Vol. 514: 71–86, 2014
doi: 10.3354/meps10961

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 6

Comparative study of sediment particle mixing in a *Zostera noltei* meadow and a bare sediment mudflat

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ABSTRACT: Seasonal changes in sediment particle mixing, surface sediment and seagrass characteristics, and benthic infaunal composition were measured in Arcachon Bay (France), within both a well-developed *Zostera noltei* meadow and a bare sediment mudflat. Sediment particle mixing intensities (measured by the normal biodiffusion coefficient D_b^N) were obtained by fitting a continuous time random walk model to *in situ* measured vertical luminophore profiles. D_b^N values (mean ± SD) were between 2.99 ± 2.75 and 22.45 ± 43.73 cm^2 yr^{-1} within the bare mudflat and between 0.39 ± 0.30 and 18.07 ± 18.14 cm^2 yr^{-1} within the *Zostera* meadow. Spatiotemporal changes in infauna and D_b^N were lower within the *Zostera* meadow, which supports the buffering effects of seagrass meadows on biological sedimentary processes. Within the *Zostera* meadow, root biomass declined during the survey, in correlation with increases in (1) the mean value and the variability of D_b^N and (2) the spatial variability of infaunal composition with a decrease in the dominant polychaete *Melinna palmata*. At this station, similarity matrices of mean D_b^N and abundances of a set of 3 infaunal species (including *M. palmata*) correlated significantly, which further supports the key role of this species in controlling sediment particle mixing through sediment stabilization. When considering the whole data set, the similarity matrices of the coefficients of variation of D_b^N and of the abundances of a set of 5 species (*Abra segmentum, Glycera convoluta, Tubificoides benedii, Heteromastus filiformis*, *Ruditapes phillipinarum*) correlated significantly, which supports the suspected role of these species in controlling sediment particle mixing.

KEY WORDS: Seagrass decline · Bioturbation · Infauna · Spatial heterogeneity · Community structure · *Melinna palmata*

INTRODUCTION

Seagrass meadows occupy less than 0.2% of the world ocean but are among the most productive ecosystems worldwide (Duarte 2002). They store a large fraction of this production, making them responsible for about 15% of carbon storage in the world's oceans (Duarte & Chiscano 1999). Seagrasses are 'ecosystem engineers,' creating complex structures that enhance the entrapment of suspended organic matter (Fonseca & Fisher 1986, Meadows et al. 2012) and oxygenate bottom water and sediment, thereby sheltering abundant and highly diverse epi- and infauna (Boström & Bonsdorff 1997, Reise 2002). Seagrass meadows are declining worldwide, and in temperate areas, major mechanisms responsible for this phenomenon include (1) eutrophication, which reduces light penetration and, combined with rising sea water temperature and sea level, inhibits seagrass growth; (2) wasting diseases inducing seagrass mor-

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tality; and to a lower extent (3) biological interactions such as herbivory or the introduction of species that can physically affect seagrasses through bioturbation (Orth et al. 2006).

Bioturbation is defined as 'all transport processes carried out by animals that directly or indirectly affect the sediment matrices' (Kristensen et al. 2012, p. 285). It includes both sediment particle mixing and bioirrigation. Through bioturbation, benthic fauna strongly affect the chemical, physical, and geotechnical properties of marine sediments (Aller 1982, Lohrer et al. 2004). Sediment particle mixing mainly results from locomotion, burrowing, defecation, and feeding by benthic macrofauna (Meysman et al. 2006). It controls the fate of sedimented particles and thereby affects the remineralization (Kristensen 2000) and resuspension (Reise 2002) of particulate organic matter.

Complex interactions occur between seagrasses and benthic infauna which most often result in negative effects of bioturbating species on seagrass growth and colonization through increased (1) physical alterations of shoots and rhizomes and (2) burial rates of seeds and seedlings (Philippart 1994, Delefosse & Kristensen 2012, Suykerbuyk et al. 2012). Conversely, many studies have revealed a negative effect of the establishment of dense root/rhizome networks on the density and burrowing activities of large bioturbators (Hughes et al. 2000, Berkenbusch et al. 2007). Nevertheless, these local negative interactions could result in an overall positive effect by maintaining spatial heterogeneity and thereby enhancing seedling recruitment (Townsend & Fonseca 1998, Meadows et al. 2012). At the whole benthic infaunal community level, seagrass meadows clearly structure community patterns and stabilize sediment (Reise 2002). To our knowledge, vertical sediment particle mixing intensity induced by the whole benthic infaunal community has never been quantitatively assessed within seagrass meadows. However, studies focusing on individual bioturbator species have shown that both their densities and bioturbation intensity tended to be higher in unvegetated areas than in seagrass meadows (Berkenbusch et al. 2007, van Wesenbeeck et al. 2007). Overall, feedback effects ('biomechanical warfare') contribute to a dynamic equilibrium between seagrasses and infauna (van Wesenbeeck et al. 2007). This suggests that seagrass meadows already affected by another stressor will be more sensitive and threatened by biomechanical disturbance induced by sediment particle mixing (Orth et al. 2006, Berkenbusch et al. 2007, Meadows et al. 2012). It also suggests that, at a local scale, seagrass degradation or disappearance would lead to the establishment of a more spatially heterogeneous infaunal community (Boström et al. 2006, Schückel et al. 2013), subsequently leading to a higher spatial heterogeneity in sediment particle mixing intensity.

Arcachon Bay, a macrotidal lagoon on the southwestern coast of France, is colonized by a *Zostera noltei* meadow, which used to cover most (70 out of 110 km^2) of the intertidal flats (Auby & Labourg 1996). In this bay, *Z. noltei* meadows protect intertidal flats from sediment erosion (Ganthy et al. 2013). They also structure macrozoobenthic communities (Blanchet et al. 2004), which present only limited seasonal changes compared to adjacent bare sediment flats (Castel et al. 1989, Bachelet et al. 2000). The surface occupied by *Z. noltei* in Arcachon Bay has diminished by a third between 1988 and 2008, and this decline has been more pronounced since 2005 (Plus et al. 2010), resulting in the replacement of large *Z. noltei* meadows by bare mudflats.

The present study focuses on sediment particle mixing as a functional response of the whole infaunal benthic community to both changes in its own structure and in seagrass meadow characteristics. We aimed to (1) quantitatively assess seasonal changes in vertical sediment particle mixing intensities within both a *Z. noltei* meadow and an adjacent bare sediment area, and (2) relate these intensities to infaunal community composition and seagrass meadow dynamics in order to (3) assess the impact of the decline of intertidal seagrass meadows on biological sedimentary processes. This was achieved through the comparisons, over a 1 yr survey, of sediment mixing intensity, sediment and seagrass population characteristics, and macrozoobenthic community structures at 2 closely related intertidal stations: a well-developed *Z. noltei* meadow and a bare sediment mudflat.

