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Influence of seagrass density and hydrodynamic forcing on advective pore-water exchange: a flume study with Thalassia testudinum mimics

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Abstract

Most studies on porewater exchange have been carried out in unvegetated contexts only, raising the question "under which conditions porewater exchange occurs within seagrass meadows". We studied how hydrodynamic conditions (velocity set at 0, 0.1 and 0.25 m s^{-1} without waves and at 0, 0.1 m s^{-1} with small waves) and meadow density (0, 245, 480 and 1300 shoots m^{-2}) affect such exchange processes within a simulated seagrass meadow in a laboratory flume. The removal rate of fluorescent dye from the porewater, was significantly affected by hydrodynamic forcing, but not by shoot density or their interaction. Exchange rates were highest at the highest current velocity (0.25 m s^{-1} without waves) and in the presence of waves (0.1 m s^{-1} with small waves); the no flow and 0.1 m s^{-1} flow without waves had a much lower exchange rate. Overall, present results suggest that porewater exchange can be as important in seagrass meadows as previously shown for bare sediments, regardless of seagrass density, hydrodynamic

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forcing can drive porewater exchange from sediment to water column. This has important implications. Via this process, particulate and/or dissolved organic nitrogen can be delivered to the root-zone of seagrasses, providing an additional nutrient source to oligotrophic seagrass meadows. Yet, increased porewater exchange and particulate organic matter may also increase the amount of metals and organic microcontaminants delivered to the sediment and seagrass roots.

Key words: Seagrass, *Thalassia,* Porewater, Hydrodynamic, fluorescence, Density

Introduction

Seagrass meadows are highly productive autotrophic marine ecosystems that provide many important ecosystem services including habitat provision to numerous marine organisms (Borg *et al.*, 2005; Mills & Berkenbusch, 2009), enhancing water transparency through sediment entrapment (Van der Heide *et al.*, 2007; Carr *et al.*, 2010) and contributing to coastal protection by sediment stabilization (Newell & Koch, 2004; Widdows *et al.*, 2008; Christianen *et al.*, 2012). In contrast to most terrestrial plants, seagrasses have high N-losses due to the combination of relatively high leaf-loss rates with little N resorption from senescing leaves (Stapel & Hemminga, 1997; Romero *et al.*, 2006). Efficient external recycling of nutrients, with substantial input of exogenous N onto the litter and efficient uptake of N released from litter, has been identified as an important mechanism to retain N in nutrient-poor tropical seagrass meadows (Vonk & Stapel, 2008). Nevertheless, N-losses are unavoidable in the open and highly dynamic shallow coastal environments where seagrasses grow, raising the question of which additional nitrogen sources are used to maintain high seagrass productivity.

Recently, it was discovered that dissolved organic nitrogen is relatively abundant and not refractory in coastal waters, even in oligotrophic systems (Bronk *et al.*, 2007). Moreover, it was discovered that seagrasses can rapidly consume this dissolved organic nitrogen, particularly via their roots (Evrard *et al.*, 2005; Barron *et al.*, 2006; Van Engeland *et al.*, 2011, 2013), thus providing a competitive advantage over other primary producers (Evrard *et al.*, 2005; Vonk *et al.*, 2008). This raises the question, which factors are determining how much organic nutrients are delivered from the water layer into the coral sand, on which many tropical seagrasses grow in oligotrophic environments. To our knowledge, little is known about the processes controlling organic nutrient exchange in vegetated sandy substrates, as previous studies have focused on advective transport of nutrients in bare sandy sediments (Huettel & Webster, 2001; Oschlies, 2002).

In cohesive and fine grained sediments, dissolved organic nutrients (DON) and particulate organic matter (POM) will only be transported by molecular diffusion and bioturbation (Precht & Huettel, 2003). In more permeable, sandy sediment, DON and POM could be transported due to pressure differences that induce porewater flow (Huettel & Webster, 2001). Surface gravity waves may also influence porewater exchange by causing oscillating flow near the seabed-water interface (Webb & Theodor, 1972; Huettel & Webster, 2001). These studies of such porewater exchange have been carried out in unvegetated contexts. It would be useful to know under which hydrodynamic conditions such exchange processes may occur within seagrass meadows, and how this depends on meadow properties such as, for example, seagrass density.

