

# Let it flow: how does an underlying current affect wave propagation over a natural seagrass meadow?

Maike Paul<sup>1,\*</sup>, Lucy Gwen Gillis<sup>2</sup>

<sup>1</sup>Forschungszentrum Küste, Leibniz Universität Hannover, Merkurstr. 11, 30419 Hannover, Germany

<sup>2</sup>Netherlands Institute for Sea Research (NIOZ) — Yerseke, Korrिंगaweg 7, 4401 NT Yerseke, The Netherlands

**ABSTRACT:** Temperate seagrass beds can be found within intertidal and tidal areas of variable hydrodynamic forcing. To investigate the interaction between hydrodynamics and seagrass plants, *Zostera noltii* meadows were exposed to a range of combinations of waves and flow in a flume. Velocity profiles were obtained to observe the evolution of hydrodynamic forcing due to the presence of a seagrass canopy. Observations under flow without waves agreed with those of previous studies and showed that turbulent kinetic energy (TKE) at the top of the canopy increased with increasing flow velocity as well as with distance from the leading edge. The highest TKE values were achieved for the highest flow velocity without waves, and the presence of waves generally led to reduced TKE values. Profiles of time-averaged downstream velocity were not affected by the presence of waves. However, flow reduction near the bed increased with higher seagrass density, resulting in an S-shaped profile for the highest density and flow velocity. Underlying currents affected wave orbital velocities, causing a reduction of orbital diameters in the free-stream region. In the canopy region, this process was superimposed by the damping effect of the seagrass meadow, but only positive flow components were reduced by seagrass presence. Streamlining and oscillating motion of seagrass leaves were observed under flow and waves, respectively. These processes did not affect the wave/flow attenuation capacity of the meadow, which indicates that the ecosystem-engineering traits of seagrasses are not compromised by increased flow velocity or in the presence of waves.

**KEY WORDS:** *Zostera noltii* · Velocity profiles · Waves · Currents · Turbulence · Flume

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## INTRODUCTION

Temperate seagrass beds can be found in intertidal and sub-tidal areas of variable hydrodynamic forcing (Larkum et al. 2006), including wave action, flow and turbulence (Peterson et al. 2004). Hydrodynamics affect pollen dispersal (Verduin et al. 2002), nutrient availability (Weitzman et al. 2013) and uptake rates of seagrass plants (Thomas & Cornelisen 2003, Cornelisen & Thomas 2004, Morris et al. 2008). In return, seagrass beds can significantly alter hydrodynamic forcing via reflection from the leaves, flow diversion, and absorption of energy through drag and motion (see Paul et al. 2014 for a comprehensive review).

These effects can have implications for sediment transport, nutrient availability within seagrass beds as well as coastal protection, and have therefore been the focus of several studies in the past.

Key seagrass traits that affect wave attenuation include shoot density (e.g. Chen et al. 2007), stiffness (e.g. Bouma et al. 2005) and leaf length (e.g. Fonseca & Cahalan 1992) or leaf area index as combining parameter (Paul et al. 2012). These studies compared surface elevation measurements at different locations along a vegetated patch to derive wave height reduction and relate this to properties of flexible vegetation. Their results also agree with observations for less flexible vegetation (e.g. salt marsh, Bouma et al.

\*Corresponding author: paul@fzk-nth.de

2010) and vegetation-like structures, e.g. plastic strips (Augustin et al. 2009). Under unidirectional flow, velocity profiles have been used to investigate the effect of flexible vegetation on turbulence and flow propagation, similar to the extensive work carried out in atmospheric sciences (see Raupach et al. 1991 for a review). Submerged vegetation behaves like a barrier and deflects part of the flow upward, which leads to reduced flow inside the canopy and enhanced velocities above it (Fonseca et al. 1982, 1983, Fonseca & Kenworthy 1987). This pattern is consistent for all seagrass species, including *Amphibolis antarctica*, which differs morphologically from other seagrasses as it has a pronounced leafless stem. A field study regarding *A. antarctica* established that this stem region led to a slight increase in flow close to the bed (Verduin & Backhaus 2000), but the overall profile yielded the same logarithmic pattern, with an inflection point at the top of the canopy (Fonseca 1990), as species with uniform biomass distribution.

The magnitude of flow reduction, however, depends on shoot density (Peterson et al. 2004) and spatial arrangement (Fonseca et al. 2007), as well as hydrodynamic parameters (Heller 1987, Gambi et al. 1990). The extensive data set by Gambi et al. (1990) has been used to validate various models (Abdelrhman 2003, Peterson et al. 2004), which are able to predict velocity profiles and fluxes within and above flexible vegetation. Gambi et al. (1990) exposed *Zostera marina* meadows of different density to a range of unidirectional flow velocities and were able to distinguish 2 zones with different dynamics within the meadow in all treatments: the first is the canopy–water interface, which has high shear stress and turbulence intensity; the second is the below-canopy zone, which, in contrast, has low shear stress and reduced turbulence intensity. The measurements showed that shear velocity and turbulence increased with distance into the meadow, but within the range of shoot densities tested (400–1200 shoots m<sup>-2</sup>) no effect of density on the velocity structure could be observed. The latter finding contradicts other observations in the field (Peterson et al. 2004) and laboratory (Fonseca et al. 1982), but can be explained by the experimental setup. Gambi et al. (1990) only covered parts of the flume width with seagrass, hence allowing the flow to move around the vegetation in addition to diverting the flow above the canopy. Flow reduction within the canopy leads to increased settling of sediment, particulate organic matter and larvae (Eckman et al. 1994, Gacia et al. 1999) and protects roots from scouring (Fonseca et al. 1982). Field studies observed resuspension in a natural *Thalassia*

*testudinum* bed under moderate hydrodynamic conditions (Koch 1999) as well as elevated levels of suspended particulate matter due to resuspension and advection inside a seagrass meadow under high wave energy during storm surges (Ward et al. 1984). Nevertheless, sedimentation rates are generally higher within seagrass meadows than in unvegetated areas (Ward et al. 1984), and seagrasses are commonly considered to prevent erosion (Fonseca & Fisher 1986, Fonseca 1996, Granata et al. 2001).

In the upper part of the canopy, turbulence and flow velocity increases (Gambi et al. 1990), which can affect the growth rate of plants by promoting nutrient uptake and photosynthesis (Fonseca & Kenworthy 1987). At low flow velocities, a pronounced diffusive boundary layer hampers nutrient uptake while enhanced flow and turbulence reduce this layer and hence promote uptake (Koch 1994), provided that enzymatic processes are not limiting nutrient uptake. Experiments with artificial seagrass revealed that the turbulent flow region in the upper part of the canopy is caused by the onset of vortex shedding (Ghisalberti & Nepf 2002). This can lead to a monami, i.e. a waving motion of the canopy, of a given frequency, as was revealed for the first time in the field by Ackerman & Okubo (1993) and can be reproduced in the laboratory if the seagrass patch is of sufficient length (Nepf & Ghisalberti 2008). These vortices and associated turbulence were investigated in detail (Nepf 2012b) and linked to the meadow's roughness density, which is a non dimensional measurement of the canopy density. Roughness density can be calculated via multiplying the leaf width, shoot density and the canopy height (Nepf 2012b). Turbulence generated by submerged vegetation also propagates downstream beyond the patch, causing a wake region with elevated Reynolds stress levels behind it. Folkard (2005) investigated the effect of such a wake region on turbulence inside a second vegetation patch downstream and suggested that the wake length determines the gap size between patches as enhanced turbulence at the beginning of the second patch will negatively affect deposition of particulate derived nutrients via organic matter.