MATERIALS AND METHODS

Study area

The present study was conducted at a site named 'Germanan,' which is located in Arcachon Bay, France (44° 42.73' N, 1° 07.94' W; Fig. 1). This site consisted of an intertidal flat characterized by the presence of 2 distinct habitats at the same hypsometric level (ca. 2 m deep at high tide) only isolated by a small channel. The first habitat corresponded to an unvegetated mud flat ('bare sediment'), whereas the second one was colonized by a well-established *Zostera noltei* meadow ('*Zostera* meadow'). Based on measurements of currents performed at these sta-

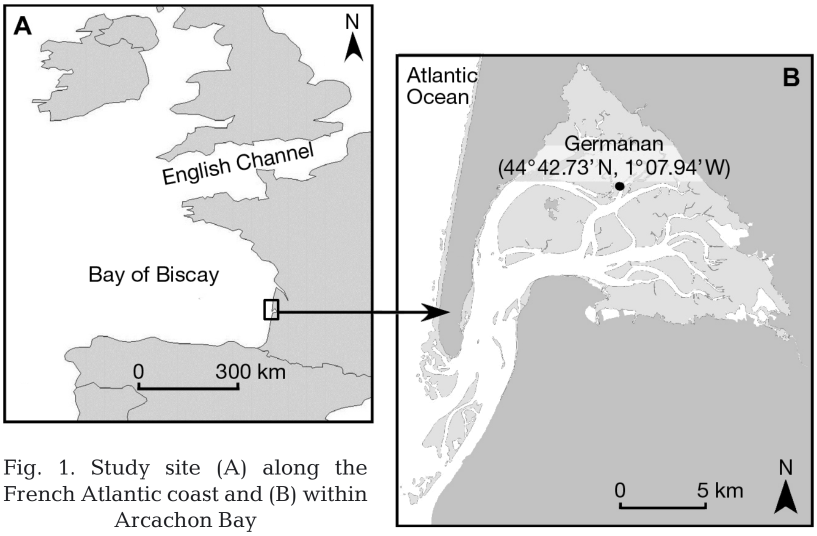

Fig. 1. Study site (A) along the French Atlantic coast and (B) within Arcachon Bay

tions, and despite slight differences between vegetated and bare sediment flats, Ganthy et al. (2013) concluded that both habitats were subject to similar hydrodynamic forcing.

Field sampling and experiments

General strategy

Experiments and samplings were performed seasonally between October 2010 and October 2011 (5 campaigns during October 2010; February, April, July, and October 2011) both at the bare sediment and the *Zostera* meadow stations.

Sediment particle mixing experiments

Sediment particle mixing was assessed through *in situ* incubations of sediment cores using luminophores as sediment particle tracers (Mahaut & Graf 1987) together with a mathematical model to fit luminophore vertical depth profiles (Maire et al. 2008).

One day prior to each experiment (i.e. each combination of Station × Season), 6 cores (height = 30 cm, ∅ = 9.6 cm) were pushed ca. 25 cm into field sediments and left for 1 full tidal cycle. Cores were placed within a ca. 3 m^2 surface. At the beginning of the experiment, 6.9 g dry wt luminophores (green eco-trace®, environmental tracing systems, sediment median grain size, D_{50} = 35 µm, density = 2.5 g cm^{-3}) were suspended in seawater and spread at the sediment surface. Three cores were sampled after 7 and 14 d, respectively, in order to overcome the known dependence on experimental duration of sediment particle mixing (Maire et al. 2007). These cores were frozen (−20°C) and sliced (0.5 cm thick sections down to 5 cm depth, 1 cm thick thereafter). After being freeze-dried, each slice was weighed and homogenized. Aliquots (2 g) of sediment were photographed under UV light using a digital camera fitted with a yellow filter.

Luminophore pixels were counted after a binarization step (based on the RGB level) for each image corresponding to a single slice using image-analysis software (Maire et al. 2006). The relative concentrations of luminophores in each slice were then used to compute corresponding vertical depth profiles.

Sediment particle mixing intensity was assessed by fitting a continuous time random walk (CTRW) model (Meysman et al. 2008a) to luminophore vertical depth profiles. This model was chosen because it proved more efficient than the biodiffusion model in describing the sediment particle mixing process over a short time scale (Maire et al. 2008, Meysman et al. 2010). The CTRW model assumes that sediment particle mixing is controlled by 2 probability distributions. The jump-length distribution defines the elementary distance a particle travels during a given mixing event. The waiting-time distribution describes the elementary time a particle waits in between 2 consecutive mixing events. The jump-length and waiting-time distributions are most often assumed to follow a Poisson process and a Gaussian distribution, respectively (Meysman et al. 2008b, 2010). For each replicate of each combination of Season × Station × Experiment duration, a single normal biodiffusion coefficient (D_b^N in cm^2 yr^{-1}) value reflecting sediment particle mixing intensity was obtained from fitted parameters according to Meysman et al. (2008b, 2010):

$$D_b^N = \frac{\sigma^2}{2\tau_c} \qquad (1)$$

where σ^2 is the variance of the jump-length distribution, and τ_c is the average of the waiting-time distribution. The fitting error (quality of the model adjustment) was expressed via the root mean square error (see Maire et al. 2007 for details). This was carried out using the TURBO package ('functions for fitting bioturbation models to tracer data') within the open source R programming framework (v2.13.1., www.R-project.org).

For all Season × Station combinations, no significant differences in D_b^N were detected between the 2 experimental durations (univariate permutational ANOVA, PERMANOVA, $p < 0.05$). Consequently, the 6 D_b^N values measured for each combination were considered as replicates for further statistical analyses.

Water and sediment characteristics

Water temperature and sediment characteristics (granulometry and organic carbon and nitrogen content of the sediment surface) were assessed for each Season × Station combination. The uppermost 1 cm of sediment from 4 cores (∅ = 6 cm) were sampled for further analyses. One core was used for sediment median grain size (D_{50}) using a laser microgranulometer (MALVERN® Master Sizer S). For determination of surface sediment carbon (particulate organic carbon, POC) and nitrogen (PON) content, the top 1 cm of the 3 other cores was sliced, freeze-dried, homogenized, and later separately analyzed. Samples for carbon analysis were decarbonated (HCl 0.3 N). Both POC and PON were assessed using a CN auto-analyzer (Thermo Flash® EA112).

Z. noltei population characteristics

For each Season × Station combination, 6 cores (internal diameter = 9.6 cm) were sampled to assess *Z. noltei* population characteristics. Sediment was sieved on 1 mm square mesh to retain leaves and roots. Shoots were first counted. Leaves and roots were then separated before being dried (60°C for 48 h) and weighed (precision: 0.1 mg).

Infauna

For each Season × Station combination, 5 replicates of sediment were sampled using a 0.04 m^2 square corer (Castel et al. 1989) and sieved on a 1 mm square mesh. Macrofauna was then fixed (4% buffered formaldehyde) and colored with Rose Bengal. Each organism was identified to the species level, counted, and its biomass assessed. Infaunal species were separated from other macrofauna, and their species richness, abundance (ind. m^{-2}), and biomass (in ash-free dry weight, g AFDW m^{-2}) were assessed.

Statistical analysis

Univariate analyses

Differences between stations and seasons in surface sediment POC and PON; total macrofaunal abundance, biomass, and species richness; infaunal abundance, biomass, and species richness; and D_b^N were assessed using univariate PERMANOVAs (Anderson 2001, McArdle & Anderson 2001) without data transformation. Euclidean distance was used, and the design consisted of 2 crossed factors, namely 'Season' (fixed, 5 levels) and 'Station' (fixed, 2 levels). Because a strong decrease in the shoot density was observed within the *Zostera* meadow in October 2011, differences between stations and seasons in D_b^N were first tested in the same way (but with only 4 levels of the Season factor) on data obtained from October 2010 to July 2011. The seasonal dynamic in D_b^N within the *Zostera* meadow from October 2010 to October 2011 was then analyzed using a single fixed factor (Season, 5 levels) PERMANOVA. Pairwise tests were also performed to highlight differences among factor modalities. The effects of factors on spatial variability (i.e. among-replicate variability) were tested using the PERMDISP procedure (Anderson 2006; same distance measure and same design as above).