Seagrass beds are well known to attenuate hydrodynamic energy by decreasing current velocity (e.g., Fonseca *et al.*, 1982; Gambi, 1990) and wave energy (e.g., Fonseca & Cahalan, 1992; Bouma *et al.*, 2005) within a seagrass meadow. This would reduce the exchange between the pore- and open-water if hydrodynamic energy from waves and currents is a direct driver of such exchange processes. The increased bottom roughness generated by vegetation such as seagrasses (Newell & Koch, 2004; Chen *et al.*, 2007) may create local hydraulic pressure gradients, which could locally enhance the exchange between the pore- and open-water. Within this study we aim to identify the relative importance of *i)* current velocity, *ii)* the presence/absence of waves and *iii)* vegetation density for the exchange between pore- and open-water within a seagrass meadow. Hence we placed *Thalassia testudinum* mimics (245, 480 and 1300 shoots m^{-2} and a bare control) into a race-track flume, in which we created flows with mean velocities of 0 (still), 0.1 (slow) and 0.25 m s^{-1} (fast) and studied the effect of the absence/presence of 0.05 m waves superimposed on a flow of 0.1 m s^{-1} (slow & wave). So we varied two parameters, shoot density (d) and hydrodynamics (h), both of which may be expected to influence the influx of DON-rich water into the porewater (Santos *et al.*, 2012). As a quantitative proxy of this influx, we measured the decrease in the amount of fluorescent dye in the pore water over a 1-hour period, assuming that influx equals outflux (= porewater exchange). We hypothesize that porewater exchange decreases with *i)* decreasing current velocity, *ii)* reducing wave energy and *iii)* increasing vegetation density. Our results on porewater fluxes in seagrass beds will elucidate which factors and processes may control the supply of additional nutrient sources to the rhizosphere, and will thereby also have implications for our understanding of the compartmentalisation and accumulation of (potential) toxic / alien dissolved molecules, like nanoparticles or medicine derivatives.

Methods

Experimental Setup

The exchange between pore- and open water in seagrass meadows was studied in a race-track flume at the Royal Netherlands Institute for Sea Research (NIOZ), Yerseke. This flume is approximately 17.55 m long, 0.6 m wide, can hold water to a of depth 0.4 m, can generate currents with mean velocities up to ~0.6 m s^{-1}, and superimpose waves on the currents (Figure 5.1; further details in Bouma *et al.*, 2005; Paul *et al.*, 2012). The test section of the flume (2 m long × 0.6 m wide) has a deepened floor, creating a space of 0.15 m depth, which was filled with coral sand collected from Indonesia with grain size 0.5 mm and permeability 1.94 × 10^{-4} m s^{-1}. The top of the sand layer was level with the flume bed next to the test section. Exchange between pore- and open water was measured as the loss from the sand layer of the fluorescent dye, which was injected upstream of fluorescent sensors placed at 0.03 m depth in the sand (Figure 5.1). Four different hydrodynamic conditions were applied: *i)* control (still, no flow and no waves, 0 m s^{-1}), *ii)* flow of 0.1 m s^{-1} (slow), *iii)* flow of 0.1 m s^{-1} in the presence of 0.05 m wave height (slow & wave), and *iv)* flow of 0.25 m s^{-1} (fast). These hydrodynamic conditions can be considered as representative for the range of conditions typically observed in shallow seagrass meaodws (Palmer, 1988; Fonseca & Cahalan, 1992; Verduin & Backhaus, 2000; Peterson *et al.*, 2004).

