi et al. (1990) (1000 shoots m^{-2}, 0.2 $m\,s^{-1}$ velocity, respectively), although they used a test bed of 0.15 m as compared with the smallest width here of 0.30 m (and occupied 32–45% of the water column). However, Gambi et al. (1990) had a 0.30 m space from test bed to wall, which was similar to the 0.35-m distance used here. Gambi et al. (1990) also reported a velocity reduction of 19.6% at the 0.5-m horizontal distance into the canopy, consistent with Fonseca et al. (1982); whereas, a 31.1% reduction (Table 1) was found here. Similarly, at the 1.0-m horizontal distance into the canopy, Gambi et al. (1990) reported a 21% reduction in velocity, whereas a 38.7% reduction was measured in this study. Reynolds number for the canopy in this study was at most a quarter of that reported by Gambi et al. (1990), partly due to their use of a different characteristic length that would consistently elevate the Re_c estimate compared to this study. Interestingly, turbulence intensity within the canopy was not unlike previous studies (e.g., Gambi et al., 1990), ranging upwards to 50–70% (Fig. 2). Moreover, these results are consistent with how flow should interact with a more deflected and tightly compressed canopy as was the case here, using artificial seagrass in lieu of natural seagrass.

Table 3
Percent change in current velocity through the artificial seagrass canopies of different widths and at positions (m) downstream into the canopy, as compared with a station located 0.25 m upstream of the test section. Values are %change in current velocity for all elevations either WITHIN or ABOVE the canopy. 'In' = within the canopy; 'Above' = over the canopy. U = profile averaged current velocity 0.25 m upstream from edge of canopy

U ($m\,s^{-1}$)	Bed width (m)	Position = 0.05		Position = 0.50		Position = 0.95	
		In	Above	In	Above	In	Above
0.123	0.30	−9.2	−2.0	−67.5	+8.4	−79.1	+4.1
	0.60	−5.1	−5.6	−70.0	+8.8	−75.6	+7.9
	1.0	−6.8	+3.7	−54.5	+28.9	−69.8	+31.6
0.209	0.30	−4.4	+0.9	−83.5	+13.1	−81.8	+7.6
	0.60	−7.3	+1.8	−75.2	+15.8	−81.6	+7.7
	1.0	−10.1	+3.9	−74.2	+13.2	−75.2	+23.3

Table 4
Two-way ANOVA of grand mean current velocity WITHIN the artificial seagrass canopy by downstream distance (position) and bed width. U = profile averaged current velocity 0.25 m upstream from edge of canopy. Bold values denote important trends

U ($m\,s^{-1}$)	Source	d.f.	F	Pr > F
0.123	Position (P)	2	22.07	**<0.001**
	Bed width (B)	2	3.10	**0.0614**
	PB	4	0.07	0.9905
0.209	Position (P)	2	23.77	**<0.001**
	Bed width (B)	2	0.40	0.6879
	PB	4	0.28	0.9188

4.2. Effects of bed width on flow

The effect of bed width on water flow was generally the same for both artificial (this study) and live seagrass canopies of similar scale (i.e., percentage of flume width occupied; Gambi et al., 1990). As the width of the test bed was increased and reached across the flume, there was less current velocity reduction by the canopy. Unlike the narrower beds around which flow was apparently deflected, water was constrained to pass through the canopy in the case of the wider test beds, resulting in higher velocities within the canopy as bed width increased. This increase in velocity through the canopy necessarily follows rules of flow continuity (Fonseca et al., 1983) and is the kind of response Nowell and Jumars (1987) have warned against for evaluating hydrodynamics of seagrass beds in flumes. However, with the exception of within-canopy, high flow conditions when canopy compression would have been at its greatest, increased bed width significantly increased both within and above-canopy velocities.

Plant canopies can alter the turbulence intensity (u_{rms}) of flow within them due to vortex shedding by shoots, and to fluttering (Anderson and Charters, 1982; Gambi et al., 1990; Ackerman and Okubo, 1993). Seagrass beds (both artificial and live) increase the turbulence intensity of flow within the canopy. For example, in this study using artificial seagrass, u_{rms} within the canopy increased with downstream distance, as well as ambient flow speeds, effects similar to those described by Gambi et al. (1990) who used natural seagrass. However, while the results from the present study did not differ markedly from Gambi et al. (1990) in %intensity, they observed an increase in u_{rms} at the surface of the canopy, with

Table 5
Two-way ANOVA of grand mean current velocity ABOVE the artificial seagrass canopy by downstream distance (position) and bed width. U = profile averaged current velocity 0.25 m upstream from edge of canopy. Bold values denote important trends

U ($m\,s^{-1}$)	Source	d.f.	F	Pr > F
0.123	Position (P)	2	3.69	**0.0348**
	Bed width (B)	2	3.47	**0.0418**
	PB	4	1.53	0.2128
0.209	Position (P)	2	10.29	**0.0005**
	Bed width (B)	2	28.10	**<0.0001**
	PB	4	0.22	0.1573