Infaunal community structure

Infaunal community structure was investigated using non-metric multidimensional scaling (nMDS). This analysis was based on Bray-Curtis similarities calculated on untransformed abundance and biomass data. Differences in infaunal compositions between seasons and stations from October 2010 and July 2011, and among seasons within the *Zostera* meadow from October 2010 to October 2011, were tested using multivariate PERMANOVAs with Bray-Curtis similarities and using 1- and 2-way crossed designs described above, respectively. Corresponding pairwise tests and dispersion analyses were performed as well (using Bray-Curtis similarities). For both abundance and biomass data, species contributing most to differences were identified using the SIMPER procedure (Clarke & Warwick 2001).

Linking D_b^N and species distribution patterns

D_b^N values were linked to species distribution patterns using an inverse BIO-ENV procedure (ENV-

BIO; Clarke & Warwick 2001). The aim was to identify infaunal species potentially responsible for spatiotemporal changes (both in mean values and variability) in D_b^N. Coefficients of variation (CVs) were used as indicators of variability (i.e. spatial heterogeneity) patterns of both D_b^N (varD_b^N) and species abundance/biomass because they have proven more useful in comparing variability among biological characteristics than standard deviations (Fraterrigo & Rusak 2008, Hewitt & Thrush 2009). ENV-BIO procedures were performed separately on abundance and biomass data and carried out on 3 distinct datasets. The first one corresponded to all Season × Station combinations, whereas the 2 others corresponded to only bare sediment and *Zostera* meadow stations, respectively. For each dataset, only the species that represented at least 3% of the total abundance or 3% of the total biomass within at least 1 replicate were selected. ENV-BIO analyses were run separately to identify (1) species whose average abundance/biomass patterns correlated best (BEST procedure; Clarke & Warwick 2001) with D_b^N patterns, and (2) species whose CVs of their abundance/biomass patterns correlated best with varD_b^N patterns. Correlations were assessed using Spearman coefficients, and corresponding significances were tested with permutation tests involving 999 random permutations. All of the above described statistical analyses were performed using the PRIMER® v6 package with the PERMANOVA+ add-on software (Clarke & Warwick 2001, Anderson et al. 2008).

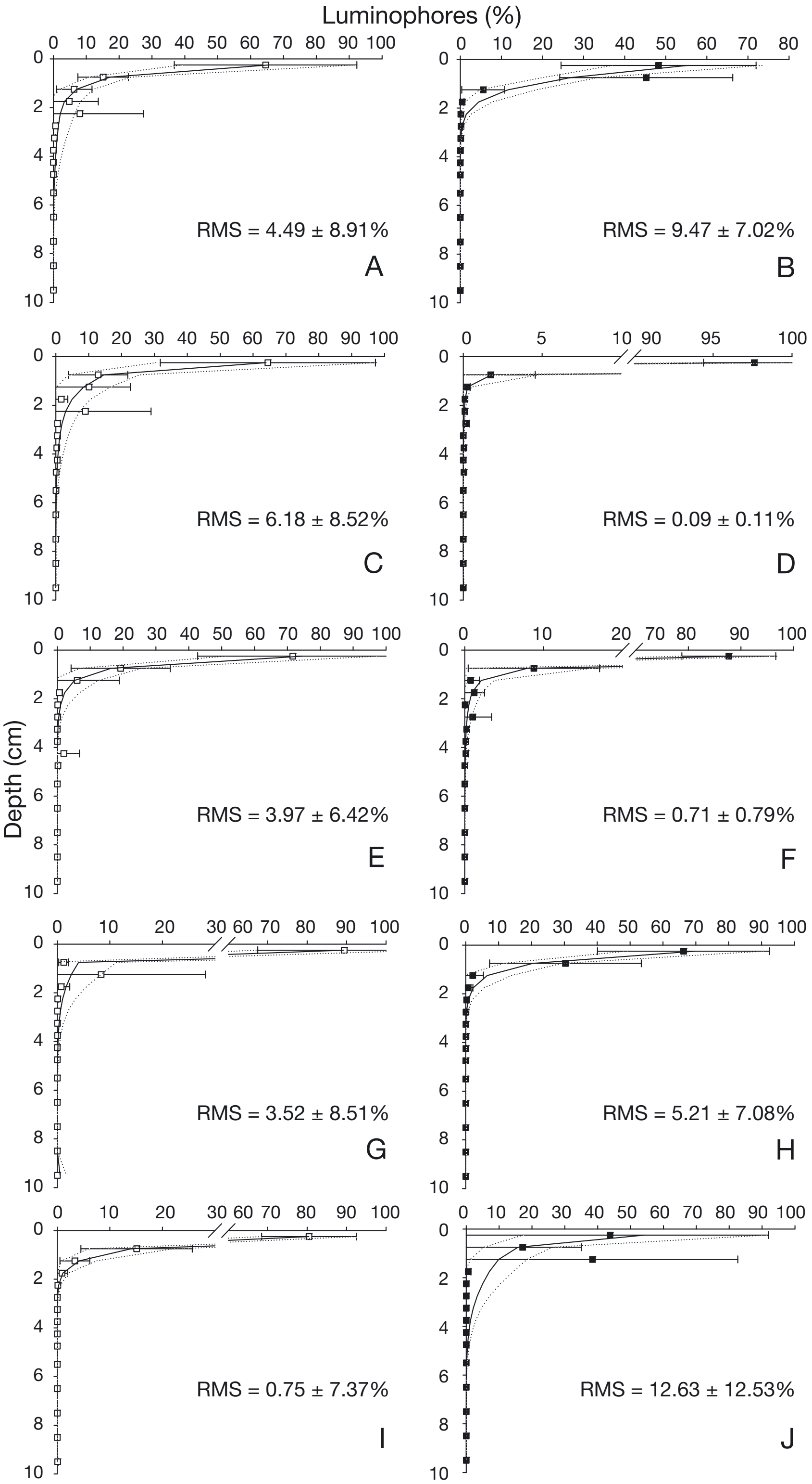

Fig. 2. Depth distribution (mean ± SD, n = 6) of luminophores, together with corresponding model fits (mean ± SD in solid and dotted lines, respectively) and fitting error (root mean square expressed in percentage, mean ± SD, n = 6) obtained both within bare sediment (open symbols) and *Zostera* meadow (black symbols) during (A,B) October 2010, (C,D) February 2011, (E,F) April 2011, (G,H) July 2011, and (I,J) October 2011

RESULTS

D_b^N

Mean depth profiles of luminophores obtained in both bare sediment and the *Zostera* meadow, together with corresponding fitting errors of the model to these profiles, are shown in Fig. 2. Fitting errors were low, indicating a good adjustment of the CTRW model to our data. Corresponding means and standard deviations of D_b^N are shown in Fig. 3. Mean D_b^N was maximal during October 2010 (22.45 ± 43.73 $cm^2\ yr^{-1}$) and minimal during October 2011 (2.99 ± 2.75 $cm^2\ yr^{-1}$) in bare sediment, whereas it was maximal during October 2011 (18.07 ± 18.14 $cm^2\ yr^{-1}$) and minimal during February 2011 (0.39 ± 0.30 $cm^2\ yr^{-1}$) in the *Zostera* meadow. Overall, D_b^N values were characterized by a high spatial variability as indicated by high standard deviations. Due to this variability, we detected no global effect, using PERMANOVA main tests, of season and station factors, and no significant interaction between these 2 factors from October 2010 to July 2011. However, a significant effect of station on the dispersion of data through PERMDISP was detected, indicating that D_b^N was more spatially variable in bare sediment during these seasons (Fig. 3).

