

# Benthic oxygen exchange over a heterogeneous *Zostera noltei* meadow in a temperate coastal ecosystem

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**ABSTRACT:** Seagrass meadows support intense but highly variable benthic metabolic rates that still need to be better evaluated to determine an accurate trophic status. The present study assessed how seagrasses and associated benthic macrofauna control spatiotemporal changes in benthic oxygen exchanges within a temperate bay. Based on seasonal sampling over a complete year cycle, the diffusive oxygen uptake (DOU), community respiration (CR) and gross primary production (GPP) were measured in a *Zostera noltei* meadow within Arcachon Bay, taking into account its spatial heterogeneity. Oxygen fluxes were assessed in sediment cores, within which benthic macrofauna and seagrass abundances and biomasses were quantified. The presence of *Z. noltei* did not significantly affect the DOU. Seasonal changes in CR and GPP correlated strongly with temperature in the presence of *Z. noltei*. The characteristics of benthic macrofauna associated with *Z. noltei* only weakly affected seasonal changes in CR. High spatial changes in both GPP and CR were mainly driven by the aboveground biomass of *Z. noltei*. When extrapolated to the whole intertidal area of the bay, in spite of limitations, our results suggest (1) overall higher contributions to CR and GPP from the seagrass meadow than from bare sediments, even though alternative primary producers in bare sediments (likely microphytobenthos) contributed significantly during winter; (2) an annual decrease in CR and GPP of 35 and 41 %, respectively, resulting from the decline in *Z. noltei* of 25 % between 2005 and 2007; and (3) a strong seasonality in the magnitude of this decrease, which was high during autumn and low during winter.

**KEY WORDS:** Benthic oxygen exchange · Seagrass · *Zostera noltei* · Benthic macrofauna · Arcachon Bay · Community respiration · Gross primary production

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## INTRODUCTION

Seagrass meadows influence both the physical environment and resident biological communities in coastal ecosystems (Orth et al. 2006, Waycott et al. 2009, Duarte et al. 2010, Fourqurean et al. 2012, McGlathery et al. 2013). They also play a major role in nutrient cycling by supporting high nitrogen and phosphorus uptake, thereby improving local water

quality (De Wit et al. 2001, McGlathery et al. 2007, Deborde et al. 2008, Delgard et al. 2016). On a global scale, seagrass ecosystems can store as much as 19.9 Pg of organic carbon (Fourqurean et al. 2012), being responsible for 20 % of the global carbon sequestration in marine sediments despite occupying only 0.1 % of the world ocean surface (Duarte et al. 2005, Kennedy et al. 2010). Waycott et al. (2009) reported an ongoing global decline in seagrasses that

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is comparable to those recorded for mangroves and coral reefs. According to those authors, seagrasses have been disappearing worldwide at a rate of  $110 \text{ km}^2 \text{ yr}^{-1}$  since 1980, with accelerating decline since 1990. Such a decline is suspected to modify the metabolic status of seagrass meadows and their role as long-term carbon sinks (McLeod et al. 2011, Fourqurean et al. 2012). Although Stutes et al. (2007) and Antón et al. (2011) suggested that threatened tropical seagrass meadows with decreasing seagrass biomass could show reduced intensities in both benthic respiration and primary production without changes in their net metabolic status, little is still known about the effect of the decline in seagrass meadows on their metabolism.