Flexible vegetation not only influences hydrodynamics, it is also affected by the acting forces analogue to terrestrial vegetation in airflow. Under a steady current, plants will bend into a more streamlined position until a maximum bending angle is reached (Vogel 1994, Boller & Carrington 2006). This streamlining reduces the frontal area of flexible vegetation and hence the form drag acting on the plants compared to stiff plants of the same size which

remain fully upright under the same hydrodynamic forcing (Vogel 1984, 1989, Koehl 1996, Järvelä 2004, Aberle & Järvelä 2013). Under wave forcing, vegetation will respond to oscillatory motion in an either whip-like or cantilever motion (Denny et al. 1998, Denny & Gaylord 2002, Paul et al. 2012). Both streamlining and swaying are controlled by the magnitude of the forcing and the biomechanical properties, e.g. stiffness of the plant (Koehl & Wainwright 1977, Paul et al. 2014). As vegetation reconfiguration alters the position of the plants in the water column, it will affect the effect vegetation has on hydrodynamics, resulting in a close interaction between the 2 processes. As a consequence, plant stiffness can be considered a driving factor in wave and flow alteration by submerged vegetation (Koehl 1984, 1996, Bouma et al. 2010, Dijkstra & Uittenbogaard 2010). In the present study, however, only one seagrass species will be investigated and the effect of stiffness on velocity profiles can therefore not be evaluated.

To date, investigations have focused on the hydrodynamic effect of seagrass traits subjected to either wave action or flow; these studies do not reflect natural conditions where both flow and waves coexist. However, it has been recognised that combined wave action and flow can result in different responses compared to each forcing individually. Recently, a combination of waves and flow was used to investigate the effect of hydrodynamics on retention times of organic matter (Gillis et al. 2014) and nutrient uptake (Weitzman et al. 2013). These studies were able to show the difference in hydrodynamics within and above a natural seagrass canopy, but could not address changes that occur when waves and/or flow travel along a vegetated stretch. The latter was investigated with respect to wave attenuation in recent studies which yielded contradicting results: Li & Yan (2007) observed enhanced wave attenuation in the presence of an underlying current in the same direction while Paul et al. (2012) found that an underlying current reduces wave attenuation over an artificial seagrass meadow. A laboratory study with stiff vegetation-like structures encompassed the hydrodynamic conditions of both these studies and a non-steady relationship between underlying flow velocity and wave attenuation was proposed (Hu et al. 2014). This would explain the earlier discrepancy of findings. However none of these studies allowed for the measurement of velocity profiles to detect turbulence fluctuations.

Most previous studies defined wave attenuation as wave height reduction obtained from surface elevation measurements, but the effect of flexible vegetation on turbulence or velocity profiles under waves

has received little attention so far. A comparative study found that the effectiveness of flow reduction in different current regimes varied with seagrass species and generally depends on flow velocity, wave frequency and distance into the meadow (Heller 1987). In a more recent study, Chen et al. (2007) investigated the effect of flow on wave attenuation by seagrass numerically, but the study is limited by the use of separate validation datasets for waves and flow only, respectively. In addition to the scarcity of data under combined waves and currents in the presence of submerged flexible vegetation, past research has mainly used artificial structures to represent seagrass plants or beds. While their behaviour visually matched that of real vegetation and such an approach gives insight in general processes, surrogates lead to a deviation from and simplification of natural conditions. The present study expands existing knowledge by exposing real seagrass canopies to waves superimposed on a range of flow velocities. The objectives of this study are to assess which hydrodynamic conditions may be favourable for seagrass growth, and whether the ecosystem engineering functions of seagrass depend on their physical environment. To achieve these objectives, this study investigates (1) how wave and flow propagation is affected by seagrass presence under naturally occurring wave and flow conditions, and (2) how seagrass responds to natural hydrodynamic conditions and how this response is linked to wave and flow attenuation.

## MATERIALS AND METHODS

### Plant material

The small, temperate seagrass *Zostera noltii* was used to study the interaction of vegetation, waves and flow. This species was specifically chosen as it colonises the intertidal zone where the combination of waves and tidal currents is most pronounced. *Zostera noltii* has ribbon-shaped leaves which are 0.5–1.5 mm wide and can be up to 22 cm long (Phillips & Meñez 1988); it shows strong seasonality in above ground biomass with high values in summer and low values in winter (Paul & Amos 2011).

Healthy and undisturbed sections of *Z. noltii* (60 × 22.5 cm) were excavated from the Oosterschelde tidal lagoon (51° 27.987' N, 4° 4.512' E) on 26 and 27 June 2013 with permission from the Province of Zeeland and Natuurmonumenten. The *Z. noltii* sections were transferred directly to the Netherlands Institute for Sea Research (NIOZ) in Yerseke. The

seagrass meadow sections were then stored in large outdoor holding tanks filled with seawater pumped directly from the Oosterschelde, to allow for recovery from transportation. After 4 d of acclimatisation the sections were placed in a flume to build a continuous seagrass meadow of 135 cm length across the width of the flume (60 cm). The flume was filled with natural seawater from the adjacent Oosterschelde and the water was changed every 4 d. Additionally, the flume was illuminated at night and during weekends to allow for photosynthesis.

Leaf dimensions were measured for 20 randomly chosen leaves throughout the meadow and were used to calculate roughness density  $\lambda$  (Nepf 2012b):

$$\lambda = \int_{z=0}^{h_c} a \, dz \quad (1)$$

where  $z = 0$  at the bed,  $h_c$  is canopy height and  $a$  is the frontal area per volume ( $a = bs$ , where  $b$  represents the leaf width and  $s$  is shoot density). Streamlining of flexible vegetation under hydrodynamic forcing results in a reduction of  $h_c$ , but also an increase in  $a$  as the same amount of biomass is compacted in a smaller volume. Consequently,  $\lambda$  is independent of hydrodynamic conditions and for a canopy with vertical uniform  $a$ , such as the strip-like *Z. noltii*, Eq. (1) simplifies to:

$$\lambda = bls \quad (2)$$

where  $l$  is leaf length.

Shoot density was evaluated by counting all shoots present in the installed seagrass meadow and dividing them by the meadow size. The meadow had an initial shoot density  $s_h = 1369$  shoots  $m^{-2}$  (high) which was reduced to  $s_l = 685$  shoots  $m^{-2}$  (low) during the course of the experiments by cutting off half of the shoots directly above the bed. These densities are representative for early summer and winter states of a natural, well established *Z. noltii* meadow in the southern North Sea (Paul & Amos 2011). Finally, all shoots were removed to evaluate the effect of only the sediment bed on hydrodynamics. As the bed consisted of natural meadow sections, the sediment was not even but provided a roughness element due to its bathymetry (Fig. 2b), which was surveyed at 2 cm increments with a ruler extending down from a horizontal bar spanning the flume at a constant height.

