The exchange of dissolved nutrients between water column and substrate pore-water due to hydrodynamic adjustment at seagrass meadow edges: A flume study

A. Adhitya[1*,5], A.M. Folkard[2], L. L. Govers[3,4,5], M.M. van Katwijk[3], H. H. de Iongh[6,7], P.M.J. Herman[1], T.J. Bouma[1*]

Running Head: Seagrass Porewater Exchange Hydrodynamic

[1]Royal Netherlands Institute for Sea Research (NIOZ) P.O. Box 140, 4400AC Yerseke, The Netherlands. Corresponding Author: Tjeerd.Bouma@NIOZ.NL and Achmad.Adhitya@NIOZ.NL

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

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

[4]Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Faculty of Science, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands

[5]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Post Office Box 11103, 9700 CC Groningen, The Netherlands

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

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

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ABSTRACT

Seagrasses need dissolved nutrients to maintain their productivity through uptake processes, from substrate pore-water via their roots and/or from water column via their leaves. Here, we present the first study of exchanges of dissolved nutrients between pore water and the water column in the vicinity of seagrass canopies. We address the following research questions, using a laboratory flume experiment: 1) How does solute exchange between open water and substrate pore water vary spatially within seagrass patches? 2) How does seagrass leaf length affect this solute exchange? 3) How does the measured rate of solute exchange compare with seagrasses' rates of uptake of dissolved nutrients? Our results indicate that solute intrusion from open water into substrate pore water is highest in the area around seagrass patches' leading edges, where flow deceleration is strongest, and decreases approximately linearly with downstream distance into the patch. The decrease in measured flow speed in the canopy fits well the predictions of previously reported models of arrays of rigid obstacles. The length of the region in which the concentration of solute that has infiltrated into the substrate at the upstream end of the seagrass patches is similar to the length scale predicted from model estimates of infiltration rate (based on the substrate permeability) and the length of time over 24-hour runs. We conclude that the mechanism we identify only pertains near canopy edges, and therefore that other mechanisms must govern nutrient supply in the interior of seagrass meadows.

Introduction

Seagrass meadows are highly productive ecosystems that provide important services such as offering nursery and other habitats to a wide range of marine species (Kennedy et al., 2010; Short et al., 2011; Cullen-Unsworth et al., 2013), contributing to shoreline protection by reducing erosion (Hendriks et al., 2007; Christiansen et al., 2013) and attenuating wave and current energy (Pujol and Nepf, 2012; Paul et al., 2012). In recent decades, seagrass meadows have decreased globally at an alarming rate (Cambridge et al., 1986; Morris and Virnstein, 2004; Waycott et al., 2009). This decline has often been linked to problems with water quality: either enhanced turbidity (van der Heide et al., 2007, Carr et al., 2010) or hypertrophic nutrient concentrations causing algae blooms (Gacia and Duarte, 2001; Apostolaki et al., 2010). In contrast to our knowledge about threats associated with high nutrient concentrations, we have a poor understanding of how seagrasses can flourish in the low nutrient (oligotrophic) environments in which they are often found, particularly in many tropical regions.

Contrary to many terrestrial macrophytes, seagrasses are poor at resorbing nitrogen from senescing leaves, resulting in high N-losses due to leaf detachment (Stapel et al., 1997; Romero et al., 2006). The high productivity and leaf-loss of seagrasses result in a nutrient paradox (Hemminga et al., 1999; Reyes and Sanson, 2001): How can seagrasses maintain their productivity if so much of their nutrients is lost via senescing leaves? Possible solutions to this paradox are that the leaves degrade within the meadow, enabling re-uptake of their nutrients by the seagrass (Peduzzi and Herndl, 1991; Apostolaki et al., 2010); trapped suspended particles may similarly contribute (Hendriks et al., 2007; Duarte et al., 2011; Kennedy et al., 2010) or seagrasses can take up dissolved organic nitrogen (DON) from sources within the bed sediment

93 (Barron et al., 2006, Vonk et al., 2008, Van England et al., 2011). Whereas these latter studies
94 show that DON may provide an important N source to seagrass roots, we lack insight into how
95 DON, or suspended matter, enters the substrate beneath seagrass meadows.

96 For bare, permeable, sandy sediment substrates, several studies have shown high rates
97 of water exchange between the open water column above the substrate and the pore water
98 within it, which may cause biological and chemical modifications of the pore water via
99 advection of suspended or dissolved matter (Huettel and Gust, 1992; Huettel and Rusch, 2000).
100 Such fluxes are generally caused by pressure gradients, which may be due to wave propagation
101 causing pressure oscillations at the sediment surface (Webb and Theodor, 1972; Shum, 1992;
102 Precht and Huettel, 2004) or to currents' interactions with seabed topography (Huettel and
103 Webster, 2001). For example, a local vertical pressure gradient of 100 Pa m^{-1}, caused by flow
104 encountering a small rise in the bed, is enough to force water several centimeters into the
105 sediment and draw pore water from more than 0.1 m beneath the sediment surface into the
106 water column (Huettel et al., 1998).

107 If advective exchange between water column and pore water (referred to hereinafter
108 as "pore water exchange") also occurs within seagrass meadows, it could provide an important
109 supply of DON to seagrass roots, which are particularly good at taking up DON (Evrard et al.,
110 2005; Vonk et al., 2008; Van England et al., 2011). Little is known about this phenomenon in the
111 presence of seagrass. Laboratory flume experiments have been reported that have provided
112 models of flow adjustments at the upstream end of vegetation(-mimic) canopies (Folkard 2005;
113 Tanino and Nepf, 2008; Chen et al., 2013). The general pattern observed in these experiments is
114 that, on encountering such a canopy, the flow adjusts to the canopy's presence such that part

of it is deflected upwards and travels at accelerated speeds over the top of the canopy, and part travels at decelerated speeds through the canopy. However, there is also a third possible flow path – just as the flow can be deflected over the canopy, it can also be deflected beneath it, into the permeable substrate. This mechanism is analogous to the enhancement of infiltration by pressure gradients around seabed topography discussed by Huettel et al. (1998) and would cause changes in the pore water exchange rate: we would expect enhanced infiltration from the open water into the substrate while the in-canopy flow decelerates as a result of the presence of the canopy. Although other laboratory experimental studies have investigated the influence of seagrass canopy structure on solute uptake rates from the open water (Thomas et al., 2000; Morris et al., 2008), this hydrodynamic mechanism of enhanced pore water exchange, which would be expected to affect nutrient supply to seagrass roots, has not previously been investigated. Hence, here we used laboratory flume experiments to elucidate and quantify pore water exchange in the presence of patches of seagrass mimics. Since the geometric configuration of the seagrass canopy might be expected to be a primary factor in determining the magnitude of this phenomenon, we investigated the influence on it of different canopy heights (leaf lengths).