Benthic metabolism is often investigated through the assessment of the dynamics of oxygen ( $\text{O}_2$ ) and/or dissolved inorganic carbon at the sediment–water interface. Several studies have investigated the metabolism of seagrass meadows using *ex situ* incubations (e.g. Hansen et al. 2000, Welsh et al. 2000), *in situ* incubations (e.g. Viaroli et al. 1996, Plus et al. 2001, Yarbro & Carlson 2008), the open-water  $\text{O}_2$  mass balance technique (Champenois & Borges 2012) and the eddy correlation technique (Hume et al. 2011, Rheuban et al. 2014a,b). Overall, the trophic status of seagrass meadows is highly variable, with net autotrophy or heterotrophy depending on the location (Duarte et al. 2010 and references therein). Many studies have assessed the temporal changes in seagrass metabolism over inter-annual (Champenois & Borges 2012), annual (Yarbro & Carlson 2008, Ouisse et al. 2010) and daily (Rheuban et al. 2014b) timescales. Conversely, little is still known about the spatial changes in benthic metabolism within a given seagrass meadow. Most of the studies cited above were performed in mature homogeneous meadows, whereas heterogeneous meadows have received only little attention, even though they are becoming more and more common as a consequence of global seagrass decline (Orth et al. 2006, Waycott et al. 2009). Further studies are therefore clearly needed to better assess the spatiotemporal changes in benthic metabolism within seagrass meadows.

Such an assessment is not trivial, because seagrasses may affect benthic metabolism directly through their own production/respiration, but also indirectly by modifying the biotic and/or abiotic characteristics of the sediment. Seagrasses may, for example, enhance organic matter cycling through seston entrapment (Ward et al. 1984, Wilkie et al. 2012) or the decomposition of dissolved root exudates and senescent plant material (Holmer et al. 2001,

Fourqurean et al. 2012). In the presence of seagrasses, the trapping of suspended particulate organic matter (POM) may result in a higher quantity and lability of sedimentary organics, which tend to stimulate benthic microbial respiration and thus positively affect sediment total  $\text{O}_2$  uptake (TOU). Sediment  $\text{O}_2$  availability can also be modified directly through radial oxygen loss from seagrass roots, although the total  $\text{O}_2$  release to the rhizosphere of *Zostera marina* beds was estimated at only 2 to 14% of the diffusive  $\text{O}_2$  uptake (Jensen et al. 2005, Fredriksen & Glud 2006). In addition, seagrasses provide a habitat for primary producers such as benthic micro- and macroalgae or epiphytic algae (McRoy & McMillan 1977, Fredriksen et al. 2010, Vafeiadou et al. 2014), and several studies have suggested that epiphyte photosynthesis might contribute significantly to primary production in seagrass meadows (Hasegawa et al. 2007, Ouisse et al. 2010). Seagrass meadows also provide a habitat for a large diversity of benthic macrofauna (Boström & Bonsdorff 1997, Fredriksen et al. 2010, Tu Do et al. 2011, Bernard et al. 2014). These organisms are known to enhance sediment  $\text{O}_2$  uptake through their own respiration and the construction of burrows that introduce secondary oxic surfaces within the sediment column (Kristensen 2000, Glud 2008, Aller 2014, Braeckman et al. 2014). Spatial changes in  $\text{O}_2$  fluxes within a heterogeneous seagrass meadow could thus result from differences in seagrass abundance and/or quantitative benthic macrofauna characteristics and composition. To date, the interactions between seagrasses and benthic macrofauna controlling benthic metabolism in coastal sediments have received little attention, such that the spatial and temporal changes in these interactions remain poorly understood (Thouzeau et al. 2007).

The present study aimed to assess how changes in seagrasses and associated macrofauna within a heterogeneous *Z. noltei* meadow influence the spatiotemporal changes in benthic metabolism. The total benthic metabolism of the seagrass community was estimated through the TOU. We also assessed the effect of the presence of seagrasses on the diffusive oxygen uptake (DOU), which represents a currently unknown component of the benthic metabolism of seagrass meadows. The studied meadow is located in Arcachon Bay (west coast of France) and is characterized by marked seasonal changes in *Z. noltei* leaf biomass (Auby & Labourg 1996). It also exhibits high spatial heterogeneity in leaf cover during summer and autumn resulting from its severe decline since 2005 (Plus et al. 2010, Auby et al. 2011, Delgard et al. 2013).