Seagrass Setup

We investigated the influence of seagrass density on porewater exchange by using seagrass mimics, an established method in studies of physical processes (e.g. Bouma *et al.*, 2005; Peralta *et al.*, 2008; Manca, 2010). Mimics were created based on morphological observations on *Thalassia testudinum* in Indonesia, and consisted of 4 leaves per shoot (0.2 m long × 0.01 m wide) on top of a 0.1 m sheath that was placed into the sediment. Four different densities of mimics were used: *i)* no mimics (i.e. 0 shoots m^{-2}, control), *ii)* 1300 shoots m^{-2}, *iii)* 480 shoots m^{-2}, and *iv)* 245 shoots m^{-2}. These mimic densities were based on the range of shoot densities as can be observed in natural *Thalassia testudinum* meadows (i.e., 48 – 1888 shoots m^{-2}; Lewis, 1984; Tomasko & Lapointe, 1991; Barry, 2013). We do realize that by using these mimics, we lack roots and rhizome systems, thereby reducing the complexity of the below ground structure to the 0.1 m sheath of the mimic that was placed inside the coarse sand. We realize that this simplification of the below-ground structure may cause a slight overestimation of the porewater exchange rates, but assume it does not affect our ability to identify the main drivers of poor water exchange.
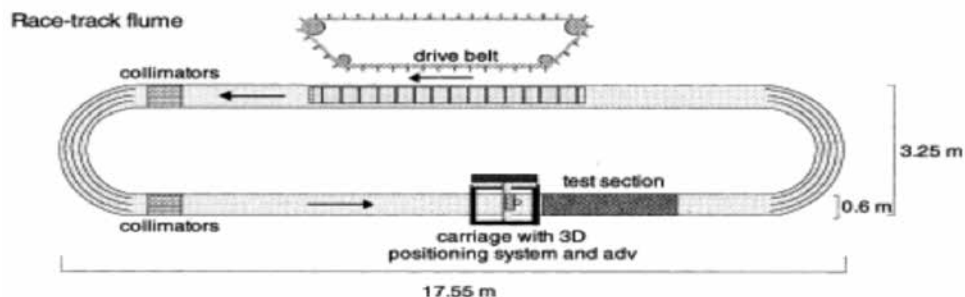
Figure 5.1
Schematic diagram of the racetrack flume tank at NIOZ, Yerseke.

Porewater Exchange Measurement
An optical fluorescent sensor (CYCLOPS; Turner Designs) was placed inside the flume at 1.2 m downstream from the leading edge of the test section at a depth of 0.03 m beneath the surface of the sediment. To enable this optical sensor to measure the fluorescent concentration inside the sediment, we placed a perforated cylindrical metal cap (0.02 m diameter x 0.03 m long; volume 9.42 ml) on the sensor head. The perforated holes were small enough to keep the coral sand out, while allowing porewater exchange. A syringe connected to a small plastic tube enabled us to inject 0.2 mg dye l^{-1} into the perforated cylindrical metal cap on top of the fluorescent sensors.

The output of the sensor was monitored for 1 hour after injection of fluorescent dye. Care was taken that the initial concentration after injection was always 0.21 mg l^{-1}. The subsequent changes in dye concentration, which we used as a proxy for the porewater exchange, were recorded for 60 minutes at 10-minute intervals. Three replicate runs were made for every vegetation density (i.e., 0, 245, 480, 1300 shoots m^{-2}) and hydrodynamic setting (i.e., 0, 0.1, 0.25 m s^{-1} in the absence of waves & 0.1 m s^{-1} with waves of 0.05 m amplitude).

Statistical Analysis
The change in dye concentration inside the sediment, was fitted with an exponential decay function:

$$C_{fl}(t) = C_0 e^{kt} \qquad (1)$$

where C_{fl} (mg l^{-1}) is the dye concentration measured at time t (minutes), C_0 is the initial dye concentration at the beginning of measurement and k is the decay constant, describing the rate that the dye concentration changes over the 60 minute measurement period. The value of k, obtained by regression for each measurement, was subsequently used in a two-way ANOVA analysis to investi-

gate which variables (hydrodynamics, density or hydrodynamics × density) are the main factors controlling porewater exchange. We defined p-values as highly significant, significant, and marginally significant when $p < 0.01$, 0.05, and 0.1, respectively. Subsequently, Tukey tests were used for post-hoc comparison, to investigate which hydrodynamic treatments differed when compared on a two by two basis.