Material and Methods

To measure the effect of seagrass canopies on pore water exchange in a spatially explicit way, we carried out experiments in a race track laboratory flume at the Royal Netherlands Institute for Sea Research (NIOZ) in Yerseke (Fig. 1a; details in Bouma et al. 2009). Coral sand collected from a natural, oligotrophic seagrass meadow in Indonesia (median grain size d_{50} = 5.8

137 x 10^{-4} m; permeability 1.6 x 10^{-11} m^2) was placed into the test section of the flume (2 m long x
138 0.6 m wide), which had a false floor to a depth of 0.15 mm, such that the top of the sand layer
139 was flush with the flume bed. The whole flume was then filled with fresh water to a height H =
140 0.40 m above the sand surface. We measured the pore water content of the sand used in the
141 flume test section by taking replicate samples of 0.5 l of the sand, placing them in a 1 l
142 graduated cylinder and covering them with water. We took the volume indicated by the surface
143 of the sand in the cylinder as the combined volume of the sand and pore water, and subtracted
144 the 0.5 l volume of the sand from this to give the pore water volume. The water volume thus
145 measured was 0.189 $\pm$ 0.004 l (mean + 1 sd; n = 5), giving a porosity (water:total volume ratio)
146 of 0.274 $\pm$ 0.004 (volumetric sand: water ratio 2.65 $\pm$ 0.05, volumetric water:sand ratio 0.378 +
147 0.006).

148 To simulate the seagrass, we used polyethylene mimics, a generally accepted approach
149 in flume studies of hydrodynamic processes within seagrass beds (e.g., Nepf & Vivoni, 2000;
150 Folkard, 2005; Bouma et al., 2009). The polyethylene used had modulus of elasticity E = 1.09 $\pm$
151 0.425 x 10^7 Nm^{-2} (N = 6). The design of our mimics was based on field observations of *Thalassia*
152 *hemprichii.* at the same location in Indonesia from where the sediment was taken. Two sets of
153 mimics were created. The first (the "long-leaved" mimics) consisted of four leaves per shoot,
154 each leaf being 0.14 m long, 0.01 m wide and 0.0001 m thick. These leaves were attached to
155 0.08 m-long sheaths that were inserted into the coral sand in the flume, so that the top of the
156 sheath was level with the sand surface, and the leaves protruded above the sand into the water
157 column. The second (the "short-leaved" mimics) consisted of two leaves per shoot, each being
158 0.1 m long, 0.01 m wide and 0.0001 m thick. These leaves were attached to 0.05 m-long

159 sheaths, which were similarly inserted into the sand such that their tops were flush with the
160 sand surface. These sheaths clearly simplify the below-ground structure of seagrass roots and
161 rhizome systems, but we assume that this does not affect our ability to elucidate the
162 mechanism of pore water exchange. In both cases, a 1 m long patch of plant mimics with a
163 density of 722 shoots m^{-2} (c.f. shoot densities observed in natural *Thalassia* meadows of 48–
164 1888 shoots m^{-2} with uniform spatial configuration, Lewis, 1984; Tomasko and Lapointe, 1991;
165 Barry, 2013), which filled the whole 0.6 m width of the flume, was fabricated and placed in the
166 flume test section, leaving 0.5 m of bare sand both upstream and downstream (Fig. 1b). Since
167 the upstream adjustment of the flow occurs over a distance comparable to the meadow height
168 (i.e. at most 0.14 m for the long leaves, and 0.1 m for the short leaves) this length of bare sand
169 should capture any variations in solute exchange due to such flow adjustments (Folkard,
170 unpublished data). We did not test a control case with no seagrass, as we assumed that there
171 would be no systematic variation in solute exchange in such a case, and that the rate of
172 exchange would be comparable to that measured 0.25 m upstream of the canopy in these
173 experiments, due to the lack of variation in bottom conditions. Along-flume locations are
174 identified using the coordinate x, where x = 0 is the upstream end of the patch (positive
175 downstream), and vertical locations using the coordinate z, where z = 0 is the surface of the
176 sand (positive upwards). The penetration of nutrients into the sediment was detected using
177 bromide as a conservative proxy tracer. Tracers are commonly used for characterizing flows in
178 surface waters, and estimating groundwater discharges (Replogle et. al., 1968; Finker and
179 Gilley, 1986). Bromide is suitable for usage in surface water (Smith and Davis., 1974; Gilley et.
180 al., 1990), and for determining hydraulic parameters both in the field (Owens, 1985; Lin et. al.,

181 2003), and laboratory (Glud et. al., 1994; Foster et. al., 1999; Rasheed et. al., 2003). Here,
182 bromide was added into the surface water at a concentration $[Br^-]_t$ of 0.1 kg m^{-3}.

183 A current with a mean speed of 0.3 m s^{-1} was passed around the flume, representing
184 typical hydrodynamic conditions observed in shallow seagrass meadows (e.g. Palmer, 1988;
185 Verduin and Backhaus, 2000). After 24 hours exposure of the sediment substrate to the flow of
186 this bromide-seeded open water, cores of the substrate were extracted to determine the
187 amount of bromide that had penetrated into them. The 24-hour period was chosen to ensure
188 that the bromide was well-mixed in the open water column, but was otherwise solely for
189 logistical convenience. The cores were extracted using 0.1 l syringes with their narrow tips cut
190 off, giving cores of approximately 0.05 m in diameter. At each location, the core was extracted
191 by positioning the syringe vertically with the base of the plunger flush with the sediment
192 surface, then pushing the sleeve of the syringe into the sediment whilst keeping the plunger
193 stationary. When the syringe was lifted away, it took with it a core of sediment that retained
194 the relative position of sediment and pore water within itself, which was immediately stored at
195 -20°C. Cores were taken at three random replicate cross-flume locations at each of nine along-
196 flume locations covering upstream of, within, and downstream of the patch: x = -0.25, -0.05,
197 0.05, 0.25, 0.5, 0.75, 0.95, 1.05 and 1.25 m (Fig. 1b). For analysis, a 0.02 m-thick section was
198 sliced from the top of each core, and this was sliced in half, to enable measurements of pore
199 water in two layers (0-0.01 m and 0.01-0.02 m). This approach followed that of Reimers et al.'s
200 (2004) in situ measurements of iodide in sediments with similar grain size. The layers were
201 defrosted and centrifuged for 2 minutes at 1000 rpm to separate the pore water from the
202 sediment. The bromide concentrations in the pore water $[Br^-]_c$ were measured using high

performance liquid chromatography (HPLC), and expressed, following Peralta et al. (2008), as relative bromide concentration ($[Br^-]_{rel}$, %), i.e. their ratio to $[Br^-]_t$, the bromide concentration in water column:

$$\left[Br^-\right]_{rel} = \frac{\left[Br^-\right]_c}{\left[Br^-\right]_t} \cdot 100\% \quad (1)$$

Velocity measurements were made using a Vectrino Acoustic Doppler Velocimeter (ADV, Nortek AS, Rud, Norway) at the same along-flume positions at which sediment samples were taken (Fig. 1b). At each location, velocities were measured at heights z_1 to z_n = 0.005, 0.03, 0.07, 0.095, 0.115, 0.13, 0.15, 0.18, 0.27 and 0.31 m. All of these measurements were made at mid channel, to minimize wall effects. At each measurement point, velocity was recorded for 120 seconds at 10 Hz. The height of the deflected canopy, h, was measured for every along-flume location at which velocity was measured, using a ruler attached to the side of the flume.