## MATERIALS AND METHODS

### Study area and sampling procedures

Arcachon Bay is a 174 km<sup>2</sup> mesotidal (tidal range: 0.8 to 4.6 m) closed bay located on the Atlantic French coast. It is connected to the Atlantic Ocean by a channel that is 2 to 3 km wide. Its intertidal area (117 km<sup>2</sup>) is covered by mudflats partly occupied by *Zostera noltei* meadows and oyster beds. Its subtidal area (57 km<sup>2</sup>) is partly colonized by *Z. marina* meadows. The present study was conducted on an intertidal flat located in the middle of the bay (Germanan site; Fig. 1). This flat is approximately 1.7 m above the mean water level with an approximate emersion period of 6 h d<sup>-1</sup> and a water height of approximately 2 m at high tide (Ganthy et al. 2013). During the study period, it was colonized by a *Z. noltei* meadow exhibiting a strong spatial heterogeneity in leaf cover during summer and autumn. At this time, the meadow typically consisted of approximate 3 m<sup>2</sup> patches with different amounts of leaf cover. Vegetated sediments (Stns Z) and adjacent bare sediments (Stn N) were sampled over 2 d every 3 mo (i.e. during each season) from October 2010 to October 2011. In vegetated sediments, 3 vegetated patches with increasing leaf cover (Stns Z1, Z2, Z3) were sampled

in October 2010 (autumn) and July 2011 (summer) to consider the spatial heterogeneity of the *Z. noltei* bed. Care was taken to sample 3 patches with leaf covers representative of the 3 different coverage classes (i.e. <25%, 25–75% and >75%) defined by Plus et al. (2010) as follows: <25% is associated with shoots scattered in weak density or very heterogeneous seagrass beds; 25–75% is associated with heterogeneous seagrass beds presenting an alternation of covered spots and patches of bare substratum; and >75% is associated with continuous and homogeneous seagrass beds with strong leaf cover. Owing to logistical constraints, Stns Z1 and Z3 could not be sampled in October 2011 (autumn). During spring and winter, the meadow was much more homogeneous and, therefore, only medium leaf density patches (Stn Z2) were sampled in February 2011 and April 2011. For all stations, care was taken to sample different patches from one season to the next to avoid artefacts resulting from previous samplings. During each season, the water temperature and salinity were measured approximately 4 h before low tide at Stns N and Z2 using a thermosalinometer (WTW 197i). During each season and for each sampled station (see above), 6 to 8 sediment cores were consistently collected manually at low tide and at noon using Plexiglas core tubes (9.1 cm diameter and 40 cm length), which were inserted into the sediment to at least 25 cm depth. Sediment cores were transported to the laboratory within 1 h of their collection and then transferred into a large tank containing high-tide water, where they were kept for approximately 4 h before the start of the measurements, which were all carried out at *in situ* temperature.

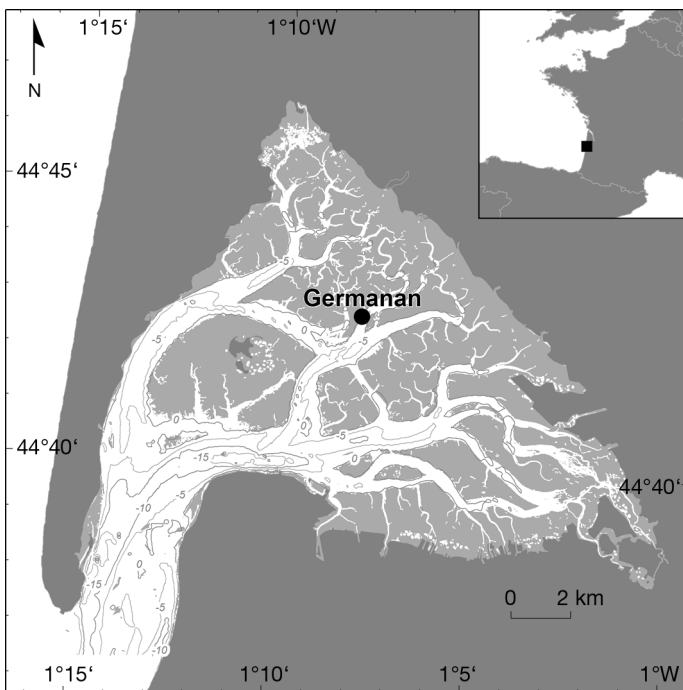


Fig. 1. Arcachon Bay (France) showing the location of the study site, 'Germanan'