Within the *Zostera* meadow, the effect of Season on D_b^N was significant (1-way PERMANOVA, pseudo-F = 3.8803, p(perm) = 0.0144). D_b^N recorded in February 2011 was significantly lower and less variable than those recorded in October 2010, April 2011, and July 2011, and only significantly less variable than in Ocotber 2011. D_b^N was also significantly more variable during October 2011 than during the 4 other sampled seasons (Table 1).

Occasionally, fewer tracers were found at the end of the incubations within bare sediment than within the *Zostera* meadow.

Water, sediment, and *Zostera* population characteristics

Water temperature and main surface sediment characteristics (D_{50}, POC, PON) are listed in Table 2. Water temperature presented typical seasonal variations, and differences in D_{50} were not well marked (Table 2). Both surface sediment POC and PON were minimal during April 2011 within bare sediment as well as within the *Zostera* meadow. Maximal values of both surface sediment POC and PON contents were recorded during October 2011 within bare sediment and during July 2011 within the *Zostera* meadow. Both POC and PON were also significantly affected by the interactions between Season and Station (PERMANOVA main test, p < 0.05). POC and PON were significantly higher within bare sediment than within the *Zostera* meadow only during October 2011 (Table 2).

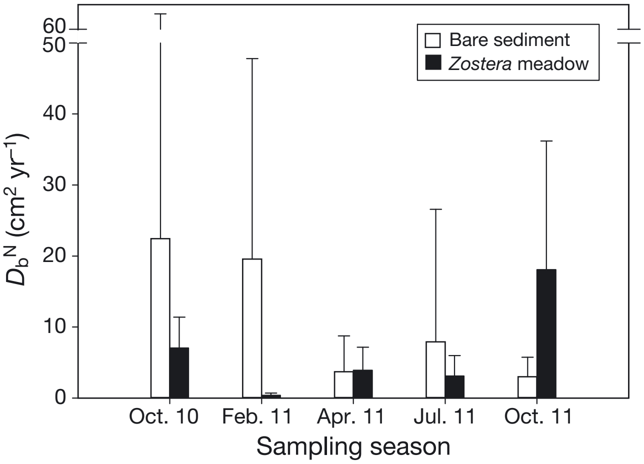

Fig. 3. Mean (± SD) particle mixing intensities (measured by the normal biodiffusion coefficient D_b^N) recorded within both bare sediment (open bars) and *Zostera* meadow (black bars) during the 5 sampling seasons

Means and standard deviations of *Zostera* shoot densities, leaf biomasses, and root biomasses are shown in Table 2. There was a significant decrease in both shoot density and root biomass between October 2010 and October 2011 (Table 2).

Benthic infaunal characteristics

Univariate parameters

Means and standard deviations of species richness, abundance, and biomass of benthic infauna are shown in Table 2. Species richness only significantly varied with Season (pseudo-F = 9.7705, p(perm) = 0.0001). It was minimal during July 2011 within both bare sediment and the *Zostera* meadow. Species richness was maximal during October 2011 within bare sediment and during October 2010 within the *Zostera* meadow.

Table 1. Seasonal dynamics of the normal biodiffusion coefficient (D_b^N) within a *Zostera* meadow: p-values obtained by pairwise permutational ANOVAs between all possible seasons within the *Zostera meadow*. Values in **bold** indicate seasons that significantly differ (p < 0.05), and ^{D} indicates combinations that present significantly different dispersions (PERMDISP analysis, p < 0.05)

	October 2010	February 2011	April 2011	July 2011
February 2011	**0.002**$^{\mathbf{D}}$			
April 2011	0.193	**0.012**$^{\mathbf{D}}$		
July 2011	0.102	**0.003**$^{\mathbf{D}}$	0.662	
October 2011	0.186^D	0.053^D	0.147^D	0.134^D

Table 2. Water temperature, median sediment grain size (D_{50}), and means ± SD of surface sediment organic contents (percent particulate organic carbon and nitrogen, % POC and % PON), *Zostera* population characteristics (shoot density, leaf and root biomasses), and infaunal characteristics (species richness, abundance, biomass) measured within *Zostera* meadow and bare sediment stations during 5 sampling seasons. Values in **bold** indicate significant differences among stations for the given sampling season (univariate permutational ANOVA, PERMANOVA pairwise comparison, $p < 0.05$). Within a given station, values linked by the same letter do not significantly differ among the considered seasons (univariate PERMANOVA pairwise comparison, $p < 0.05$). AFDW: ash-free dry weight

	October 2010		February 2011		April 2011		July 2011		October 2011	
	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow
Water temp. (°C)	14.5	14.5	6	6	16.5	16.5	21.5	21.5	14.5	14.5
D_{50} (µm)	27.2	43.9	37.8	61.4	26.2	46.5	32.5	32.2	29.8	25.0
% POC	–	–	2.23 ± 0.61^{ac}	2.32 ± 0.47^{a}	1.64 ± 0.31^{a}	1.03 ± 0.04^{b}	2.63 ± 0.19^{b}	2.86 ± 0.47^{ac}	**2.68 ± 0.35^{bc}**	**2.08 ± 0.07^{c}**
% PON	–	–	0.19 ± 0.02^{a}	0.17 ± 0.02^{a}	0.17 ± 0.03^{a}	0.14 ± 0.02^{b}	0.25 ± 0.01^{b}	0.31 ± 0.06^{abc}	**0.29 ± 0.04^{b}**	**0.23 ± 0.02^{c}**
Shoot density (shoot m^{-2})	0	10339 ± 987^{a}	0	12560 ± 2644^{a}	0	14362 ± 3902^{a}	0	10029 ± 5929^{ab}	0	6052 ± 1317^{b}
Leaf biomass (g AFDW m^{-2})	0	36.18 ± 7.84^{a}	0	9.84 ± 1.89^{b}	0	22.14 ± 6.29^{c}	0	40.27 ± 4.92^{a}	0	38.10 ± 7.28^{a}
Root biomass (g AFDW m^{-2})	0	123.10 ± 10.09^{a}	0	95.69 ± 18.93^{b}	0	72.25 ± 18.57^{bd}	0	47.58 ± 8.04^{c}	0	54.55 ± 18.38^{cd}
Infaunal species richness (no. of species)	12 ± 3^{ac}	12 ± 1^{a}	12 ± 2^{ac}	9 ± 3^{ab}	10 ± 1^{a}	9 ± 3^{ab}	5 ± 2^{b}	8 ± 2^{b}	14 ± 2^{c}	11 ± 2^{ab}
Infaunal abundance (ind. m^{-2})	**5405 ± 1807^{a}**	**7960 ± 1455^{a}**	**2490 ± 438^{b}**	**5440 ± 1463^{bc}**	**2895 ± 1298^{ab}**	**8175 ± 2803^{ab}**	**494 ± 350^{c}**	**6962 ± 755^{ab}**	2595 ± 681^{b}	3285 ± 1814^{c}
Infaunal biomass (g AFDW m^{-2})	**4.11 ± 3.50^{ab}**	**16.82 ± 11.62**	6.12 ± 3.14^{a}	15.52 ± 15.57	8.54 ± 6.52^{a}	15.47 ± 4.07	**1.98 ± 1.24^{b}**	**11.83 ± 5.81**	**5.47 ± 2.57^{a}**	**14.27 ± 9.31**

Infaunal abundance varied significantly with Season × Station (pseudo-F = 5.3252, p(perm) = 0.0020). Within bare sediment, infaunal abundance was significantly lower during July 2011 than during the 4 other sampling seasons (Table 2). Conversely, it was maximal during October 2010. This last value was significantly higher than the one recorded during October 2011 (Table 2). A similar trend toward a significantly lower infaunal abundance during October 2011 than during October 2010 was found within the *Zostera* meadow (Table 2). Infaunal abundances were always significantly higher in the *Zostera* meadow than in bare sediment, except during October 2011 (Table 2).