Variations in the mean flow speed (U, m s^{-1}) were calculated separately for the regions above (U_a) and within (U_b) the seagrass canopy, as averages of the flow speed measurements at each measurement height z_i, weighted by the distance between adjacent measurement heights:

$$U_a = \frac{1}{(H-h)}\left\{U(z_j)\left(\frac{z_j+z_{j+1}}{2}-h\right)+\sum_{i=j+1}^{n-1}U(z_i)\left(\frac{z_i+z_{i+1}}{2}-\frac{z_{i-1}+z_i}{2}\right)+U(z_n)\left(H-\frac{z_{n-1}+z_n}{2}\right)\right\} \quad (2)$$

$$U_b = \frac{1}{h}\left\{U(z_1)\left(\frac{z_1+z_2}{2}\right)+\sum_{i=2}^{j-2}U(z_i)\left(\frac{z_i+z_{i+1}}{2}-\frac{z_{i-1}+z_i}{2}\right)+U(z_{j-1})\left(h-\frac{z_{j-2}+z_{j-1}}{2}\right)\right\} \quad (3)$$

where z_j is the first measurement point above the top of the canopy and n is the total number of measurement points in the profile.

Results

Hydrodynamic flow adjustment due to the canopy – The flow was slower inside both the long and short seagrass meadows than above them (Fig. 2). Flow within the seagrass canopies gradually decelerated with distance away from leading edge, implying (due to conservation of mass) that flow within the canopies had a component moving upwards and out of the canopies. The horizontal velocity gradient (rate of reduction of downstream flow speed) was larger in the long seagrass than in the short seagrass (Fig. 3). The adjustment length (X_D) over which this reduction in in-canopy speed takes place, and the mean in-canopy flow speed achieved at the end of the adjustment (U_1) are predicted by Chen et al. (2013), for canopies of rigid obstacles, to be given by

$$X_D = \frac{3(1-\phi)}{C_D a}\left(1 + 2.3 C_D a\, h\right) \quad (4)$$

$$U_1 = \frac{U}{1 - \frac{h}{H}\phi + \sqrt{\frac{C_D a\, h}{2C(1-\phi)}\left(\frac{H-h}{H}\right)^3}} \quad (5)$$

where ϕ is the canopy solid volume fraction, C_D the canopy drag coefficient, a the frontal area per canopy volume, and $C = K_c\,(\delta_e/H)^{1/3}$, where K_c is an empirical coefficient which Chen et al. (2013) find to be 0.07 ± 0.02 (here, we use 0.07) and δ_e is the penetration length scale of vortices in the overflow into the top of the canopy, which we calculate (following Nepf et al. 2007) as $0.23/C_D a$. The leaf mimics used in the present experiments had widths of ~0.0001 m, which implies solid volume fractions of $\phi = 0.0018$ for the short-leaved canopy and $\phi = 0.0048$ for the long-leaved canopy. There is uncertainty, however, about the appropriate values of C_D

243 for our canopies. Tanino and Nepf (2008) have investigated C_D for arrays of solid cylinders, and
244 numerous studies have reported values of C_D for a wide range of – mainly terrestrial – flexible
245 vegetation (see e.g. Wu et al., 1999), but drag coefficient values for seagrass canopies are not
246 well known, and are likely to be highly dependent on canopy structure (Peterson et al., 2004).
247 We therefore use our data and Chen et al.'s equations to back calculate values for C_D for our
248 canopies. Doing this give values of C_D = 1.5 for the long-leaved canopy, and C_D = 2.1 for the
249 short-leaved canopy. Using these values in (4) and (5) gives X_D = 0.64 m and U_1 = 0.027 ms^{-1} for
250 the short-leaved canopy, and X_D = 0.66 m and U_1 = 0.031 ms^{-1} for the long-leaved canopy. These
251 provide a predicted velocity decay that fits our data in the long-leaved case reasonably well, but
252 in the short-leaved case, our data shows more of a linear decay in in-canopy flow speed (Figure
253 3) rather than the exponential decay assumed by Chen et al. and observed elsewhere for arrays
254 of rigid obstacles (e.g. Belcher et al. 2003).

255 **Bromide penetration in the pore-water** – Despite the large degree of variation in the
256 data, Figure 4 shows that the relative bromide concentration $[Br^-]_{rel}$ was highest around the
257 leading edge of canopy in both depth layers in both the short- (Figure 4a) and long-leaved
258 (Figure 4b) canopies. The horizontal distance over which the solute is predicted to be able to
259 travel through the substrate in the 24 hours for which the experiment was run can be predicted
260 from the infiltration speed. This can be calculated, following Nepf and Koch (1999), as

261 $$V_D = \frac{KU^2}{gd} \qquad (6)$$

262 where K is the sediment permeability (1.6 x 10^{-11} m^2), and d, the distance over which the flow
263 deceleration at the front end of the canopy, is taken (from Figure 3) to be approximately the

mean value of X_D, 0.65 m. This gives $V_D = 2.22\times10^{-6}$ m s^{-1}, which over 24 hours gives a horizontal penetration distance of 0.19 m, which is of the same order of magnitude as the length over which the maximum levels of measured bromide concentration in the substrate are sustained, in both of the canopies at both depths.

The rate at which the bromide infiltrates into the substrate can be compared to the rate of uptake of nutrients by seagrasses. The value of V_D calculated above implies a volumetric rate of water infiltration of 2.94×10^{-6} m^3 s^{-1} per m^2 of bed surface area. If we assume that the concentration of dissolved, bioavailable nitrogen in coastal waters is 0.00005-0.0005 g l^{-1} (Cozzi and Giani, 2007), this would imply 0.00053– 0.0053 x 10^{-3} kg N (m^2 sediment surface)$^{-1}$ hr^{-1} of dissolved nitrogen exchange between the water column and sediment. Rates of nitrogen uptake by seagrasses vary greatly but a typical value is 5 μmol (g dry weight)$^{-1}$ hr^{-1} i.e. 70 μg N (g dry weight)$^{-1}$ hr^{-1} (e.g. Vonk et al., 2008). Touchette and Burkholder (2000) give a range of 5-270 μg N (g dry weight)$^{-1}$ hr^{-1} for ammonium uptake. If the density of real seagrass is estimated as 910 kg m^{-3} (e.g. Folkard, 2005), then the short-leaved canopy used here represents a dry weight seagrass mass of 0.13 kg (m^2 sediment bed surface area)$^{-1}$, and the long-leaved canopy 0.325 kg (m^2 sediment bed surface area)$^{-1}$. This implies that the solute exchange rate can be written as 4.1-41 μg N (g dry weight)$^{-1}$ hr^{-1} for the short-leaved seagrass, and 1.6-16 μg N (g dry weight)$^{-1}$ hr^{-1} for the long-leaved seagrass. These values are the same order of magnitude as typical range of uptake rates of nitrogen by seagrasses, if arguably towards the lower end of that range.