### Diffusive O<sub>2</sub> fluxes

Oxygen microprofiles were measured using Clark-type microelectrodes (Revsbech 1989). For each season except in October 2010, replicate depth profiles of the O<sub>2</sub> concentration (n > 5) were randomly performed in single cores collected at Stns N and Z2. This sampling design was chosen partly because of technical and time constraints, and partly because previous studies have shown that, over the spatial range considered during the present study, biogeochemical heterogeneity is mainly associated with the smallest (e.g. <16 cm<sup>2</sup>, according to Deflandre 2001) spatial scales (see also Stockdale et al. 2009). Sensors with a 50 μm tip diameter (Unisense A/S) were positioned using a motor-driven micromanipulator controlled by a portable computer. At Stn Z2, owing to

sensor fragility, O<sub>2</sub> profiles could only be measured in a core with a relatively low shoot density compared to those used for the total O<sub>2</sub> flux measurements. Linear calibration was achieved using the O<sub>2</sub> concentration of the overlying water measured by Winkler titration (Grasshoff et al. 1999) and the zero oxygen in the anoxic part of the sediment. Oxygen profiles were processed using the PRO<sub>2</sub>FLUX software (Deflandre & Duchêne 2010). DOU was computed according to Fick's first law applied to sediments (Berner 1980):  $DOU = \phi \times D_s \times dC/dz$ , where  $\phi$  is the sediment porosity,  $dC/dz$  is the concentration gradient and  $D_s$  is the bulk sediment molecular diffusion coefficient corrected for tortuosity, i.e.  $D_s = D_0/\theta^2$ , where  $\theta$  is the tortuosity and  $D_0$  is the diffusion coefficient in water (Broecker & Peng 1974) at *in situ* temperature (Li & Gregory 1974).  $D_s$  was estimated as  $D_s = D_0/[1 + 3(1 - \phi)]$  (Iversen & Jørgensen 1993). The steady-state O<sub>2</sub> gradient was assessed based on the fitting of the depth profile of the O<sub>2</sub> concentration. A full description of this method can be found in Rasmussen & Jørgensen (1992), De Wit (1995) and De Wit et al. (1997).

#### Total O<sub>2</sub> fluxes: community respiration and gross primary production

For all stations and seasons, incubations under light and dark conditions were performed on 5 to 6 replicate sediment cores. These cores were sealed with a waterproof cap and their overlying water was constantly stirred (ca. 30 rpm) with a Teflon-coated magnetic bar. Light with an intensity of 170  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  at the sediment surface was supplied by fluorescent tubes (Arcadia FMW30) during incubations under light. This intensity was in the range of that occurring in the field under immersion. Based on measurements carried out over a tidal flat in Arcahon Bay during May and September 1994, Isaksen & Finster (1996) reported that the light intensity reaching the *Z. noltei* canopy could be high (i.e. 700 to 1300  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) under emersion, but drastically decreased during rising tide because of strong shading by incoming turbid waters. Under a 50 cm water cover, the light intensity that these authors measured around midday was, for example, less than 150  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Water samples were collected at the beginning and end of the incubation. They were analyzed for O<sub>2</sub> by Winkler titration (Grasshoff et al. 1983). Incubation durations were adjusted (2 to 4 h) to ensure that O<sub>2</sub> concentrations never dropped by more than 30% of their initial values. Total O<sub>2</sub> fluxes ( $F$ ) were computed as follows:

$F_{\text{dark/light}} = [(C_{\text{end}} - C_{\text{start}}) \times V]/(A \times T)$ , where  $C_{\text{end}}$  and  $C_{\text{start}}$  are end and starting oxygen concentrations, respectively,  $V$  is the volume of the water column,  $A$  is the sediment surface area and  $T$  is the incubation duration. Community respiration (CR) ( $CR = -F_{\text{dark}}$ ) measured in the dark was added to net community production (NCP) ( $NCP = F_{\text{light}}$ ) measured in the same core under light conditions to calculate gross primary production (GPP) ( $GPP = NCP + CR$ ).