Results

Comparisons of the loss of dye concentration from the sediment over time, showed that hydrodynamic forcing appeared to have a much stronger effect on porewater exchange than meadow density (Figure 5.2). When the dye concentrations decreased over time, they followed an exponential decay curve, allowing us to estimate the k-values by fitting our measurements to equation 1. Measurements for the zero flow runs showed a slight increase in dye concentration (Figure 5.2A). We cannot explain this result, other than that perhaps some dye might have been retained in the injection syringe and gradually diffused out. Overall, the regression lines obtained by fitting equation 1, had SE s ranging from 0.0005 to 0.013 (Table 5.1). The observation that hydrodynamics had a stronger effect on porewater exchange than vegetation density was confirmed by our statistical tests on the fitted k-values (Table 5.2). Only the hydrodynamic treatment had a highly significant effect ($p < 0.01$), whereas the density effect was marginally significant ($p < 0.10$); there was no significant interaction. The subsequent post hoc Tukey test on the highly significant results showed that the fast (i.e., 0.25 m s^{-1} in the absence of waves) and slow-wave (i.e., 0.1 m s^{-1} with waves) treatments had a similar significantly faster porewater exchange rates than the slow (i.e., 0.1 m s^{-1} no waves) and still (i.e., 0 m s^{-1} no waves) treatments (Figure 5.3). The porewater exchange under slow flow was significantly faster than in the still treatment, where exchange is fully dependent on diffusion.

Table 5.1
Time decay constant (k) values (mg l^{-1} min^{-1}) derived by fitting equation 1 to dye concentrations from each run, averaged over 3 replicates for each density (0, 245, 480, 1300 shoots m^{-2}) and hydrodynamic (still, slow, fast, slow wave) treatment. Values are means (n = 3; ±SE).