Infaunal biomass only significantly varied with Station (pseudo-F = 17.786, p(perm) = 0.0002). Lowest biomasses were recorded during July 2011 within both bare sediment and the *Zostera* meadow. Highest biomasses were recorded during April 2011 and October 2010 within bare sediment and the *Zostera* meadow, respectively. Infaunal biomass was significantly higher within the *Zostera* meadow than within bare sediment during October 2010 and July and October 2011.

Community structure (multivariate)

The results of the nMDS suggested that the compositions of benthic infauna differed between bare sediment and the *Zostera* meadow (Fig. 4). This was confirmed by PERMANOVA and PERMDISP results, which showed that from October 2010 to July 2011, both the mean composition and the variability of benthic infaunal composition were significantly affected by Season × Station interactions (pseudo-F = 6.4634, p(perm) = 0.0001 and significant PERMDISP).

Overall, there were clearly stronger seasonal changes in benthic infaunal composition within bare sediment than within the *Zostera* meadow (Fig. 4, Table 3). An exception to this general pattern was October 2011, with (1) different benthic infaunal composition within bare sediment and *Zostera* meadow, and also (2) a more variable benthic infaunal composition within the *Zostera* meadow than in October 2010 (Fig. 4, Table 4). Infaunal biomasses showed the same general pattern, but with less marked differences in mean compositions and especially in variability.

SIMPER analysis carried out on abundance data showed that *Zostera* meadow assemblages

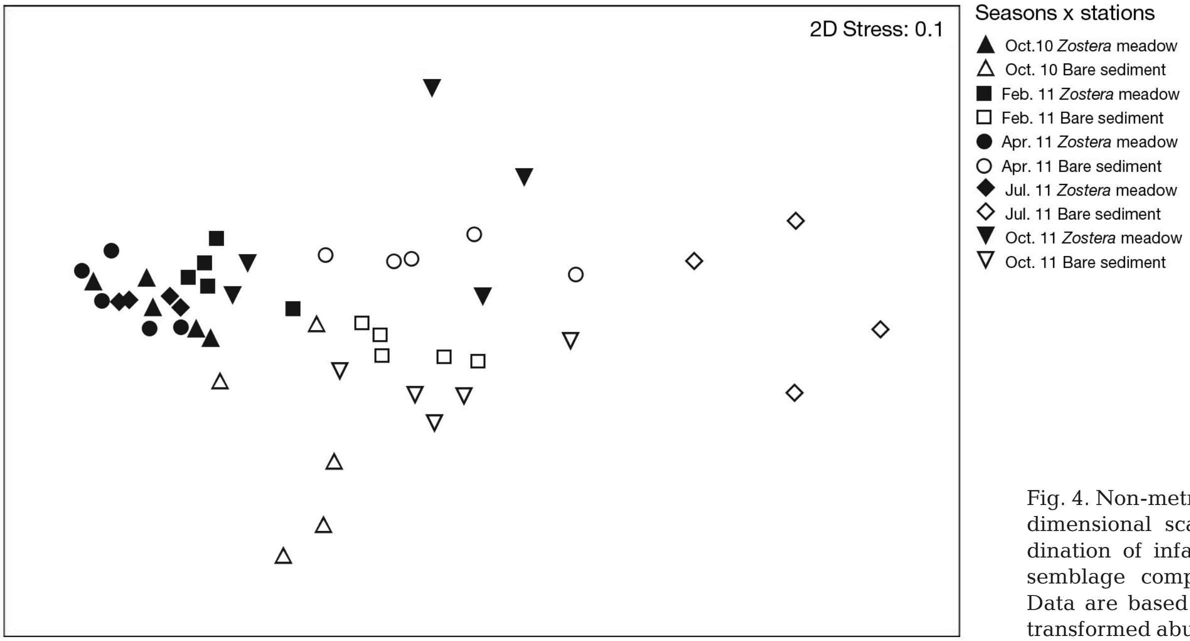

Fig. 4. Non-metric multidimensional scaling ordination of infaunal assemblage compositions. Data are based on non-transformed abundances

Table 3. Pairwise comparisons of average dissimilarity percentages among infaunal abundance assemblages given by SIMPER analyses from October 2010 to July 2011. Values in **bold** indicate assemblages that significantly differ (permutational ANOVA pairwise tests, $p < 0.05$), and ^{D} indicates assemblages that present significantly different multivariate dispersions (PERMDISP analysis, $p < 0.05$)

		October 2010		February 2011		April 2011		July 2011
		Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment
October 2010	Bare sediment							
	Zostera meadow	**54.4**						
February 2011	Bare sediment	**49.1**	**60.8**					
	Zostera meadow	**51.8**	**32.1**	**53.0**				
April 2011	Bare sediment	**61.1**	**68.5**	**44.2**	**59.0**			
	Zostera meadow	**62.5**	24.1	**67.5**	**35.6**	**70.4**		
July 2011	Bare sediment	**89.8**	**93.1**^{D}	**77.0**^{D}	**91.7**^{D}	**76.8**	**94.5**	
	Zostera meadow	**61.0**^{D}	20.3	**65.6**^{D}	**33.6**^{D}	**66.6**^{D}	20.9^{D}	**91.9**^{D}

had an overall similarity of 61.9% mostly due to the polychaetes *Melinna palmata* and *Heteromastus filiformis*, whereas bare sediment assemblages had an overall similarity of 44.0% mostly due to the polychaetes *M. palmata*, *H. filiformis*, *Aphelochaeta marioni*, and *Nephtys hombergii*, the bivalve *Abra segmentum*, and the oligochaete *Tubificoides benedii*. Within-station similarities changed with Season from 51.1% in October 2011 to 87.7% in July 2011 within the *Zostera* meadow, and from 50.7% in July 2011 to 70.8% in February 2011 within bare sediment. They were always higher within the *Zostera* meadow than within the bare sediment, except in October 2011. SIMPER analysis also showed that both between-station and seasonal differences in infaunal compositions were mostly driven by differences in the abundances of the 5 above-mentioned species (Table 5). The 2 dominant polychaetes *H. filiformis* and *M. palmata* contributed to all between-station dissimilarities because of their higher abundances within the

Table 4. Pairwise comparisons of average dissimilarity percentages among infaunal abundance assemblages given by SIMPER within a *Zostera* meadow. All assemblages significantly differed (permutational ANOVA pairwise tests, $p < 0.05$), and all presented significantly different multivariate dispersions (PERMDISP analysis, $p < 0.05$)

	October 2010	February 2011	April 2011	July 2011
October 2011	57.6	47.2	62.9	62.5

Table 5. Abundance means ± SD of infaunal species that represented at least 3 % of the total abundance in at least 1 replicate, together with results of SIMPER analysis. Species names in **bold** indicate those that contributed to 90 % of dissimilarity between overall bare sediment and *Zostera* meadow assemblages. Letters in the Seasons SIMPER column relate to a pairwise comparison of species between seasons: lowercase (within bare sediment) and uppercase (within *Zostera* meadow) letters indicate species that contributed to 90 % of dissimilarity between October 2010 and February 2011 (a/A), October 2010 and April 2011 (b/B), October 2010 and July 2011 (c/C), October 2010 and October 2011 (d/D), February and April 2011 (e/E), February and July 2011 (f/F), February and October 2011 (g/G), April and July 2011 (h/H), April and October 2011 (i/I), and between July and October 2011 (j/J). Values in **bold** indicate species that contributed to 90 % of dissimilarity between bare sediment and *Zostera* meadow stations during the given season