#### Sediment characteristics

Porosity, particulate organic carbon (POC) and particulate organic nitrogen (PON) were measured during all seasons (except October 2010) at Stns N and Z2. These parameters were measured in the upper 0 to 0.5 cm sediment layer. Sediment porosity was determined from the water content calculated after freeze-drying the samples, by using a porewater density of 1.03 g cm<sup>-3</sup> and a dry density of 2.65 g cm<sup>-3</sup>, which is the mean density of sandy muds. Sediment porosity was corrected for salt content using seawater salinities (Burdige 2006). Sediment POC and PON contents were measured on 3 replicate cores. Samples were freeze-dried and analyzed with an automatic CN analyzer (Thermo Flash EA1112). POC measurements were performed after removal of carbonates (0.3 M HCl, 24 h) from 10 mg dry weight (DW) of powdered samples.

#### Seagrass and benthic macrofauna characteristics

At the end of each incubation (see 'Total O<sub>2</sub> fluxes' above), sediment from each core was carefully passed through a 0.5 mm sieve to collect plant material and benthic macrofauna. The seagrass material was divided into aboveground (AG) and belowground (BG) samples. The number of shoots per core was counted. The DW of leaves (alive) and roots/rhizomes (dead and alive) was assessed by drying to constant weight at 70°C. Benthic macrofauna was fixed in 4% buffered formaldehyde and stained with rose bengal. Organisms were counted, separating epifauna and infauna based on the portion of the habitat that they primarily occupied (see Bouma et al. 2009). Corresponding species lists are given in the Appendix. Epifauna and infauna biomasses were determined as the ash-free dry weight (AFDW) after desiccation (48 h at 60°C) and combustion (4 h at 450°C). The number and the small surface of the cores used in the present study possibly led to an

undersampling of benthic macrofauna. As a comparison, Bernard et al. (2014) also sampled Stns N and Z2 for infauna during the same seasons of the same years, but collected a 0.2 m<sup>2</sup> sediment surface (versus primarily 0.042 m<sup>2</sup> during the present study). They extensively presented and discussed spatiotemporal changes in the composition of benthic infauna. As a consequence, because both flux and macrofauna data originated from the same sediment cores, we first restricted the use of our macrofauna data to the incorporation of both epi- and infauna characteristics in stepwise regression models to describe the spatiotemporal changes in CR and GPP (see 'Statistical analysis' below). Nevertheless, because one of the hypotheses underlining the upscaling of our flux data to the whole intertidal area of Arcachon Bay (see 'Upscaling to the whole intertidal area of the bay' below) is that the macrofauna collected in our experimental cores were indeed representative of the benthic macrofauna present in the field, we also qualitatively compared our infauna data with those collected by Bernard et al. (2014) at the same stations and seasons. The same approach was used for epifauna data based on a comparison with unpublished data (G. Bernard pers. comm.).

### Statistical analysis

POC, PON, DOU, CR, GPP, *Z. noltei* and macrofauna data measured during the whole monitoring period at Stns N and Z2 were first analyzed by testing the effects of 'season' (fixed, 5 levels) and 'station' (fixed, 2 levels) factors using univariate 2-way permutational ANOVA (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) without preliminary data transformation using Euclidean distances. CR, GPP, *Z. noltei* and macrofauna data measured in October 2010 and July 2011 along the leaf cover gradient were analyzed by testing the effects of 'season' (fixed, 2 levels) and 'station' (fixed, 4 levels) factors using the same procedure. In both cases, pairwise tests were performed to assess the differences between factor levels. All these analyses were performed with the PRIMER v6 package and the PERMANOVA+ add-on software (Clarke & Warwick 2001, Anderson et al. 2008).