|		Vegetation density (shoots m^{-2})			
		0	**245**	**480**	**1300**
		k			
Hydro-dynamic forcing	**still**	-0,001 (0,003)	0,005 (0,003)	0,008 (0,001)	0,002 (0,001)
	slow	-0,011 (0,012)	-0,016 (0,007)	-0,018 (0,008)	-0,006 (0,0005)
	fast	-0,046 (0,005)	-0,026 (0,013)	-0,032 (0,011)	-0,032 (0,009)
	slow wave	-0,039 (0,004)	-0,014 (0,006)	-0,038 (0,003)	-0,018 (0,007)
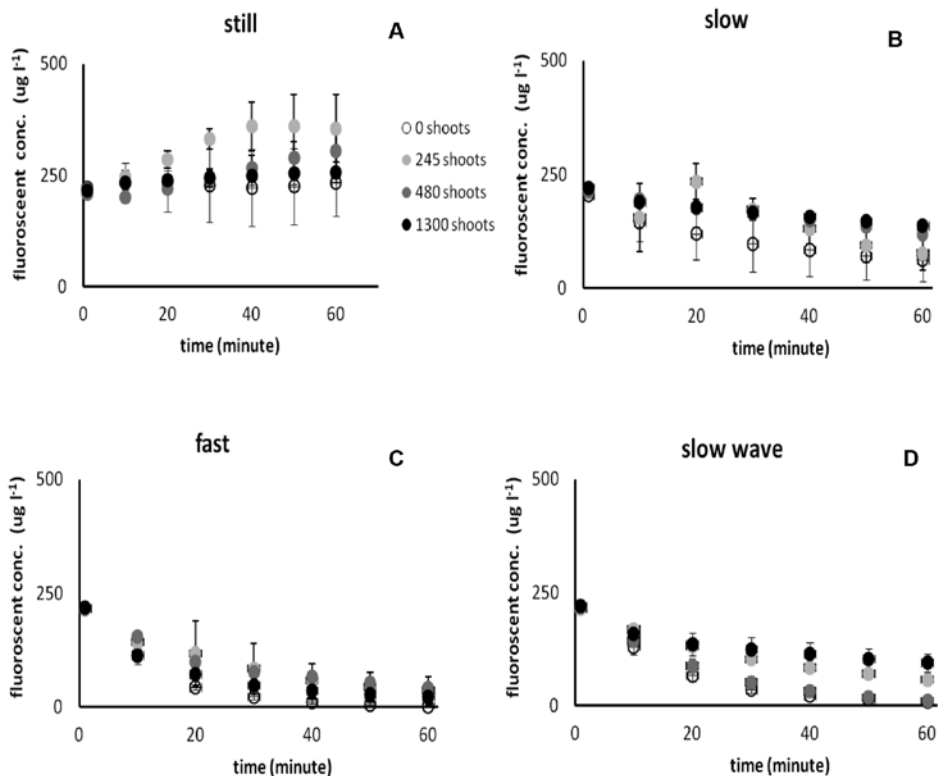
Figure 5.2
Porewater exchange, quantified as the change in dye concentration, plotted against time, under four different hydrodynamic conditions: (A) Still (flow velocity 0 m s^{-1}, no waves) (B) Slow (0.1 m s^{-1}, no waves) (C) Fast (0.25 m s^{-1}, no waves) and (D) Slow wave (0.1 m s^{-1} and waves of 0.05 m amplitude). In each graph, the average fluorescent concentration (mean $\pm$ SE, n = 3) is plotted at 10 minute intervals during 60 minutes of measurements for four different seagrass shoot densities (0, 245, 480 and 1300 shoots m^{-2}).

Table 5.2
Two-way full factorial ANOVA analysis of the variation of the values of the decay constant (k) with shoot density (d) and hydrodynamic treatment (h).

Independent Variables	Df	F Value	Pr (> F)
hydrodynamics	3	23.681	2.91e-08
vegetation density	3	2.653	0.0654
hydrodyn. X dens.	9	1.193	0.3328
Residuals	32		
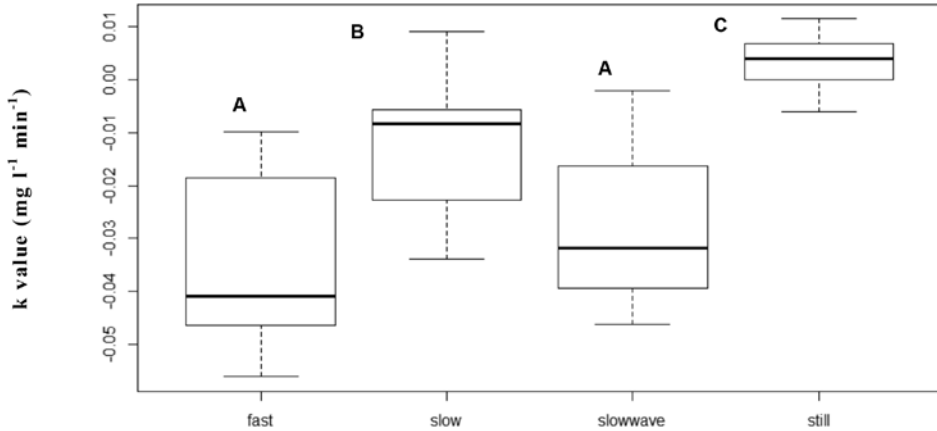
Figure 5.3
Box and whisker plots showing the significantly different groups (as indicated by letters) of the time decay constant (k, mg l^{-1} min^{-1}) for the four hydrodynamic treatments.