Discussion

Effect of the seagrass canopy on hydrodynamics – Our experiments demonstrate the well-established pattern of flow adjustment at the upstream end of a submerged vegetation canopy (e.g. Folkard, 2005; Tanino and Nepf, 2008; Chen et al., 2013), whereby part of the flow travels at accelerated speeds over the top of the canopy, and part travels at decelerated speeds through the canopy. They also indicate the third element of flow that we theorize above - the enhancement of infiltration from the open water into the substrate while the in-canopy flow decelerates as a result of the presence of the canopy. This flow is negligible in terms of water discharge (in these experiments, its velocity scale is ~10^{-6} ms^{-1}, compared to ~10^{-2} ms^{-1} for the canopy through-flow and ~10^{-1} ms^{-1} for the overflow) but, as discussed below, important for nutrient budgets.

The magnitude of the reduction in flow speed observed in both the long- and short-leaved cases here is in good agreement with the predictions of Chen et al. (2013), which are derived from a two-layer flow model of flows through arrays of rigid obstacles (c.f. the flexible obstacles used here). This model assumes that the layers are connected via turbulent stresses in the shear zone at the top of the canopy which are assumed to scale on the square of the velocity difference between the layers and the length scale of the vortices within the shear zone. The latter, in turn, are assumed to scale on the reciprocal of the product of the canopy drag coefficient (C_D) and frontal area per unit volume (a). The adjustment length measured in these experiments, over which this reduction in flow speed (X_D) occurs, fits well the predictions of Chen et al. (2013) for our long-leaved canopy (Figure 5b), but appears to be slower, and more linear rather than exponential, in our short-leaved canopy. Reasons for this are unclear; one possibility is that relatively sparse canopies of flexible obstacles allow preferential flow

paths to be set up that lead to a more gradual flow decay rate at the start of the canopy (where the flow is faster and more able to deflect the obstacles). But this is purely speculative, and the distinction between flow decay in canopies of rigid and flexible obstacles suggested by our data requires further investigation.

Effects of hydrodynamic adjustment to the seagrass canopy on solute exchange – The horizontal length scale over which the highest levels of bromide concentration within the sediment cores persists into the canopy (~0.2 m) matches well that predicted from the assumption that the solute exchange between the open water and the substrate results from the infiltration of the flow into the substrate due to its deceleration by the canopy. This supports the hypothesis that the enhanced solute exchange is due to increased flow infiltration as a result of the deceleration of the in-canopy flow. The lack of distinction between the bromide concentrations in the 0-0.001 m and 0.001-0.002 m depth cores indicates that the infiltrating water spreads more deeply than these depths. In the present study, we concentrated on the horizontal extent of nutrient delivery to the substrate. The relationship between the depth of infiltration and the depth of seagrass roots is also likely to be important for determining seagrasses' nutrient uptake rates, and requires further investigation. The variability in measured bromide concentrations (Figure 4) is quite high, and as a result there is no clear difference in them between the short- and long-leaved cases studied here.

Effects of solute exchange on seagrass canopy – The fact that our estimates of nutrient exchange rate are in the same range of orders of magnitude as the rate of nutrient uptake by seagrasses indicates that nutrient exchange between the open water and sediment at seagrass canopy edges is an important process for determining seagrass nutrient uptake in these

330 regions. Seagrasses can take up dissolved nutrients from both pore water and open water
331 (Stapel et al., 1997, Hemminga et al., 1999), but pore water nutrient concentrations are
332 generally higher (Okubo et al., 2002; Larned et al., 2004), especially in the oligotrophic waters
333 typically found in tropical seagrass environments. This implies that pore water nutrient
334 concentrations, and thus the rates of infiltration of water into the sediment are an important
335 determinant of seagrass growth rates at the upstream edges of seagrass canopies. By
336 extension, one can hypothesize that there is likely to be exfiltration of relatively nutrient-rich
337 interstitial water from the sediment into the water column at the downstream end of canopies,
338 where the near-bed open water pressure is reduced. This, therefore, is likely to be an important
339 mechanism for replenishment of nutrients in the open water. We conclude from this study that
340 the nutrient transfer rate from the open water to the pore water is determined primarily by the
341 infiltration of the flow into the substrate due to its deceleration by the canopy – as well as the
342 ambient nutrient concentration (Nishihara and Ackerman, 2006), which we have not considered
343 here. This has the effect of causing pore water dissolved nutrient concentrations to decrease
344 with increasing distance from seagrass canopy edges (over a distance of ~0.5-1 m in our study).
345 This finding has important ecological implications, as it implies favorable nutrient conditions for
346 clonal expansion at the edges of seagrass patches, which can increase the seagrass growth rate
347 and thus facilitate patch and meadow expansion. However, this also raises the question of how
348 nutrients can be delivered to pore water in the interior of seagrass meadows, where our results
349 suggest nutrient concentrations would be very low if they were purely determined by the
350 mechanism we have identified as being important here, as there is no flow deceleration here.

Future studies are therefore required to identify the mechanisms that ensure sufficient nutrient supply to seagrasses in the interior of seagrass meadows.