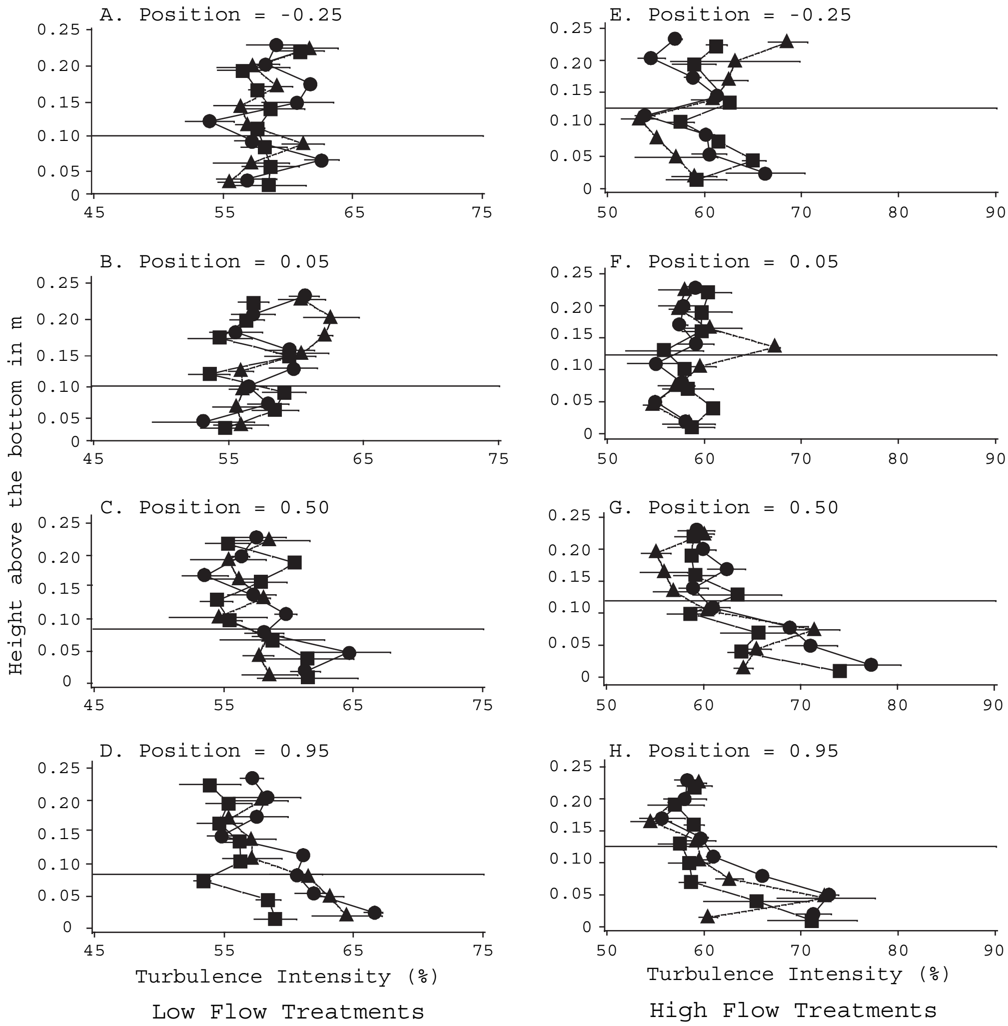

Fig. 2. Turbulence intensity profiles for each position (0.25 m upstream of the test bed, and within the test bed at different distances from its upstream edge [0.05 m, 0.50 m, 0.95 m]), at each of two flow treatments (0.123 [low] and 0.209 m s^{-1} [high]), and three test bed widths (circles = 0.3, squares = 0.6, triangles = 1.0 m). Note different turbulence intensity (%) axes for each of the two flow treatments. Horizontal line is the deflected canopy height. Error bars are one standard error of the mean; if not visible then they are less than the size of the symbol.

a slight reduction closer to the bottom; whereas here, there was no clear increase in u_{rms} at the canopy surface and u_{rms} remained high to within 0.02 m of the bottom. This difference is likely due to the greater deflection of the artificial seagrass and perhaps less fluttering by the artificial seagrass. We attribute this departure from previously observed canopy flow structure (Gambi et al., 1990) to the fact that at the higher velocities, the artificial canopy was more compressed than a natural canopy would have been, reducing inter-shoot spacing, blade spacing, and flow penetration into the canopy and thus, reducing turbulence intensity. Nonetheless, turbulence intensity in the narrower beds was slightly greater than in the wider beds, especially as ambient flow velocity increased.