### Hydrodynamic conditions and instrumentation

The experiments were carried out under controlled conditions in the racetrack wave flume at NIOZ. This flume permits unidirectional flow of up to  $0.45 \text{ m s}^{-1}$ ,

and regular waves of varying heights and periods. For a detailed description of the flume, see Paul et al. (2012). The water depth was set to 30 cm to ensure a layer of water above the vegetation for all treatments. Four different flow velocities ( $0.05$ ,  $0.1$ ,  $0.2$  and  $0.3 \text{ m s}^{-1}$ ) were generated. The high density meadow and the unvegetated case were exposed to each flow velocity once with and without superimposed regular waves (wave height 4 cm and period 1.1 s). The same treatments were completed for the low density meadow; however flow velocities of  $0.05$  and  $0.2 \text{ m s}^{-1}$  were omitted. This setup resulted in 9 hydrodynamic conditions and a total of 23 different treatments of which 13 covered the combined waves and flow cases.

The meadow was installed with its leading edge 850 cm downstream of the wave paddle to enable waves and flow to fully develop before reaching the vegetation. Velocity profiles were obtained at the leading edge ( $x = 0$ ) as well as 45 cm, 90 cm and 135 cm downstream along the central axis of the flume. Each profile consisted of 13 points in the vertical ( $z$ ), spaced 1.5 cm apart and starting 1 cm above the bed ( $z = 0$  being at the bed). Consequently, each profile covered a water depth of 19 cm and hence provided information about flow velocities and turbulence within as well as above the meadow. At each position, the 3D velocity components were recorded with an Acoustic Doppler Velocimeter (ADV, Vectrino, accuracy of  $\pm 0.5\%$  of measured value  $\pm 1 \text{ mm s}^{-1}$ , Nortek) at 100 Hz for 2 min. To obtain high quality data, the sampling volume of the ADV needed to be undisturbed for the duration of the measurement. As moving seagrass leaves may intrude into the sampling volume and hence could corrupt the velocity data, a small area (approximately  $4 \times 4 \text{ cm}$ ) was cleared of vegetation at each profile location. These gaps were too small to significantly affect the flow pattern and wave propagation (Folkard 2011), but large enough to provide high quality velocity measurements below the top of the canopy.

Plant reconfiguration under hydrodynamic forcing was recorded through the glass flume wall. The tip heights of 10 plants were traced onto a transparent grid. During runs when plants moved under wave forcing, the upper and lower positions of the leaf tips were recorded.

### Data analysis

Quality of ADV data is characterised by its correlation and to ensure high quality during analysis, data

points with a correlation <85% were removed from the data set. In addition, flow velocity outliers (exceeding 3 standard deviations from the mean) were removed, and the despiking algorithm of Mori et al. (2007) was applied to smooth data and close gaps. In the region 8.5–11.5 cm above the bed, instrument ringing (reflections of the acoustic signal which reduces signal quality) occurred due to the geometry of the flume. Consequently, some time series in this region did not contain sufficient data for further processing and were removed from the analysis. The instantaneous velocity contains 3 components and can be written as

$$u(t) = \bar{u} + u_w(t) + u'(t) \quad (3)$$

at time  $t$  where  $\bar{u}$  is the time-averaged component dominated by the unidirectional flow,  $u_w$  is the fluctuation due to waves (and equals zero in the flow only cases) and  $u'$  is the fluctuating component due to turbulence (Stapleton & Huntley 1995). To determine  $u_w$ , a zero-phase, forward and reverse digital filter, which ensures zero phase distortion, was used (Thompson et al. 2012). The filter was applied to time series of the downstream ( $u$ ) and vertical ( $w$ ) flow component where appropriate, while the cross-stream velocity component ( $v$ ) is assumed to be uncontaminated from wave motion in all cases due to the one dimensional forcing of the wave paddle. For all runs, the fluctuating components ( $u'$ ,  $v'$ ,  $w'$ ) were consequently used to calculate turbulent kinetic energy (TKE) (Jonsson et al. 2006):

$$TKE = \frac{1}{2} (\overline{u'^2} + \overline{v'^2} + \overline{w'^2}) \quad (4)$$

For runs with waves, average orbital velocities were determined by calculating the minimum and maximum velocity for each wave cycle, then averaging these over all waves within a run. Data cleaning, pre-processing and all calculations were done in MATLAB. We used 1-way ANOVA to compare the blade tip excursion (the distance between highest and lowest point of the oscillation) with flow velocity ( $n = 10$ ), the presence and absence of waves with maximum canopy height and different flow velocity with maximum canopy height. A 2-way ANOVA was used to compare maximum canopy height at different flow velocities with and without waves ( $n = 10$ ). In all

cases  $p < 0.05$  was considered significant. Prior to testing, normality of the data was assessed using a D'Agostino-Pearson test. Least squares difference (LSD) post hoc testing was performed following ANOVA. All statistical testing was completed using the R programming platform (R Development Core Team 2012).

## RESULTS

The plants had a mean  $\pm$  SD leaf length of  $6.2 \pm 0.5$  cm and bent under hydrodynamic forcing, resulting in a non-linear reduction of  $h_c$  to less than 30% of its still-water value at a flow velocity of  $0.3 \text{ m s}^{-1}$  (1-way ANOVA,  $p < 0.05$ ,  $F = 131$ ,  $n = 20$ ; Fig. 1). Canopy height was not significantly different in the presence and absence of waves (1-way ANOVA,  $p > 0.05$ ,  $F = 2.8$ ,  $n = 50$ ; Fig. 1). A significant difference in canopy height was seen between the presence and absence of waves and flow velocities (2-way ANOVA,  $p < 0.05$ ,  $F = 7.8$ ,  $n = 10$ ; Fig. 1); this occurred at 0, 0.05, 0.1 and  $0.2 \text{ m s}^{-1}$  (LSD test,  $p < 0.05$ ). For velocities of 0.05, 0.1 and  $0.2 \text{ m s}^{-1}$ , canopy height was greater in the presence of