REFERENCES

Apostolaki, E., Holmer, M., Marba, N., Karakassis, I. (2010). Degrading seagrass (*Posidonia oceanica*) ecosystems: a source of dissolved matter in the Mediterranean. Hydrobiologia 649: 13-23

Barron, C., Middelburg, J.J., Duarte, C.M. (2006). Phytoplankton trapped within seagrass (*Posidonia oceanica*) sediments are a nitrogen source: An in situ isotope labeling experiment. Limnol. Oceanogr. 51: 1648–1653

Barry, S. C., Frazer, T. K., Jacoby, C. A. (2013). Production and carbonate dynamics of *Halimeda incrassate* (Ellis) Lamouroux altered by *Thalassia testudinum* Banks and Soland ex Konig. Jour. Exp. Mar. Bio. Ecol. 444: 73-80

Belcher, S.E., Jerram, N., and Hunt, J.C.R. (2003) Adjustment of a turbulent boundary layer to a canopy of roughness elements. J. Fluid Mech. 488: 369-398

Bouma, T. J., Friedrichs, M., Klaassen, P., van Wesenbeeck, B. K., Brun, F. G., Temmerman, S., van Katwijk, M. M., Graf, G., Herman, P. M. J. (2009). Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. Mar. Ecol. Prog. Ser. 388: 293-297

Cambridge, M.L., Chiffings, A.W., Brittan, C., Moore, L., McComb, A.J. (1986). The loss of seagrass in cockburn sound, western Australia II. possible causes of seagrass decline. Aquatic Bot. 24: 269-285

Carr, J., P. D'Odorico, K. McGlathery, and P. Wiberg. (2010). Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. Journal of Geophysical Research 115: G03011. doi:10.1029/2009JG001103

Chen, Z., Jiang, C., and Nepf, H.M. (2013) Flow adjustment at the leading edge of a submerged aquatic canopy. Water Resour. Res., 49: 5537-5551

Christiansen M.J.A., van Belzen J., Herman P.M.J., van Katwijk M.M., Lamers L.P.M., van Leent P.J.M., Bouma T.J. (2013). Low-Canopy Seagrass Beds Still Provide Important Coastal Protection Services. PLoS ONE 8(5): e62413. doi:10.1371/journal.pone.0062413

Cozzi, S., and Giani, M. (2007) Determination of Organic Nitrogen and Urea, in L.M.L. Nollet and L.S.P. de Gelder (eds.) Handbook of Water Analysis 2nd edition. London: CRC Press

Cullen-Unsworth, L. C., Nordlund, L. M., Paddock, J., Baker, S., McKenzie, L. J., Unsworth, R. K. F. (2013). Seagrass meadows globally as a coupled social–ecological system: Implications for human wellbeing. Marine Pollution Bulletin, 83 (2): 387-397

Duarte, C.M., Kennedy, H., Marba, N. and Hendricks, I.E. (2011) Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. Ocean Coast. Manage. 51: 671-688

Evrard, V., Kiswara, W., Bouma, T. J., Middelburg, J. J. (2005). Nutrient dynamics of seagrass ecosystems: ^{15}N evidence for the importance of particulate organic matter and root systems. Mar. Ecol. Prog. Ser. 295: 49-55

Finkner, S.C. and Gilley J.E. (1986). Sediment and dye concentration effects on fluorescence. Appl. Eng. Agri. 2: 104-107

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

Foster, S., Glud, R.N., Gundersen, J.K., Huettel, M. (1999) In situ study of bromide tracer and oxygen flux in coastal sediments. Est. Coast. Shelf Sci. 49: 813-827

Gacia, E. and Duarte, C.M. (2001). Sediment retention by a mediterranean *Posidonia oceanica* Meadow: The Balance between Deposition and Resuspension. Estuar. Coast. Shelf Sci. 52: 505-514

Gilley, J.E., Finkner, S.C., Doran, J.W., Kottwitz E.R. (1990). Adsorption of bromide Tracers onto sediment. Appl. Eng. In Agri. 6: 35-38

Glud, R.N., Gundersen, J.K., Jorgensen, B.B., Revsbech, N.P., Schulz, H.D. (1994). Diffusive and total oxygen uptake of deep sea sediments in the eastern south Atlantic Ocean: in situ and laboratory measurements. Deep Sea Res. 41: 1767-1788

Hemminga, M.A. and Marba, N. and Stapel, J. (1999). Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems. Aquatic Botany, 65: 141-158

Hendricks, I.E., Sintes, T., Bouma, T. and Duarte, C.M. (2007). Experimental assessment and modeling evaluation of the effects of seagrass (*P. oceanica*) on flow and particle trapping. Mar. Ecol. Prog. Ser. 356: 163-173

Huettel, M., Gust, G. (1992). Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. Mar. Ecol. Prog. Ser. 82: 187-197

Huettel, M and Rusch, A. (2000). Transport and degradation of phytoplankton in permeable sediment. Limnol. Oceanogr. 45 (3): 534-549

Huettel, M. and Webster I. T. (2001). Porewater flow in permeable sediments. *In* Boudreau, B.P. and Jorgensen, B.B [eds.], The benthic boundary layer. New York: Oxford Univ. Press, pp. 144-179

Huettel, M., Ziebis, W., Forster, S., Luther III, G. W. (1998). Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochimica et Cosmochimica Acta, 62 (4): 613-631

Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. Global Biogeochemical Cycles, 24, GB4026, doi: 10.1029/2010GB003848

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G.T. (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446: 285-302

Larned, S. T., Nikora, V. I., Biggs, B. J. F. (2004). Mass transfer-limited nitrogen and phosphorus uptake by stream periphyton: A conceptual model and experimental evidence. Limnol. Oceanogr. 49: 1992–2000

Lewis, F. G. (1984). Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrate. Mar. Ecol. Prog. Ser. 19: 101-113

Lin, A.Y.C., Debroux, J.F., Cunninghan, J.A., Reinhard, M.(2003). Comparison of Rhodamine-WT and bromide in the determination of hydraulic chracteristics of constructed wetlands. Ecol. Eng. 20 (1): 75-88

Madsen, O.S. (1978) Wave-induced pore pressures and effective stresses in a porous bed. Géotechnique 28 (4): 377-393

Morris, L.J. and Virnstein, R. W. (2004). The Demise and Recovery of Seagrass in the Northern Indian River Lagoon, Florida. Estuaries 27 (6): 915 - 922

Morris, E.P. and 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. and Koch, E.W. (1999). Vertical secondary flows in submersed plant-like arrays. Limnol. Oceanogr. 44 (4): 1072–1080

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

Nepf, H.M., Ghisalberti, M., White, B., and Murphy, E. (2007), Retention time and dispersion associated with submerged aquatic canopies, Water Resour. Res., 43, W04422, doi:10.1029/2006WR005362

Nishihara G.N. and Ackerman J.D. (2006). The effect of hydrodynamics on the mass transfer of dissolved inorganic carbon to the freshwater macrophyte *Valissneria americana*. Limnol. Oceanogr. 51 (6): 2734-2745

Okubo, A., Ackerman, J.D., Swaney, D.P. (2002). Passive diffusion in ecosystems. *In:* Okubo, A. and Levin, S. (eds.) Diffusion and Ecological Problems: New Perspectives. New York: Springer Verlag, pp 31–106

Owens, L.B., Van Keuren, R.W. and Edwards, W.M. (1985). Groundwater quality changes resulting from a surface bromide application to a pasture. Journ. Environ. Qual. 14: 543-548

Palmer, M.A. (1988). Epibenthic predators and marine meio-fauna: separating predation, disturbance and hydrodynamic effects. Ecology 69: 1251-1259