Nowell and Jumars (1987) suggested that with decreasing test bed width there should be greater intrusion of flow into the canopy from the side (as evidenced by the slackening of current velocity over the canopy by the 1.0-m distance, meaning that flow could have been penetrating the canopy more effectively). Increased flow intrusion into the canopy for the narrower bed widths likely contributed to increased turbulence intensity within the canopy as seen here, especially as inter-shoot spaces increase with decreasing mean velocity. However, we are uncertain as to how this translates into shoot

Table 6
Two-way ANOVA of turbulence intensity WITHIN the artificial seagrass canopy by downstream distance (position) and bed width. U = profile averaged current velocity 0.25 m upstream from edge of canopy. No significant effects were found for turbulence intensity ABOVE the canopy (not shown); only position under high flow approached significance ($p = 0.0851$). Bold values denote important trends

U (m s^{-1})	Source	d.f.	F	Pr > F
0.123	Position (P)	2	14.99	**0.001**
	Bed width (B)	2	1.6	0.2202
	PB	4	0.73	0.5815
0.209	Position (P)	2	13.9	**0.002**
	Bed width (B)	2	2.71	**0.0936**
	PB	4	3.01	**0.0459**

density effects. Given that the choice of bed width will determine the magnitude of change in various hydrodynamic attributes in and around the canopy, what then is the appropriate choice of bed width for a controlled flow study?

We propose that the choice of test bed width should depend upon the mechanism under study. For example, if one wanted to enhance turbulence as a means of testing efficiency of molluscan filter feeders within the bed (sensu Eckman, 1987; Irlandi, 1996), then varying bed width may be a simple means to create a gradient of turbulence within the test bed, without changing any other feature of the canopy. If examination of near-field flow interactions with newly established small patches was the intent, then narrow patches, isolated from wall effects would be appropriate. But because many seagrass beds are quite broad with respect to the direction of flow and flow deflection around the canopy is not possible, then scaling of bed width in flume studies to constrain flow as would be expected in natural settings, would be an appropriate choice.

4.3. Relevance of bed width scaling to development and maintenance of seagrass beds

Perhaps as important as its role as a manipulative tool, the effect of bed width should be considered in the context of what bed width represents in a natural setting. Many submersed species begin occupation of new space isolated from parent populations through either colonization by seed or plant fragments, initially forming very small patches (author's pers. obs.). When these new patches form, they will likely possess hydrodynamic characteristics more like the narrow test bed used here, than the wide bed where flow characteristics may be more representative of older, more established patches, or perhaps even larger continuous-cover beds.

Small patches do reduce velocity, but may have a disproportionate effect on turbulence (sensu Koch et al., in press), producing a level of turbulence that may be similar to larger beds but within a short horizontal distance. The results of such a phenomenon are intriguing as, contrary to general perceptions of seagrasses acting to create more quiescent conditions and accelerating accumulation of fine sediments, we have observed small patches with elevated levels of turbulence, which can produce sediment surfaces with coarser, rather than finer sediment within the patch (Fig. 3; albeit under oscillatory flow). Any similar winnowing of fines under unidirectional flow would also effectively armor the sediment and help protect the small patch from being uprooted at high flows, a process that suggests an ontogeny of canopy flow behavior as beds expand. Similarly, in restoration projects, where newly installed plantings often occur as isolated patches or clumps of plants, these hydrodynamic interactions may assist in survival and suggest experimentation with sediment armoring techniques.

The increased percent reduction in current velocity with decreasing bed width suggests that small patches, if of sufficient length in the downstream direction, are inherently able to retain sediment over a greater range of current velocities than wider beds, over the same horizontal distance. Given that the higher test velocity in this experiment ($0.203\ m\,s^{-1}$) was near the threshold velocity required for bedload transport of most sand in the Beaufort area ($\sim 0.3\ m\,s^{-1}$, Fonseca and Fisher, 1986), it seems likely that small patches in nature should experience enhanced velocity reduction but comparatively high levels of turbulence intensity as compared to wider beds, as seen in the flume studies. This could translate directly into improved patch survival, especially if accompanied by the increased armoring effects as seen in Fig. 3.

Fig. 3. A small eelgrass patch on an intertidal flat near Oakland, California, August 2003. Note the presence of coarser, sorted sediment within the patch as compared to the unvegetated, surrounding area.

5. Conclusions

1. Artificial seagrass canopies qualitatively have the same effects on flow as real beds, but not quantitatively; careful engineering of artificial shoots to accurately mimic natural seagrass appears to be required (sensu Ghisalberti and Nepf, 2002).
2. Increased bed width increased within-canopy flow velocity and turbulence intensity (decreased turbulence intensity within the canopy, when it occurred, may have been exacerbated by comparatively [to natural seagrass] high canopy deflection and compaction making these results conservative regarding potential turbulence intensity levels).
3. Bed width significantly influences within and over-canopy flow behavior and in simulations, bed width should be chosen so as to mimic the desired field conditions.
4. Bed width also influences turbulence intensity within the canopy.
5. Flow-dependent processes within seagrass beds may have a predictable otogeny as the bed grows and changes width normal to the direction of flow.
6. Ontogenetic changes in flow-dependent processes within seagrass beds may provide clues to adaptive strategies by which these communities develop and maintain themselves across different flow regimes.

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