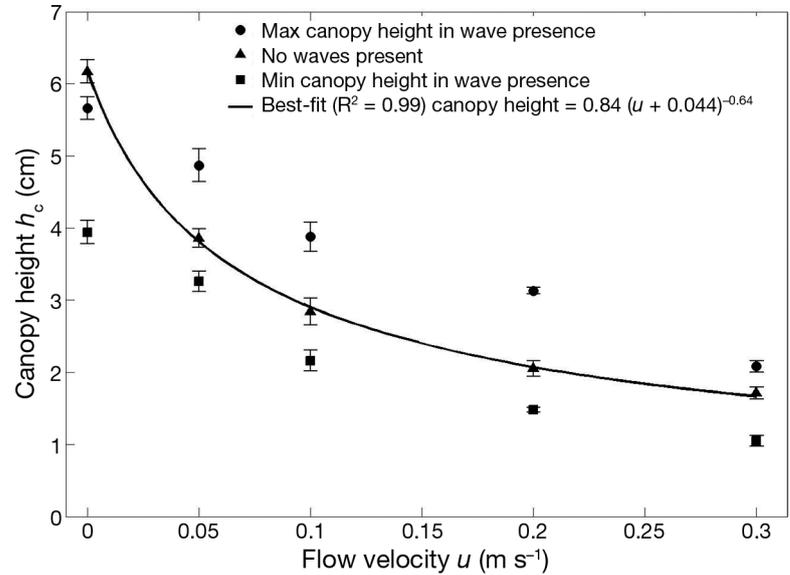


Fig. 1. Relationship between *Zostera noltii* canopy height  $h_c$  and flow velocity  $u$ , and the minimum and maximum heights of canopy flapping under wave forcing. Note that canopy height is given in cm and flow velocity is given in  $\text{m s}^{-1}$ , which also applies to the best-fit equation. There was a significant difference between maximum canopy height and flow velocity (1-way ANOVA,  $p < 0.05$ ,  $F = 131$ ,  $n = 20$ ). No significant difference was found between canopy height and the presence/absence of waves (1-way ANOVA,  $p > 0.05$ ,  $F = 2.8$ ,  $n = 50$ ). However, a 2-way ANOVA showed a significant difference ( $p < 0.05$ ,  $F = 7.8$ ,  $n = 10$ ) between the different flow velocities and the presence or absence of waves; this occurred at 0, 0.05, 0.1 and  $0.2 \text{ m s}^{-1}$  (LSD test,  $p < 0.05$ ). Data are means  $\pm$  SE

waves; this was reversed for the  $0 \text{ m s}^{-1}$  velocity, under which canopy height was reduced in the presence of waves. Exposure to waves led to an oscillating motion of the leaves. Blade tip excursion, i.e. the distance between highest and lowest point of the oscillation, did not change significantly with increasing underlying flow ( $1.55 \pm 0.2 \text{ cm}$ , 1-way ANOVA,  $p > 0.05$ ,  $F = 1.8$ ,  $n = 10$ ). Compared to flow-only treatments, the canopy was compressed beneath the wave trough and more elevated under the wave crests. The only exceptions were the no-flow treatments, where the upper limit of the tip excursion did not reach  $h_c$ . This may be caused by the short wave period, which did not allow the leaves to reach a full upright position before they were pressed down again by the next wave. The reduction of  $h_c$  with increasing flow velocity led to a compaction of the canopy at constant roughness density  $\lambda$ . The high-density meadow had a roughness density of  $\lambda \approx 0.1$  which corresponds to a transitional canopy, while the low density meadow is best described as a sparse canopy ( $\lambda \approx 0.04$ ) according to Nepf (2012a).

Cross-stream velocities ( $v$ ) showed very small fluctuations around zero in all cases, indicating negligible wall effects along the central axis of the flume. Vertical ( $w$ ) and downstream ( $u$ ) velocities, however, showed fluctuations caused by both wave and seagrass presence. Time-averaged vertical velocity profiles with and without superimposed waves were identical (data not shown), and similar to previous observations (Morris et al. 2008), suggesting that data processing effectively removed the wave signal. Downstream velocity profiles showed a clear evolution of flow along the meadow (Fig. 2A). Flow reduction with increasing seagrass density occurred near the bed, which extended upwards with distance from the leading edge of the meadow. This profile evolution was more pronounced with increasing flow velocity and seagrass density. For the high-density and highest velocity treatment, a velocity profile with an inflection point near the top of the canopy occurred at location 135 cm downstream of the meadow's leading edge (Fig. 2A). This profile shape agrees well with observations by Nepf (2012a) for transitional canopies ( $\lambda \approx 0.1$ ). The onset of such a

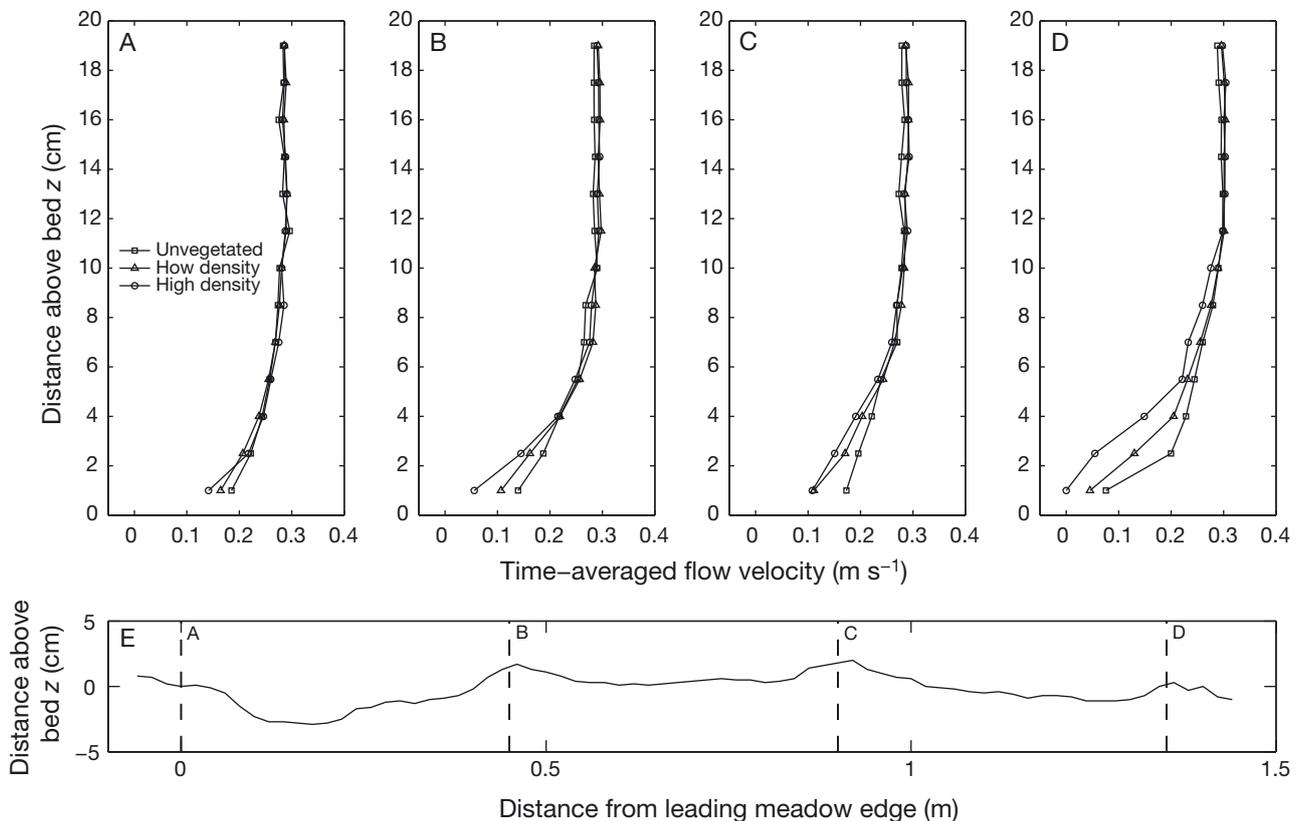


Fig. 2. (A–D) Time-averaged velocity ( $u$ ) profiles for different *Zostera noltii* shoot densities at an applied flow velocity of  $0.3 \text{ m s}^{-1}$  in the presence of waves for the unvegetated, low-density ( $685 \text{ shoots m}^{-2}$ ) and high-density ( $1369 \text{ shoots m}^{-2}$ ) cases. (E) Bed elevation of the vegetation patch. The dashed lines indicate the profile locations for plots A–D

profile shape could also be seen for the low-density meadow, but the meadow length within this study was not sufficient to fully develop the inflection point at such a low shoot density.