Paul, M., Bouma, T.J., Amos, C.L. (2012). Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. Mar. Ecol. Prog. Ser. 444: 31-41

Peduzzi, P., Herndl, G.J. (1991). Decomposition and significance of seagrass leaf litter (*Cymodocea nodosa*) for the microbial food web in coastal waters (Gulf of Trieste, Northern Adriatic Sea). Mar. Ecol. Prog. Ser. 71: 163-174

Peralta, G., Van Duren, L. A., Morris, E. P., Bouma, T. J. (2008). Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. Mar. Ecol. Prog. Ser. 368: 103-115

Peterson, C.H., Luettich Jr, R.A., Micheli, F., and Skilleter, G.A. (2004) Attenuation of water flow inside seagrass canopies of differing structure. Marine Ecology Progress Series 268: 81-92

Precht, E., Huettel, M. (2004). Rapid wave-driven advective pore water exchange in a permeable coastal sediment. J Sea. Res. 51: 93-107

Pujol, D. and Nepf, H. (2012). Breaker-generated turbulence in and above seagrass meadow. Continental Shelf Res. (49): 1-9

Rasheed, M., Badran, M.I., Huettel, M. (2003). Influence of sediment permeability and mineral composition on organic matter degradation in three sediments from the Gulf of Aqaba, Red Sea. Estuar. Coast. Shelf. Sci. 57: 369-384

Reimers, C. E., Stecher III, H. A., Taghonb, G. L., Fuller, C. M., Huettel M., Rusch, A., Ryckelynck, N., Wild, C. (2004). In situ measurements of advective solute transport in permeable shelf sands. Continental Shelf Research 24: 183-201.

Replogle, J.A., Meyers, L.E. and Brust, K.J. (1966). Flow measurements with fluorescent tracers. ASCE J Hydraulics. Div. 5: 1-14

Reyes, J. & Sansón, M. (2001). Biomass and production of the epiphytes on the leavesof *Cymodocea nodosa* in the Canary Islands. Botanica Marina 44: 307-313

Romero, J., Lee, K. S., Perez, M., Mateo, M. A. and Alcoverro, T. (2006). Nutrient dynamics in seagrass ecosystems. *In* Larkum, A.W.D., Orth, R.J. and Duarte, C.M. [eds.] Seagrasses: biology, ecology and conservation. New York: Springer, pp. 227-254

Short, F.T., Polidor, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freemen, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Kenworthy, W.J., Nafie, Y.A.L., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Van Tussenbroek, B., Vegara, S.G., Waycott, M., and Zeiman, J.C. (2011). Extinction risk assessment of the world's seagrass species. Biological Conservation 144: 1961-1971

Shum, K.T. (1992). Wave-induced advective transport below a rippled water-sediment interface. J Geophys. Res. (Oceans) 97: 789-808

Smith, S.J. and Davis, R.J. (1974). Relative movement of bromide and nitrate through soils. Journ. Environ. Qual. 3: 152-155

Stapel, J., Aarts, T.L., van Duynhoven, B.H.M., de Groot, J.D., van den Hoogen, P.H.W., Hemminga, M.A. (1996). Nutrient uptake by leaves and roots of the seagrass Thalassia hemprichii in the Spermonde Archipelago, Indonesia. Mar. Eco. Prog. Ser. 134: 195-206

Tanino, Y., and Nepf, H.M. (2008), Laboratory investigation of mean drag in a random array of rigid, emergent cylinders, J. Hydraul. Eng., 134 (1): 34–41

Thomas, F. I. M., Cornelisen, C. D. and Zande, J. M. (2000). Effects of water velocity and canopy morphology on ammonium uptake by seagrass communities. Ecology 81: 2704 – 2713.

Tomasko, D. A., Lapointe, B. E. (1991). Productivity and biomass of Thalassia testudinum as related to water column nutrient availability adn epiphyte levels: field observations and experimental studies. Mar. Ecol. Prog. Ser. 75: 9-17

Touchette, B.W., and Burkholder, J.M. (2000) Review of nitrogen and phosphorus metabolism in seagrasses. J. Exp. Mar. Biol. Ecol. 250: 133–167

Van der Heide, T., Bouma, T.J., Van Nes, E.H., Van de Koppel, J., Scheffer, M., Roelofs, J.G.M., Van Katwijk, M.M., Smolders, A.J.P. (2007). Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10: 1311-1322

Van Engeland, T., Bouma, T. J., Morris, E. P., Brun, F. G., Peralta, G., Lara, M., Middelburg, J. J. (2011). Potential uptake of dissolved organic matter by seagrasses and macroalgae. Mar. Ecol. Prog. Ser. 471: 71-81

573 Verduin, J. J., Backhaus J. O. (2000) Dynamics of plant-flow interactions for the seagrass
574 Amphibolus antartica: field observations and model simulations. Estuar Coast. Shelf Sci. 50:
575 185-204
576
577 Vonk, J. A., Middelburg, J. J., Stapel, J., Bouma, T. J. (2008). Dissolved organic nitrogen uptake
578 by seagrasses. Limnol. Oceanogr. 53 (2): 542-548
579
580 Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine,
581 A., Fourqurean, J.W., Heck Jr, K.L., Hughes, A.R., Kendrick, G.A., Kenworhty, W.J., Short, F.T.,
582 Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal
583 ecosystems. Proc. Nat. Acad. Sci. 106 (30): 12377-12381
584
585 Webb, J.E., and Theodor, J. (1972). Wave-induced circulation in submerged sands. Journal of
586 Marine Biology Association UK 52: 903-914
587
588 Wu, F.-C., Hsieh, W.S., and Chou, Y.-J. (1999) Variation of roughness coefficients for
589 unsubmerged and submerged vegetation. Journal of Hydraulic Engineering 125: 934-942
590

Figure Legends

Figure 1: a) Plan view of the racetrack flume tank at NIOZ, Yerseke; b) Plan view of the simulated seagrass meadow placed in the test section of the flume, showing locations of measurements of nutrient penetration.

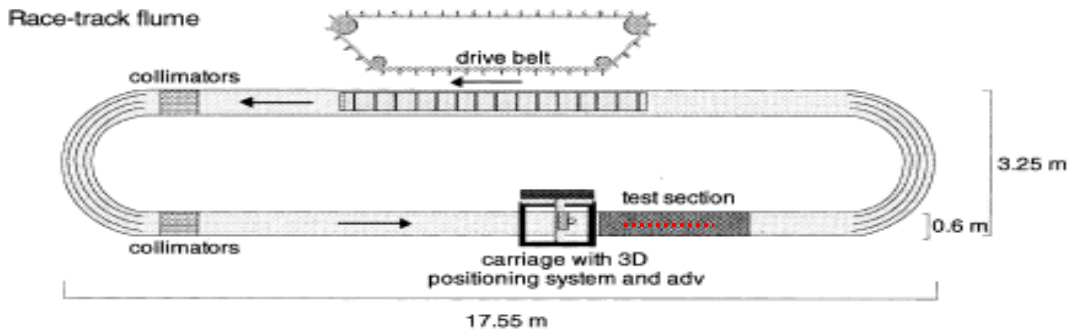
Figure 2: Flow profiles for (a) short-leaved and (b) long-leaved seagrass canopies. Filled symbols represent u profiles (normalized to u at z= 0.3 m). The dotted lines indicate the location of the canopy where long-leaved seagrass bent to similar height as short-leaved seagrass height.