Discussion

Our results provide quantitative insight into which factors determine porewater exchange within a seagrass meadow. As a quantitative proxy for the influx of water into the sediments, we measured changes in fluorescent dye concentration in the sediment over time resulting from outflux (as outflux = influx = porewater exchange). We found that hydrodynamic forcing was the main factor affecting this exchange process, while vegetation density (including the absence of vegetation) had little effect. Hence, porewater exchange may be equally important in seagrass meadows as previously shown for bare sediments.

Effects of hydrodynamic forcing and vegetation density on porewater exchange

The significant effect of current velocity and waves on porewater exchange in our experiment with vegetated permeable sediments confirms previous studies on bare submerged permeable sands (Webb & Theodor, 1972; Huettel & Webster, 2001; Santos *et al.*, 2012). Additionally, our study demonstrates the cumulative effect of currents and waves; the combination of a current velocity of 0.1 m s^{-1} with waves of 0.05 m amplitude has an effect on porewater exchange similar to that of a fast velocity of 0.25 m s^{-1} without waves.

In fine sediment, porewater exchange is mainly influenced by diffusion and bioturbation rather than advection (Aller, 2001). In contrast, in more permeable sediments like the coral sands on which many tropical seagrass meadows occur,

porewater flux will be influenced by hydrodynamic forces (Huettel & Rusch, 2000).

Our study shows that vegetation density tends to influence porewater exchange as well, but not linearly and only to a marginally significant degree ($0.05 < p < 0.1$). The vegetation mimics used are flexible, resembling the seagrass *Thalassia testudinum*, but lacking roots and rhizomes. The latter may have caused a slight overestimation of the porewater exchange rates, but is not expect to alter the main drivers of poor water exchange. The non-linear and minor effect of the shoot density probably reflects two processes. On the one hand, hydrodynamics may be attenuated by the vegetation. This has been shown for current velocity – largely due to the bending of the leaves (Gambi *et al.*, 1990; Koch & Gust, 1999) – and for waves (Fonseca & Cahalan, 1992; Bouma *et al.*, 2005). On the other hand, at low shoot densities and/or under strong hydrodynamic forcing, the shoots can cause turbulence due to their increasing the bottom roughness (Newell & Koch, 2004; Chen *et al.*, 2007), or, at low shoot densities, due to them forming obstacles for the water flow (Luhar *et al.*, 2008; Nepf & Vivoni, 2000). But since the vegetation effects are only marginally significantly, porewater exchange may be equally important in seagrass meadows as previously shown for bare sediments, implying important consequences for seagrass functioning.

Ecological implications of porewater exchange

Our study shows that the abundant, non-refractory dissolved organic nitrogen in coastal waters (Bronk *et al.*, 2007) could become available to the plant roots by pore water influx, as (1) the porewater exchange rate is high in the relatively porous sediments tested here; and (2) is generally not diminished by the presence of the vegetation.In oligotrophic coastal systems, seagrass maintain a high productivity through some N resorption from senescing leaves (Stapel & Hemminga 1997; Romero *et al.*, 2006), but particularly by efficient external recycling of nutrients via detritus (Vonk *et al.*, 2008). These sources of nitrogen may therefore function as an important additional nitrogen source to seagrass beds in its highly dynamic habitat. In addition, particulate organic matter may accumulate in the sediment (e.g. Santos *et al.*, 2012) and partially be retained with the sediment acting as a filter. Subsequent remineralisation by the microbial community may supply additional nitrogen and phosphorus to the plant roots, with the exact pathways requiring further investigation.

Rapid exchange between surface water and sediment may also have its downside. Metals and organic microcontaminants dissolved in water or sorbed to particulate matter are delivered to the sediment and the seagrass roots as well. While slow exchange allows deeper layers to remain at the level of pollution that pertained at the time of their deposition, fast transport will cause a larger part of the sediment to be in equilibrium with the surface water column. The implication

of porewater exchange within seagrass meadows for contaminations is a topic requiring more research in the near future.

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