	Seasons SIMPER	October 2010		February 2011		April 2011		July 2011		October 2011	
		Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow	Bare sediment	*Zostera* meadow
Abra segmentum	**b-C-d-e-f-F-h-g-G-H-i-j-J**	30 ± 41	15 ± 14	65 ± 14	40 ± 38	**775 ± 318**	**15 ± 14**	125 ± 122	181 ± 90	**125 ± 115**	**120 ± 54**
Ampelisca brevicornis		5 ± 11	0	0	0	10 ± 13	0	0	0	20 ± 32	0
Aphelochaeta marioni	**a-A-b-B-c-C-d-D-e -f- g-G- h-i-I-j-J**	**2310 ± 1827**	**460 ± 373**	310 ± 167	10 ± 14	30 ± 67	10 ± 22	56 ± 113	19 ± 24	**505 ± 255**	**125 ± 88**
Cerastoderma edule		15 ± 14	60 ± 42	15 ± 22	40 ± 42	30 ± 21	10 ± 14	19 ± 24	13 ± 14	15 ± 22	40 ± 38
Clymenura clypeata	e-h-i	15 ± 22	40 ± 52	5 ± 11	0	70 ± 84	20 ± 21	0	0	**25 ± 43**	**40 ± 76**
Galathowenia oculata		0	0	0	0	0	0	0	0	0	15 ± 33
Glycera convoluta	a-c-d-f-J	185 ± 76	65 ± 29	55 ± 27	80 ± 57	45 ± 27	50 ± 40	6 ± 13	13 ± 14	35 ± 29	70 ± 27
Hediste diversicolor	g	0	5 ± 11	35 ± 29	0	20 ± 27	0	0	6 ± 13	0	0
Heteromastus filiformis	**a-A-b-B-c-C-d-D-e-E-f-F-g-G-h-H-i-I-j-J**	**405 ± 160**	**855 ± 368**	**425 ± 165**	**1065 ± 455**	**370 ± 177**	**680 ± 705**	**0**	**256 ± 149**	**190 ± 117**	**830 ± 409**
Mediomastus fragilis	A-C-E-G-H	**0**	35 ± 22	**20 ± 27**	**170 ± 132**	5 ± 11	35 ± 55	19 ± 24	156 ± 55	15 ± 22	0
Melinna palmata	**a-A-b-B-c-C-d-D-e-E-f-F-g-G-h-H-i-I-j-J**	**2000 ± 884**	**6115 ± 1661**	**1170 ± 434**	**3535 ± 928**	**1165 ± 624**	**6745 ± 2013**	**156 ± 52**	**6050 ± 805**	**1015 ± 477**	**1475 ± 1688**
Nemertea		0	0	5 ± 11	35 ± 42	45 ± 45	20 ± 21	0	0	0	0
Nephtys hombergii	e-g-i-j-J	25 ± 18	30 ± 41	60 ± 38	0	20 ± 21	5 ± 11	75 ± 35	0	**100 ± 50**	**10 ± 22**
Notomastus latericeus	g-J	40 ± 89	0	0	20 ± 45	0	5 ± 11	0	31 ± 63	**40 ± 45**	**85 ± 78**
Pseudopolydora pulchra		30 ± 33	0	20 ± 32	0	0	0	0	0	25 ± 25	0
Pygospio elegans	a-b-B-e-H-f-g-h-i-j	0	0	120 ± 82	0	180 ± 201	110 ± 232	19 ± 38	0	40 ± 55	15 ± 14
Ruditapes philippinarum		0	15 ± 22	15 ± 22	35 ± 65	0	55 ± 97	0	6 ± 13	5 ± 11	45 ± 27
Streblospio shrubsolii	a-b-c-d-g-i-j	**175 ± 229**	**0**	10 ± 14	0	10 ± 22	0	0	0	**105 ± 76**	**10 ± 22**
Tubificoides benedii	**a-A-B-C-d-D-e-E-f-F-g-G-h-H-i-I-j-J**	45 ± 62	160 ± 104	**100 ± 92**	**355 ± 276**	**80 ± 82**	**395 ± 355**	19 ± 38	206 ± 139	**250 ± 97**	**380 ± 159**

Table 6. Best results of the ENV-BIO analysis within (A) the entire data set, (B) bare sediment, and (C) *Zostera* meadow. Text in **bold** indicates significant results ($p < 0.05$), i.e. best correlations found. D_b^N: normal biodiffusion coefficient

	D_b^N vs. abundance	D_b^N variability vs. abundance variability	D_b^N vs. biomass	D_b^N variability vs. biomass variability
(A)				
ρ (Spearman)	0.368	**0.728**	0.425	0.686
p	0.569	**0.046**	0.607	0.09
Species	*Mediomastus fragilis*	***Abra segmentum*; *Glycera convoluta*; *Heteromastus filiformis*; *Tubificoides benedii*; *Ruditapes phillipinarum***	*Abra segmentum*; *Diopatra biscayensis*; *Mediomastus fragilis*	*Heteromastus filiformis*; *Mediomastus fragilis*; *Ruditapes phillipinarum*; *Streblospio shrubsolii*; *Tubificoides benedii*
(B)				
ρ (Spearman)	0.491	0.83	0.491	0.5
p	0.854	0.329	0.984	0.835
Species	*Abra segmentum*; *Mediomastus fragilis*; *Nephtys hombergii*	*Melinna palmata*; *Tubificoides benedii*	*Cerastoderma edule*; *Glycera convoluta*; *Heteromastus filiformis*; *Nephtys hombergii*; *Pygospio elegans*	*Streblospio shrubsolii*; *Tubificoides benedii*
(C)				
ρ (Spearman)	**0.964**	0.842	0.879	0.503
p	**0.024**	0.187	0.448	0.855
Species	***Aphelochaeta marioni*; *Mediomastus fragilis*; *Melinna palmata***	*Abra segmentum*; *Cerastoderma edule*	*Aphelochaeta marioni*; *Mediomastus fragilis*	*Cerastoderma edule*; *Tubificoides benedii*

Zostera meadow than within bare sediment. These 2 species also contributed to seasonal differences in both bare sediment and the *Zostera* meadow, with lower abundances in July 2011 within bare sediment and a strong decrease of *M. palmata* in October 2011 within the *Zostera* meadow (Table 5).

Linking D_b^N and infaunal species distributions patterns

The results of the ENV-BIO procedure are shown in Table 6 for correlations between D_b^N (varD_b^N) and infaunal species compositions within the whole data set (Table 6A), bare sediment stations (Table 6B), and *Zostera* meadow stations (Table 6C).

When considering the whole data set, the ENV-BIO procedure highlighted a significant correlation ($\rho = 0.728$, $p = 0.046$) between the similarity matrices based on varD_b^N, and the abundances of 5 species (*A. segmentum, Glycera convoluta, H. filiformis, T. benedii,* and *Ruditapes phillipinarum*; Table 6A). Another significant correlation ($\rho = 0.964$; $p = 0.024$) was detected within the *Zostera* meadow between the similarity matrices based on D_b^N and the abundances of 3 species, namely *A. marioni*, *Mediomastus fragilis*, and *M. palmata* (Table 6C). In contrast, no significant results were found within bare sediment (Table 6B).