Figure 3: Downstream development of the mean flow speeds over the canopy (U_a; clear symbols) and within the canopy (U_b; filled symbols) for (a) short-leaved and (b) long-leaved seagrass canopies. The dotted line indicates the predictions of the model of Chen et al. (2013) – see text for details. The thick black lines indicate the location of the seagrass canopy.

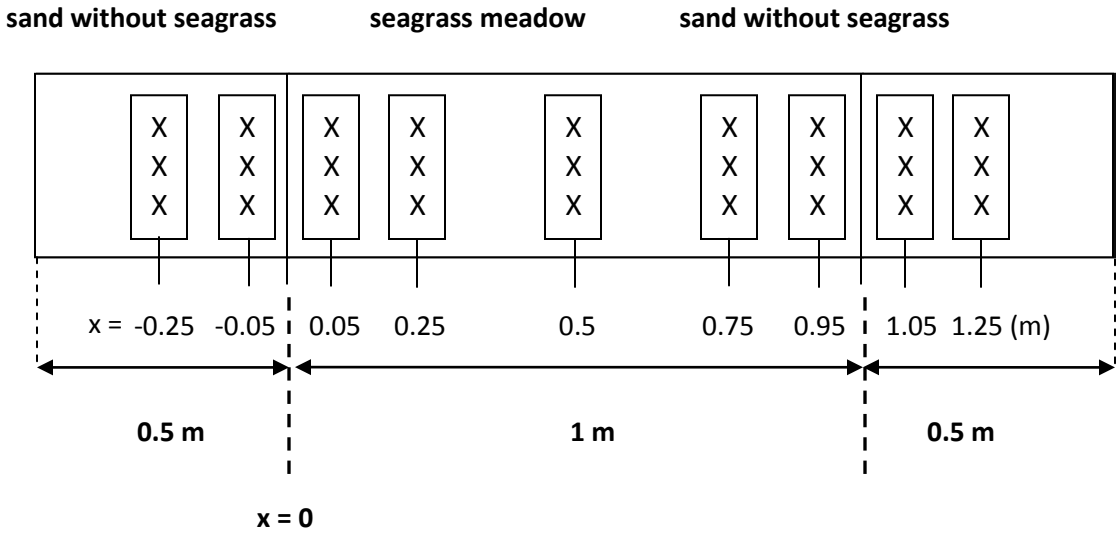
Fig. 4 Relative bromide concentration, as defined in equation (1), in the pore water measured after 24 hours of running the flow, for (a) the short-leaved seagrass canopy; and (b) the long-leaved seagrass canopy. Clear symbols represent relative bromide concentration in 0.01 m depth; filled symbols represent relative bromide concentration in 0.02 m. Error bars show standard deviation of samples measured at the three parallel locations for each x-position shown in Fig. 1b.

Figure 1

a. Race Track Flume



b. Seagrass Setup and Hydrodynamic Scheme



632 **Figure 2**

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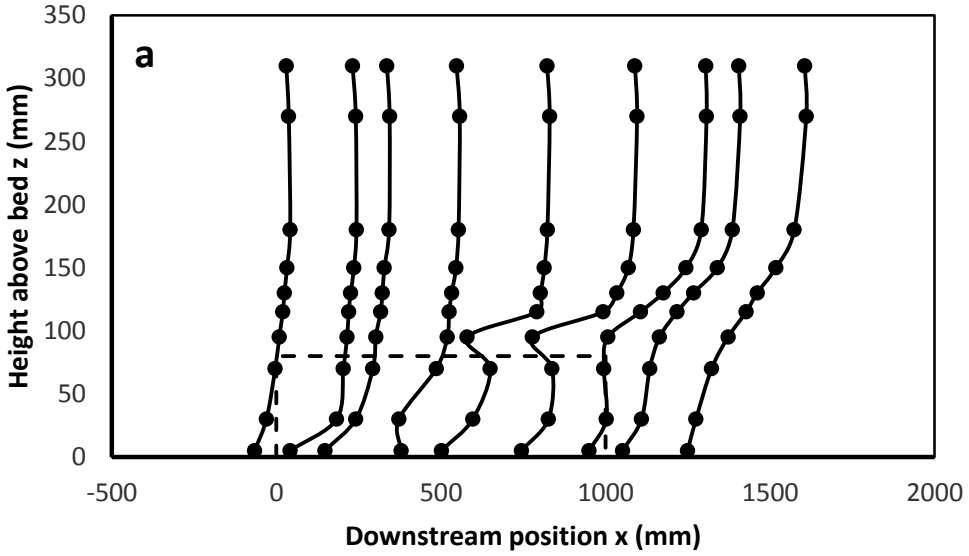

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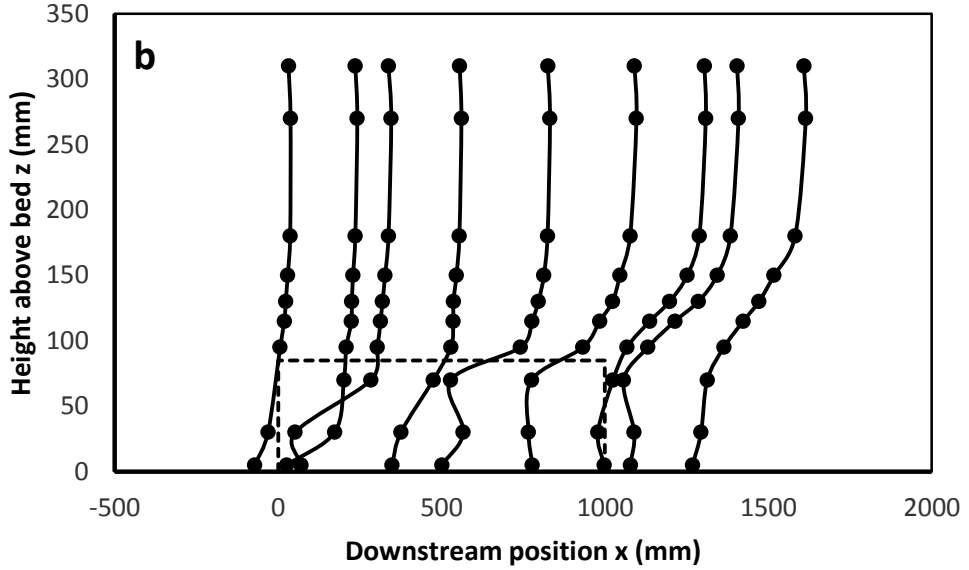