A similar development along the patch was observed for TKE for all treatments. Generally, treatments with waves yielded lower TKE values compared to treatments without waves, which only reversed close to the water surface in all cases (Fig. 3). In the lower part of the water column ( $z < 10$  cm), TKE developed a peak at the leading edge just above the bed which moved up the profile with increasing distance into the meadow for both densities (Fig. 3). This development was clearly visible in the treatments without waves, but its onset could also be observed for the treatments with waves. It should be noted that a slight increase of TKE near the bed was also observed over the bare bed, which is attributed to the bathymetry of the natural bed as this poses a roughness element in itself (Fig. 2E).

A direct comparison of TKE near the top of the canopy ( $z = 5.5$  cm) confirmed the pronounced increase of TKE into the meadow in all no-wave treatments with vegetation, while in the unvegetated treatments the existing bed roughness only led to

10–20% of the increase caused by vegetation (Fig. 4). Adding waves to low-velocity treatments did not change the order of magnitude of TKE, but restricted the TKE evolution along the meadow (Fig. 4A). At a flow velocity of  $0.1 \text{ m s}^{-1}$  without waves, TKE increased by 316% for the low-density and 287% for the high-density treatments, while with waves the change was  $-4\%$  and  $32\%$ , respectively. At high velocities, the overall magnitude of TKE was reduced (Fig. 4B) and the relative TKE increase varied little between treatments without waves (127% and 247% for the low- and high-density meadows, respectively) and with waves (131% and 185%, respectively). For the high-velocity treatments without waves, an increasing trend with seagrass density was visible, but it did not reflect in the absolute values of the treatments with waves or in the low-velocity treatments.

The interaction of waves and flow was also visible in the minimum and maximum wave orbital velocities. In the wave-only treatments, the maximum orbital velocities were almost constant along the profile, while the minimum velocities decreased towards the surface (Fig. 5A). With increasing flow velocity, the profile shape became more logarithmic (Fig. 5B–E), with reduced values towards the bed. A

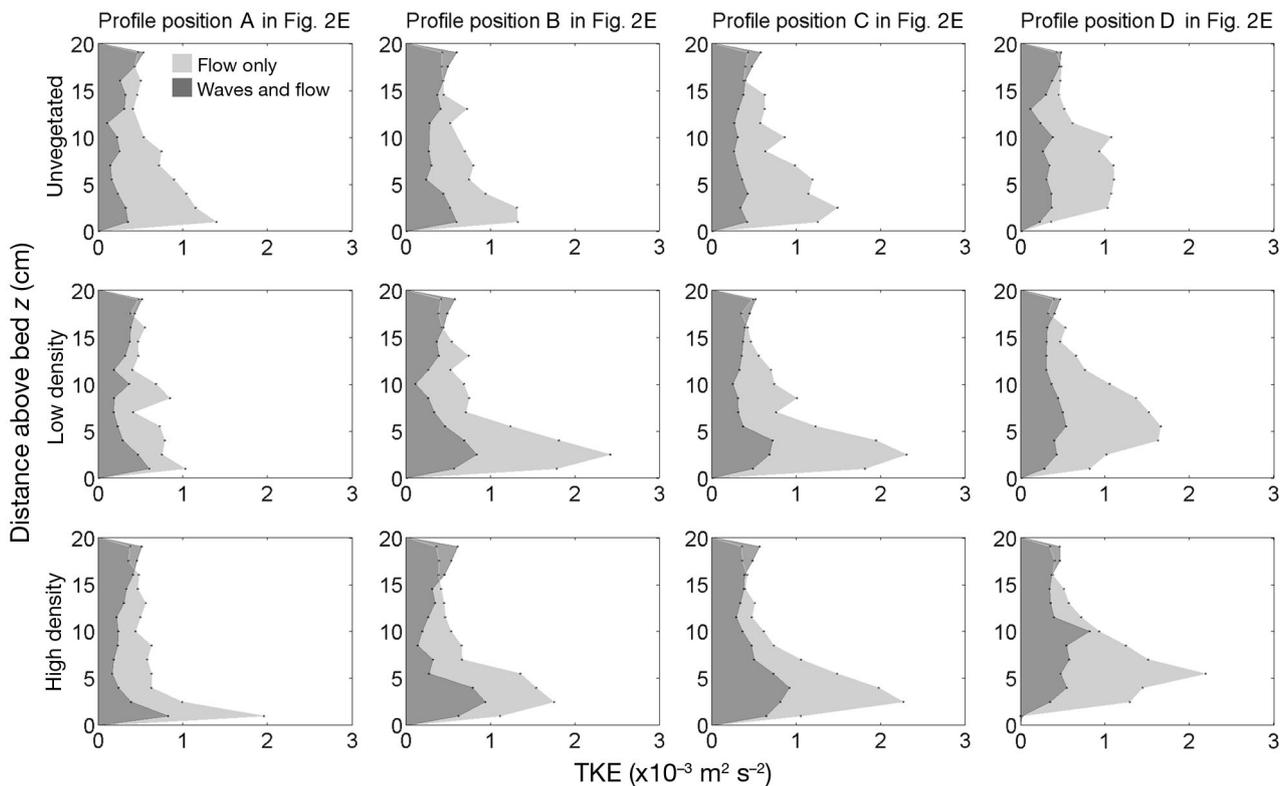


Fig. 3. Turbulent kinetic energy (TKE) profiles for an underlying current of  $0.3 \text{ m s}^{-1}$  for different *Zostera noltii* seagrass densities in the absence (light grey) and presence (dark grey) of waves