DISCUSSION

Sediment particle mixing intensity (D_b^N)

The D_b^N values obtained during the present study (Fig. 3) are in the same order of magnitude as literature data regarding sediment particle mixing intensities measured in coastal environments using a large variety of methods (Josefson et al. 2002, Gilbert et al. 2003, Wheatcroft 2006, Duport et al. 2007, Teal et al. 2008). D_b^N measured within bare sediment (Fig. 3) are largely consistent with D_b reported in intertidal mudflats, from 1.8 to 108 cm^2 yr^{-1} (Clifton et al. 1995), from 4 to 5 cm^2 yr^{-1} (Herman et al. 2001), and from 6 to 52 cm^2 yr^{-1} (Widdows et al. 2004). Measuring sediment particle mixing through core incubation clearly limits the (hydrodynamical or biological) lateral movements of particles to a maximal length defined by the core diameter. Although the reduction of biologically driven lateral transport was limited here because of the small size of the present infauna (see below) compared to the diameter of the used cores, hydrodynamical lateral transport was clearly limited by the use of cores projecting ca. 5 cm above the sediment surface.

Overall, our D_b^N measurements were characterized by high among-replicate variability (Fig. 3). Previous studies have also shown high variability in vertical luminophore profiles within replicated sediment cores during *in situ* sediment particle mixing experiments (Wheatcroft 2006, Duport et al. 2007, Gilbert et al. 2007). This mostly explains why we failed to detect any significant effect of both Season and Station using PERMANOVAs. More generally, within-treatment variability reflects the degree of small-scale spatial heterogeneity in sediment particle mixing processes, closely linked to those of infaunal species distribution and activities.

Overall comparison of the *Zostera* meadow and bare sediment

Sediment particle mixing (D_b^N)

From October 2010 to July 2011, D_b^N was significantly less variable and tended to be lower within the *Zostera* meadow than within bare sediment (Fig. 3). This suggests that sediment particle mixing was less intense and particularly more spatially homogeneous within the *Zostera* meadow, which is consistent with the consideration of seagrasses as sediment stabilizers (Orth 1977, Townsend & Fonseca 1998, Reise 2002, Meadows et al. 2012) through the creation of dense root/rhizome networks (Reise 2002). The presence of seagrasses should result in lower sediment particle mixing due to (1) sediment compaction (Hughes et al. 2000, Berkenbusch et al. 2007) and (2) the exclusion and/or inhibition of the activity of large bioturbators (Berkenbusch et al. 2007, van Wesenbeeck et al. 2007). The fact that more particles seemed to occasionally have been washed away within bare sediment tends to confirm this stabilizing effect, but is difficult to assess because it was not linked with any experimental factor.

Infauna

Infaunal compositions clearly differed between the *Zostera* meadow and bare sediment (Fig. 4). Similar differences have already been observed both in Arcachon Bay (Blanchet et al. 2004, Do et al. 2013) and in other seagrass meadows (Boström & Bonsdorff 1997, Fredriksen et al. 2010). These differences result from several processes, including (1) the creation of dense root/rhizome networks, which provide protection for many prey species (Summerson & Peterson 1984), and (2) the accumulation of organic matter through both enhanced sedimentation (Fonseca & Fisher 1986, Wilkie et al. 2012) and the decay of plant materials (Castel et al. 1989, Rossi & Underwood 2002).

Species richness never differed between the *Zostera* meadow and bare sediment (Table 2). The composition of infauna in the *Zostera* meadow was characterized by high abundances of the deposit-feeding polychaetes *Melinna palmata*, *Heteromastus filiformis*, and *Aphelochaeta marioni* and the oligochaete *Tubificoides benedii* (Table 5), as already reported (Bachelet et al. 2000, Blanchet et al. 2004, Do et al. 2013). Interestingly, these species were also present, albeit in lower abundances, in bare sediment (Table 5). Differences between the *Zostera* meadow and bare sediment thus mostly resulted from (1) higher abundances of *M. palmata*, *H. filiformis*, *T. benedii* and *Abra segmentum*, and (2) lower abundances of *A. marioni* within the *Zostera* meadow (Table 5). This suggests that the bare sediment infaunal community corresponds to an impoverished *Z. noltei* meadow sub-community. A similar pattern (i.e. higher infaunal abundance in a seagrass meadow but similar species richness and composition as within bare sediment) was reported by Fredriksen et al. (2010) along the Norwegian coast. This was attributed to the fact that the corresponding *Z. marina* meadow and bare sediment stations were directly adjacent, which was also the case during the present study. Interestingly, this phenomenon has also been observed in tidal flats structured by other engineers such as tube-building polychaetes (Volkenborn et al. 2009).

For all given Seasons except October 2011, the compositions of infauna were also much more (spatially) homogeneous within the *Zostera* meadow than within bare sediment, as indicated by (1) the higher among-replicate Bray-Curtis similarity within the *Zostera* meadow than within bare sediment, and (2) the corresponding dispersion of replicates in the nMDS based on infaunal compositions (Fig. 4). A similar effect was suggested by Blanchet et al. (2004), who showed that benthic faunal compositions at stations with low above- and below-ground *Zostera* biomass were highly heterogeneous. Such differences in variability within the *Zostera* meadow and bare sediment can be related to differences in spatial homogeneity between the 2 habitats. This may refer to (1) food availability and (2) the occurrence of *Z. noltei* root/rhizome networks. Within the *Zostera* meadow, buried leaf debris and enhanced sedimentation provide an abundant and homogeneous food source for benthic infauna. Conversely, infaunal abundance and composition within bare sediment are mostly conditioned by the heterogeneous distribution of (1) spots of buried leaf debris and (2) deposition in pits/hollows. This hypothesis is supported by (1) the more variable surface sediment POC contents recorded within bare sediment than within the *Zostera* meadow during the present study (except in July 2011; Table 2) and (2) the higher variability in abundance within bare sediment of the oligochaete *T. benedii* and the polychaete *M. palmata* (Table 5), which are associated with high concentrations of sedimentary organics (Rossi & Underwood 2002).

Higher spatial heterogeneity within bare sediment compared to the *Zostera* meadow may also result from the sole effect of the distribution pattern of any spatial structures within the sediment column (heterogeneous distribution of buried debris versus homogeneous dense root/rhizome networks). Inert buried debris can enhance local abundance of oligochaetes (Rossi & Underwood 2002), and dense *Zostera* root/rhizome networks are known to provide shelter from predation for small species (Summerson & Peterson 1984). According to Brenchley (1982), polychaete tube mats, such as the dense mats created by *M. palmata* at our study stations, induce similar and additional structuring effects as *Zostera* root/rhizome networks.

Spatio-temporal changes within the *Zostera* meadow and bare sediment

Within the *Zostera* meadow, all sampled Seasons except October 2011 were characterized by (1) relatively low D_b^N associated with low varD_b^N and (2) similar and low among-replicate variability in the composition of benthic infauna. Low variability in infaunal composition should therefore result in low variability in D_b^N, thereby facilitating the assessment of the effect of environmental factors on sediment particle mixing. Two lines of evidence suggest that this is indeed the case.

First, D_b^N measured within the *Zostera* meadow during February 2011 was lower and significantly less variable than during all other sampled seasons (Fig. 3, Table 1), which is in good agreement with the negative effect of low temperature on sediment particle mixing (Grémare et al. 2004, Maire et al. 2006, 2007). Along the same line, the low D_b^N recorded in April 2011 could be related to a lower organic content of the sediment in this particular season (Table 2), which again is in good agreement with the positive effect of food availability on sediment particle mixing (Maire et al. 2006, 2007, Wheatcroft 2006).