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640 **Figure 3**

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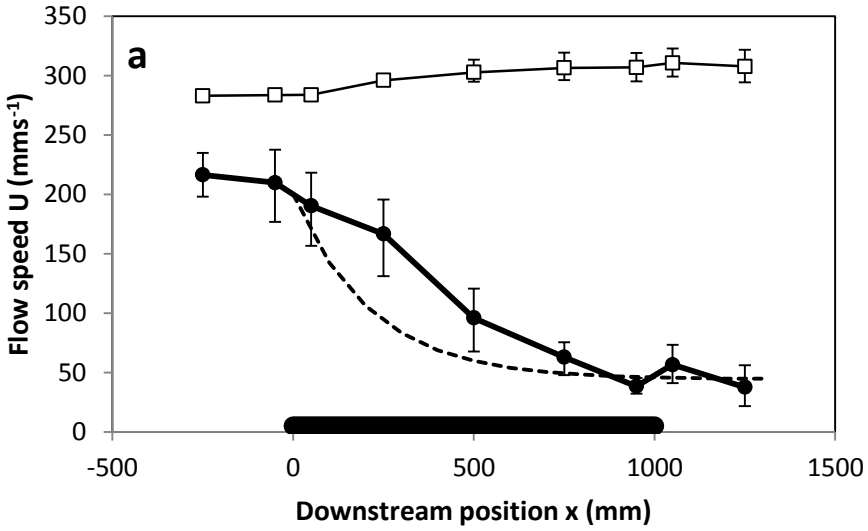

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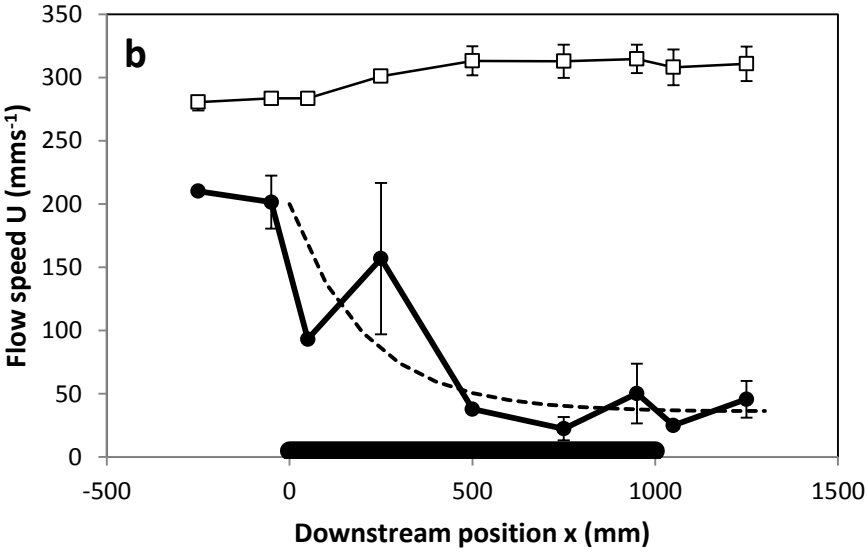

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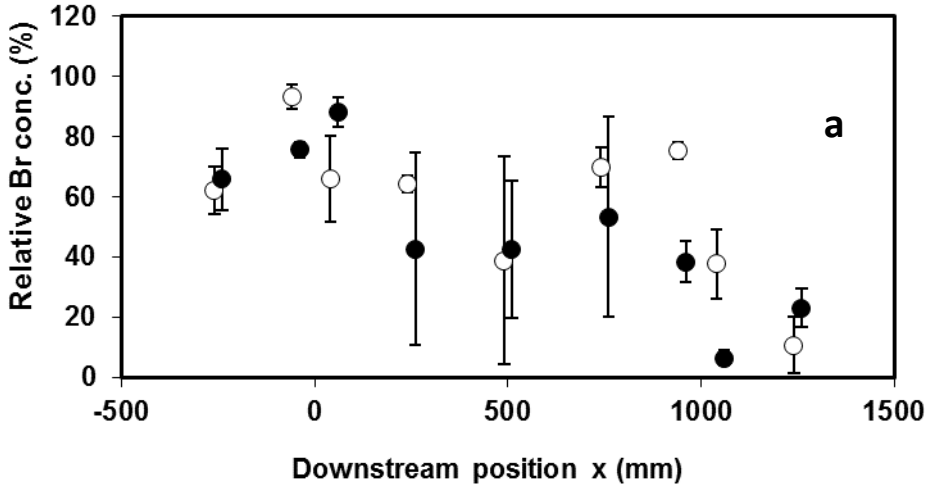
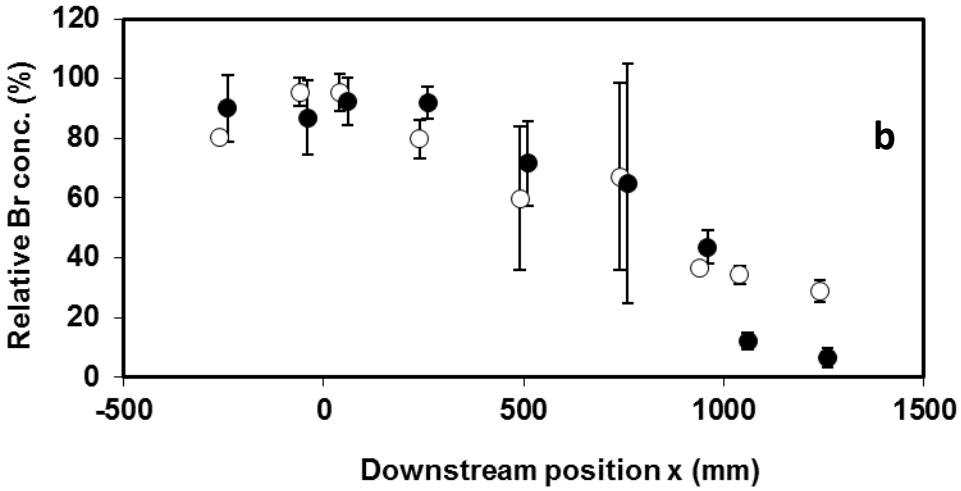
Figure 4


Relative Br conc. (%)
120
100
80
60
40
20
0
-500
0
500
1000
1500
Downstream position x (mm)
a


Relative Br conc. (%)
120
100
80
60
40
20
0
-500
0
500
1000
1500
Downstream position x (mm)
b