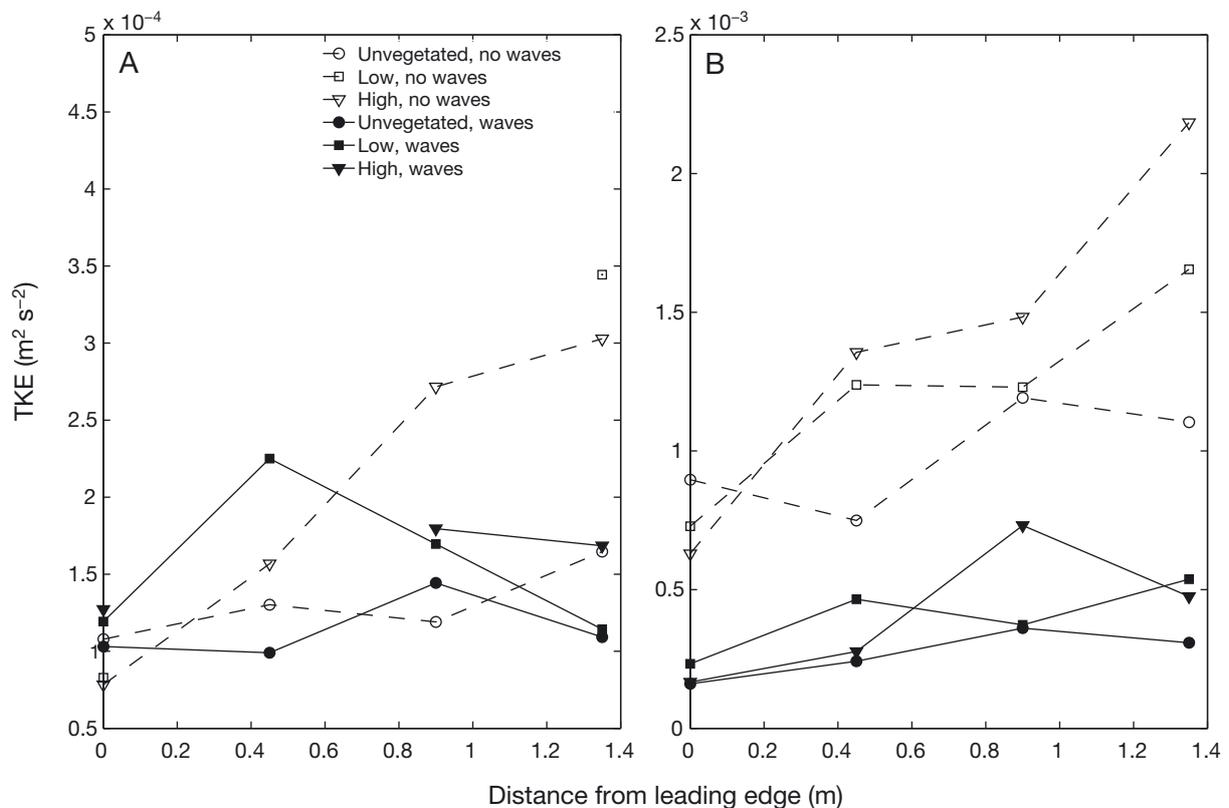


Fig. 4. Turbulent kinetic energy (TKE) evolution at the top of the *Zostera noltii* canopy ( $z = 5.5$  cm) for (A)  $0.1 \text{ m s}^{-1}$  flow and (B)  $0.3 \text{ m s}^{-1}$  flow. Note the different scales along the y-axis for increased visibility

pattern formed where minimum velocities decreased strongly towards the surface at low flow velocities. With increasing flow velocities, this pattern became less pronounced but a slight trend remained during all treatments. Due to the different developments of minimum and maximum orbital velocity profiles, the mean orbital diameter decreased with increasing underlying flow velocity (Fig. 6) throughout the water column. In the free-stream region ( $z > 10$  cm) the mean orbital diameter remained unaffected by the vegetation and decreased by over 30% at the highest underlying flow velocity of  $0.3 \text{ m s}^{-1}$  compared to the no-flow scenarios in all cases. In the canopy region (up to 5.5 cm), the evolution of a logarithmic profile was superimposed by a damping effect of the seagrass meadow, resulting in the onset of an S-shaped profile as observed for the mean flow velocities (Fig. 2A). The damping effect increased with seagrass density, but only affected positive incident velocities, i.e. orbital flow against wave passage was not affected by seagrass. Consequently, the mean orbital diameter in the canopy region was most affected by seagrass presence for the medium flow velocities in this study, decreasing by >10% from the

unvegetated to the high-density case, while at the lowest and highest flow velocities, the orbital diameter remained almost constant or within the measurement accuracy of the ADV (Fig. 6).

## DISCUSSION

These results highlight the complex interaction between seagrass, waves and unidirectional flow, which is likely to have an impact on the optimum habitats of different seagrass species. In the presence of seagrass, mean flow velocities near the bed decreased, yielding an S-shaped profile for the highest density and flow velocity. The orbital velocities in the presence of waves were reduced by an underlying flow, but were relatively robust against seagrass presence. Seagrass presence decreased only the net positive velocities, while net negative velocities remained unaffected. This effect was independent of the shape of the seagrass canopy, which changed with hydrodynamic forcing.

Flexible seagrass leaves bend and align themselves with flow (Fonseca & Koehl 2006, Backhaus &