Second, there was a clear decline in root biomass within the *Zostera* meadow (Table 2) between October 2010 and October 2011. The infaunal abundance during October 2011 did not significantly differ within the *Zostera* meadow and bare sediment (Table 2). Infaunal composition within the *Zostera* meadow was also significantly more heterogeneous during October 2011 than October 2010 (Fig. 4, Table 4). This mainly resulted from a decrease in the polychaete *M. palmata* between October 2010 and 2011, and to a lower extent from (1) a decrease in the opportunistic polychaete *A. marioni* and, (2) an increase in the oligochaete *T. benedii*. Such enhanced abundances of *T. benedii* following a seagrass mortality event have already been reported and attributed to organic enrichment through the decay of buried plant material (Rossi & Underwood 2002). Since the variability in the composition of infauna and D_b^N were higher in bare sediment than in the *Zostera* meadow, we attribute differences (both in absolute values and variability) in infaunal composition and in D_b^N recorded in October 2011 to a degradation of the *Zostera* meadow and thus to a convergence to bare sediment conditions. Blanchet et al. (2004) reported a significant effect of *Z. noltei* meadow on the composition of benthic infauna in Arcachon Bay for shoot densities higher than ca. 6000 shoots m^{-2}. This threshold value corresponded to the shoot density recorded within the *Zostera* meadow during October 2011 (Table 2), supporting the occurrence of a positive effect of a decline of the *Zostera* meadow on sediment particle mixing. In contrast, the facts that (1) both D_b^N and varD_b^N were low during October 2010 and April and July 2011 and (2) infaunal composition did not significantly differ among these 3 seasons (Fig. 4, Tables 2 & 3) support the importance of this threshold and are therefore in accordance with the postulated role of *Zostera* meadows in buffering seasonal environmental changes (De Wit et al. 2001, Bachelet et al. 2000).

The analysis of temporal changes in bare sediment was more complex due to higher among-replicate variability both in D_b^N and infaunal composition. The low D_b^N (with low associated variability, Fig. 3) recorded in April 2011 could nevertheless be related to a lower organic content of the sediment in this particular season, as was also the case for the *Zostera* meadow (Table 2).

Control of sediment particle mixing intensity (D_b^N) by infaunal composition

During the present study, we looked at a possible effect of infaunal composition by using an ENV-BIO procedure carried out through 12 modalities (3 data sets, 2 modalities corresponding to mean values and CVs, and 2 modalities corresponding to the use of abundance and biomass as the basis for the computation of similarity between infaunal compositions).

No significant results were obtained when using biomass as a basis for the computation of similarity in infaunal compositions (Table 6). This was surprising, since biological processes are more often cued by biomass rather than by abundance (Rice et al. 1986, Wheatcroft et al. 1990). A possible explanation is that during the present study, sediment particle mixing was mostly cued by small organisms (see below), exhibiting no major spatio-temporal changes in their individual biomass.

The only significant result when using mean abundance values was obtained for the *Zostera* meadow data set (Table 6), where the combined abundances of the 3 polychaetes *A. marioni*, *M. palmata*, and *Mediomastus fragilis* correlated best with spatio-temporal changes in D_b^N. Interestingly, the analysis of (1) temporal changes in the abundances of these organisms and (2) their sediment particle mixing modes are coherent with their postulated role in the control of sediment particle mixing.

The cirratulid *A. marioni* was abundant when mean sediment particle mixing intensity was high (i.e. during October 2010 and 2011) and was scarcer during the other sampling seasons (Table 5), which is not unexpected since this species is a downward conveyor (Bouchet et al. 2009, Garcia 2010). Conversely, the capitellid *M. fragilis* was absent in October 2011 when mean D_b^N was the highest (Table 5, Fig. 3), which concurs with the fact that this species is a head-down upward conveyor (Quintana et al. 2007, Garcia 2010). The ampharetid *M. palmata* was always the dominant species within *Zostera*. Its abundance dramatically decreased in October 2011 when D_b^N was the highest, which here again is consistent with its sediment mixing mode. This gregarious (Oyenekan 1988) tube-building polychaete develops dense populations, particularly when sediment organic matter concentrations are high (Cacabelos et al. 2011) such as within *Zostera* meadows (Dauvin et al. 2007, Table 5). *M. palmata* constructs mucus-lined tubes covered with sediment particles (Fauchald & Jumars 1979) forming dense tube mats that impact sediment structure (Cacabelos et al. 2011) from the surface to a few centimeters deep, leading to a sediment compaction effect, which is superimposed on the one induced by *Zostera* root/rhizome networks (Brenchley 1982). *M. palmata* is consequently considered to be a sediment stabilizer, which is in accordance with the correlation between its low abundance and the high D_b^N measured during October 2011. Given its often (very) high abundances, *M. palmata* is a key species in contributing to low D_b^N within the *Zostera* meadow.

As stated above, macrobenthic species abundance, species richness, and species composition increase in variability when communities are subject to increasing levels of disturbance (Warwick & Clarke 1993, Hewitt & Thrush 2009). Variability in ecological patterns and processes is also more sensitive to disturbance than their mean values (Fraterrigo & Rusak 2008), explaining that a significant correlation between D_b^N and species abundances patterns was obtained for the whole data set when using the CV as an index of variability, whereas it was not the case when using mean values (Table 6). The combined CV of *A. segmentum*, *Glycera convoluta*, *H. filiformis*, *T. benedii*, and *Ruditapes philippinarum* correlated best with spatio-temporal changes in varD_b^N. In most cases (i.e. 4 out of 5), changes in the abundances of these species together with their sediment particle mixing modes agreed with the available literature regarding their potential role in the control of sediment particle mixing. The small deposit-feeding biodiffusor bivalve *A. segmentum* reworks sediment down to a few centimeters (Maire et al. 2006, 2007, Garcia 2010). The high variability in its abundances recorded within bare sediment during October 2010 and July 2011 could therefore partly explain the high corresponding varD_b^N. *G. convoluta* is a gallery-diffusor (François et al. 1997). It locally increases D_b^N by extending its semi-permanent burrow while prospecting the sediment (Garcia 2010). The capitellid polychaete *H. filiformis* and the oligochaete *T. benedii* are both upward conveyors (Quintana et al. 2007, Garcia 2010), which therefore contribute to decrease D_b^N when present.

CONCLUSIONS

Sediment particle mixing processes and infaunal community structure were less intense and heterogeneous and also less subject to seasonal variations within the *Zostera noltei* meadow than within adjacent bare sediments. This tends to confirm the structuring and buffering effects of seagrass meadows on biological sedimentary processes.

The observed decline in meadow structure down to a structuring shoot-density threshold previously reported in the literature was accompanied by increases in both the amplitude and the spatial variability of sediment particle mixing intensity and changes in infaunal composition.

Showing a significant correlation between mean D_b^N and mean abundances of a set of 3 species including the polychaete *Melinna palmata*, the present study underlines that within the *Zostera* meadow, sediment mixing is regulated by the dense population of *M. palmata* that plays a synergistic role with the *Zostera* root/rhizome network. Consequently, when the *Zostera* meadow and associated *M. palmata* population decline, sediment particle mixing intensity becomes more intense and particularly more spatially heterogeneous.

Acknowledgements. This work is part of G.B.'s PhD thesis (University of Bordeaux). G.B. was supported by a doctoral grant from the French 'Ministère de l'Enseignement Supérieur et de la Recherche.' This work was funded through the IZOFLUX (ANR blanche), BIOMIN (LEFE-CYBER and EC2CO-PNEC), the 'Diagnostic de la Qualité des Milieux Littoraux,' and the 'OSQUAR' (Conseil Régional Aquitaine) programs.

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Editorial responsibility: Erik Kristensen, Odense, Denmark

Submitted: September 20, 2013; Accepted: July 19, 2014
Proofs received from author(s): September 29, 2014