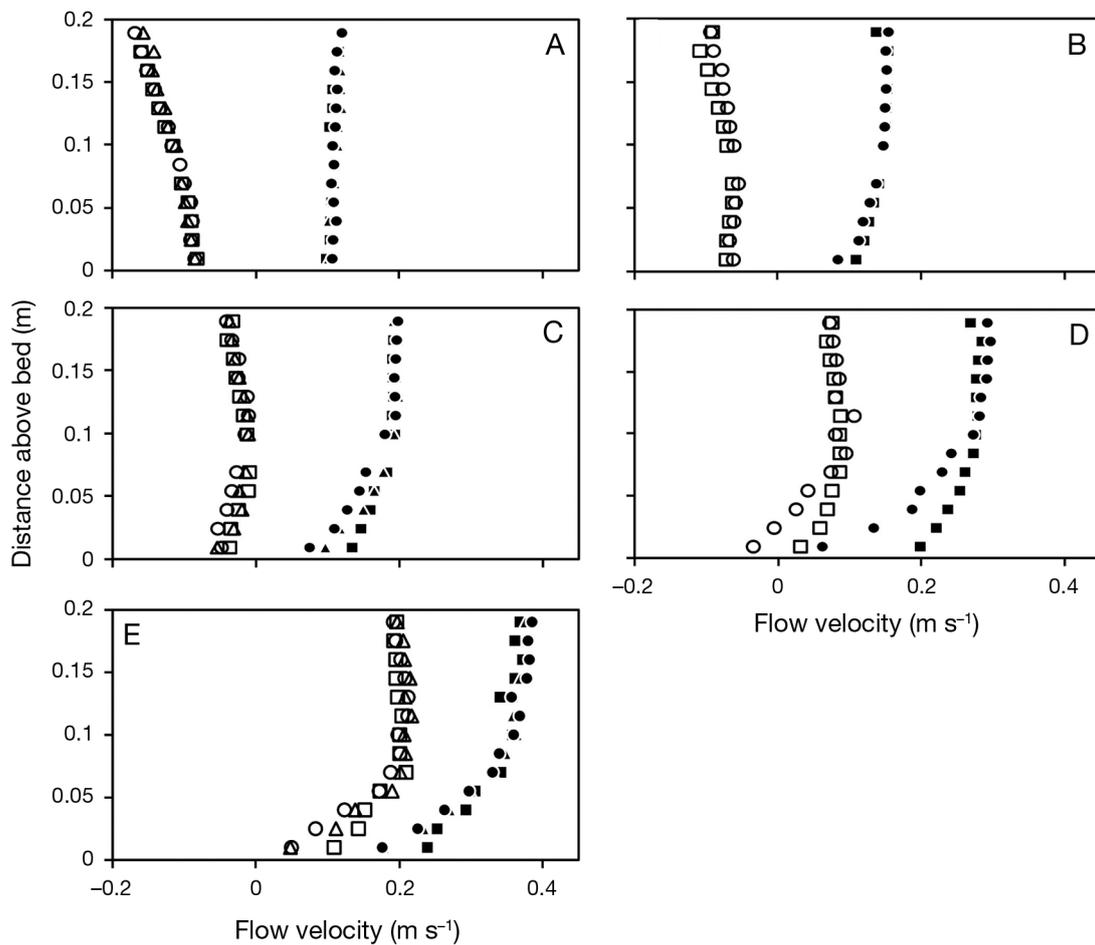


Fig. 5. Minimum (open symbols) and maximum (filled symbols) orbital velocity profiles 90 cm downstream from the meadow's leading edge for the unvegetated case (squares), the low-density case (triangles) and the high-density case (circles) (A) in the absence of an underlying current, and in the presence of an underlying current with velocity (B)  $0.05 \text{ m s}^{-1}$ , (C)  $0.1 \text{ m s}^{-1}$ , (D)  $0.2 \text{ m s}^{-1}$ , and (E)  $0.3 \text{ m s}^{-1}$ . The difference between minimum and maximum orbital velocities in different sections of the profiles are given in Fig. 6

Verduin 2008), which causes a reduction in  $h_c$  with increasing flow velocity. In the absence of waves, the observed reduction followed a negative power law ( $h_c = 0.84 [u + 0.044]^{-0.64}$ ) that predicted the degree of compaction with increasing flow velocity and suggested that beyond a given flow velocity, compaction will not continue to increase. Fonseca et al. (1982) observed that *Zostera marina* reached its maximum bending angle at a flow velocity of  $0.5 \text{ m s}^{-1}$ , and a similar response was also observed in macroalgae that behaved like rigid bodies once the velocity exceeded a critical threshold (Boller & Carrington 2006). Beyond this full compaction state, the effect of vegetation on the flow field would remain constant with increasing flow velocity, and the drag force acting on the plants would become independent of leaf length (Luhar & Nepf 2011). While such a compaction would yield optimum streamlining and

reduced drag, it may not be beneficial for the vegetation from a physiological point of view. Leaf shading would limit light availability in fully compacted meadows (Zimmerman 2003, Nikora 2010). And while the enhanced turbulence in the upper part of the canopy can promote nutrient uptake in this region (Fonseca & Kenworthy 1987), compaction can restrict water and nutrient exchange between the canopy region and the free stream above (Neumeier & Ciavola 2004, Thompson et al. 2004). Leaves located further down in the canopy could therefore suffer nutrient and photosynthesis deficiency; however, this speculation only applies to this particular case study species. There are examples of various seagrass species that are found in environments where current/wave velocities are reported to reach values  $>0.3 \text{ m s}^{-1}$  (Phillips 1980, Dierssen et al. 2003).

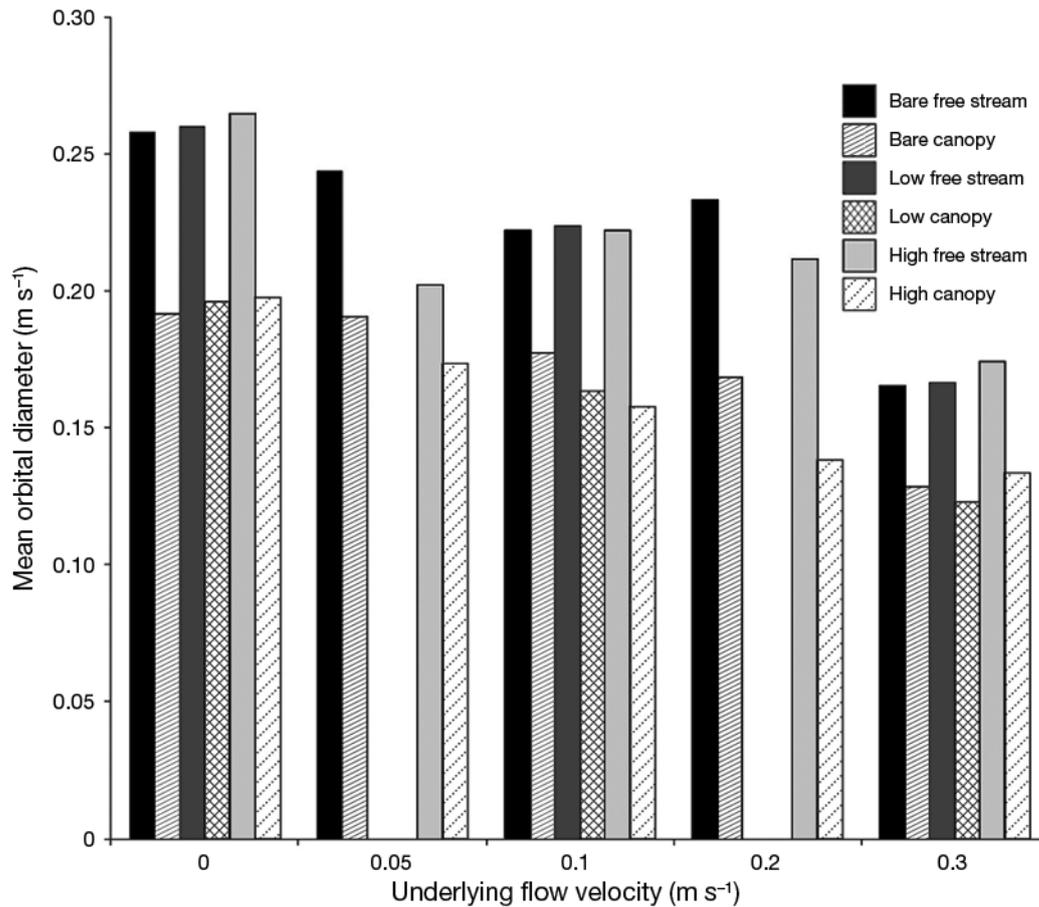


Fig. 6. Mean orbital diameters ( $\text{m s}^{-1}$ ) for the free-stream ( $z > 10$  cm) and canopy ( $z < 5.5$  cm) region for the different scenarios. The low-density meadow was not exposed to flow velocities of  $0.05 \text{ m s}^{-1}$  or  $0.2 \text{ m s}^{-1}$

In the presence of waves, seagrass leaves showed an oscillating motion, the upper and lower limit of which followed a pattern similar to that of  $h_c$  for the flow-only treatments. The magnitude of tip excursion ( $1.55 \pm 0.2$  cm), however, remained almost constant. In a study with artificial seagrass, a higher tip excursion was recorded for the wave-only case compared to the treatment where a current of  $0.1 \text{ m s}^{-1}$  was superimposed on the waves (Paul et al. 2012). However, all surrogates were longer than the real seagrass used in the present study. Moreover, the study using surrogates indicated that the difference between the flow and no-flow treatments decreased with decreasing leaf length. The present data could therefore be a natural continuation of the trend observed in the earlier study. In that case, the combined data suggest that in wave-exposed environments, long seagrasses are more affected by an underlying current than short seagrasses. Short seagrasses would move with the oscillatory motion of the waves, irrespective of underlying flow velocities.

This blade motion would be reduced for long seagrass under the same hydrodynamic conditions. However, this movement results in the opening and closing of the canopy, which is important for nutrient exchange (Thomas & Cornelisen 2003) and light availability (Zimmerman 2003). Short seagrasses could therefore have an advantage in regions where waves and currents co-occur.

As roughness density  $\lambda$  is independent of hydrodynamic forcing, the computed values apply to all hydrodynamic treatments in this study. The high-density meadow ( $\lambda \approx 0.1$ ) yielded velocity profiles that resemble profiles for a transitional canopy according to the definition by Nepf (2012a). This definition and associated velocity profile shapes were derived based on experiments with rigid vegetation surrogates (Nepf et al. 2007). This type of vegetation does not bend or become streamlined and hence keeps a constant  $h_c$  independent of flow velocity. In this study, flexible vegetation was used, which had a constant leaf length but variable  $h_c$  during the exper-

iments as it became streamlined under hydrodynamic forcing. The results therefore confirm that, for flexible strip-like vegetation, Eq. (2) can be used to derive  $\lambda$  and the proposed canopy categories and their associated velocity profiles are also applicable for such canopies. Additionally, Eq. (2) corresponds to the one-sided leaf area index, which has successfully been used to compare the wave attenuation capacity of different surrogate canopies (Paul et al. 2012). It has also been proposed as a suitable factor to evaluate flow resistance in riverine ecosystems (Järvelä 2004). The congruence of roughness density and leaf area index supports the observation that the effect of vegetation on mean flow velocities is independent of the compacted canopy height  $h_c$  and solely depends on the still-water dimensions of the meadow. This agrees with measurements of wave attenuation by artificial seagrass (Paul et al. 2012) and natural salt marsh (Bouma et al. 2010), where the amount of biomass rather than the plant's position in the water column determined wave attenuation.

It is therefore possible that plants bend and streamline under hydrodynamic forcing to reduce the drag acting on their leaves (Luhar & Nepf 2011), and in the same instance reduce approaching flow and waves. The latter is an important ecosystem engineering property that enables a seagrass species to generate environmental conditions suitable for further colonisation, by both its own seedlings and those of other species (Bos et al. 2007, van Katwijk et al. 2009). The independence of these ecosystem engineering functions from canopy compaction enables seagrasses to colonise habitats with a wide range of hydrodynamic forcing properties.

A comparison of TKE profiles in the absence and presence of waves (Fig. 3) showed that the peak at the top of the canopy is more pronounced in the absence of waves. Other processes may therefore dominate turbulence under wave forcing, the seagrass meadows having only a secondary impact. This may be caused by the back and forth motion of flexible seagrass under waves, which reduces the relative velocity between the leaves and the surrounding water (Bradley & Houser 2009). Consequently, turbulence generated by seagrass may be reduced to a level lower than the ambient prevailing turbulence due to waves. A similar explanation may be true for the reduction of orbital velocities. In the wave-only case, seagrass motion may be almost synchronous with the water motion and the relative velocity may be close to zero. Hence the plants may not have a significant effect on the orbital velocities, at least not along the length of seagrass meadow observed here.

It is hypothesised that orbital velocities would be reduced behind a longer seagrass meadow, when the wave interacts with the seagrass meadow over several wave lengths. Once an underlying current is in place, seagrass motion cannot keep up with the elevated orbital velocities for the whole duration of the wave cycle. The resulting increased relative velocity between leaves and water would generate increased drag. As a result, the orbital velocities are reduced to oscillate around zero for underlying velocities as high as  $0.2 \text{ m s}^{-1}$  in this study (Fig. 5). The presence of negative velocities for a short period of the wave cycle facilitates the opening and closing of the canopy, hence promoting nutrient exchange and light penetration, which would otherwise be reduced by the streamlined shape of the meadow. However, during this study, no quantitative measurements of plant motion were possible to support this hypothesis. The magnitude of velocities and plant motion may differ in field settings, where currents and waves often approach a seagrass meadow at oblique angles. In such a case, the complexity of wave–flow interactions increases (Grant & Madsen 1979) and the vegetation moves in a more 3D manner by streamlining in the direction of flow and oscillating in the direction of wave propagation. However, the scenario investigated here, i.e. current and waves along the same vector, provides valuable insight in the fundamental underlying processes.

## CONCLUSIONS

A natural *Zostera noltii* meadow was transplanted into a flume and exposed to a range of flow velocities, both with and without superimposed waves. The measurement of 3D velocity profiles along the central axis of the meadow was used to assess the effect of the seagrass on flow evolution, and how this differs in the presence and absence of waves. Moreover, the effect of hydrodynamic forcing on plant bending was observed. Plant bending was only affected in the mean  $h_c$  due to reconfiguration under the unidirectional flow, while the oscillatory movement caused by orbital wave motion remained constant throughout all treatments.

The results show that the response of hydrodynamics to seagrass presence (e.g. flow reduction) and the response of seagrass to hydrodynamics (e.g. streamlining) can act in parallel, without directly affecting each other. Both processes depend on hydrodynamic forcing, for instance (1) increasing flow velocities reduce  $h_c$  through streamlining and (2) increasing

relative velocities increase attenuation of wave orbital motion. But a reduced  $h_c$  does not lead to reduced flow damping near the bed and vice versa. This reveals that the ecosystem engineering functions of seagrass do not depend on their physical environment, which was a key question of this study. Moreover, the data indicate seagrass preferences regarding the hydrodynamic forcings of a habitat. We speculate that high flow velocities will lead to canopy compaction, which will potentially reduce light availability and nutrient exchange, making areas dominated by high flows less suitable for seagrass colonisation. If waves co-occur with a unidirectional flow, the opening and closing of the canopy under wave forcing facilitates these physiological processes, suggesting that seagrass meadows benefit from light to moderate wave exposure irrespective of an underlying current. However, there may be a trade-off between increased nutrient uptake and increased potential of dislodgement of the plants. It has been found that longer-leaved species are known to reduce the drag exerted on the roots in wave-exposed environments, allowing for increased anchorage (Larkum 1976, van Katwijk & Hermus 2000, Koch et al. 2006). Our work here also provided additional evidence for both of these mechanisms, where the oscillatory motion of seagrass leaves in the presence of an underlying current decreased with increasing leaf length, thus allowing for increased exposure to nutrient-rich water but also decreasing the drag on the leaves.

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