Relationships between seagrass and benthic macrofauna characteristics and between total oxygen fluxes and biotic/abiotic parameters were investigated using pairwise correlations. Subsequently, stepwise regression was used to produce overall models linking changes in CR and GPP with both biotic (seagrass

and macrofauna) and abiotic (temperature) parameters. Note that relationships between macrofauna parameters and GPP were not tested because macrofauna cannot directly affect primary production. Parameters were included in the model only if their addition significantly improved the proportions of the explained CR and GPP variances. Pairwise correlations and stepwise regressions were performed using JMP software (SAS Institute).

### Upscaling to the whole intertidal area of the bay

The studied intertidal flat is part of a heterogeneous *Z. noltei* meadow that partially covers the intertidal zone of Arcachon Bay. All surface area covered by *Z. noltei* throughout the entire bay was evaluated in late summer 2005 and 2007 by Plus et al. (2010) and Auby et al. (2011), respectively, taking into account 3 different coverage classes: <25%, 25–75% and >75%. During the present study, Stns Z1, Z2 and Z3 were positioned to be representative of these 3 classes, and Stn N was positioned to be representative of the whole intertidal area covered by bare sediments. During summer and autumn, the meadow was heterogeneous. Stns Z1, Z2 and Z3 in July 2011 and October 2010 were thus each considered representative of 1 of the 3 abovementioned coverage classes. In winter and spring, the studied meadow was relatively homogeneous, and the station with medium leaf density (i.e. Z2) was assumed to be representative of the entire meadow. For each season, the CR and GPP rates of the whole vegetated and bare areas were estimated by multiplying each individual flux measured during the present study by the corresponding surfaces in 2005 and 2007, as evaluated by Plus et al. (2010) and Auby et al. (2011), respectively. In this way, we were able to assess the seasonal changes in metabolic rates of the whole intertidal area of Arcachon Bay and compare them between 2005 and 2007.

## RESULTS

### Abiotic parameters

During the study period, the salinity ranged from 29.3 to 34.6 (Table 1). The maximum (21.5°C) and minimum (6°C) temperatures were recorded in July and February 2011, respectively. Temperatures were similar (i.e. approximately 15°C) in April 2011 and October 2010 and 2011. The porosity at Stns N and Z

Table 1. Temperature and salinity of bottom water, sediment porosity and particulate organic carbon (POC) and nitrogen (PON) measured during each sampling period in bare (N) and vegetated (measured only at Stn Z2) sediments. POC and PON are given as the mean  $\pm$  SD (n = 3). **Bold:** significant difference between dates (n vs. n - 1) within the same station (i.e. N or Z) (p < 0.05); \*significant difference between N and Z within the same season (p < 0.05). na: not available; porosity, POC and PON were not measured in October 2010 because of technical problems

Sampling date	Stn	Temp. (°C)	Salinity	Porosity (vol/vol)	PON (%)	POC (%)
Oct 2010	N	14.5	34.5	na	na	na
	Z2	14.5	34.5	na	na	na
Feb 2011	N	6	29.3	0.8	0.19 $\pm$ 0.02	2.23 $\pm$ 0.61
	Z2	6	29.3	0.66	0.17 $\pm$ 0.02	2.32 $\pm$ 0.47
Apr 2011	N	16.5	30	0.77	0.17 $\pm$ 0.03	1.64 $\pm$ 0.31
	Z2	16.5	30	0.69	<b>0.14 <math>\pm</math> 0.02</b>	<b>1.03 <math>\pm</math> 0.04</b>
Jul 2011	N	21.5	34.6	0.71	<b>0.25 <math>\pm</math> 0.01</b>	<b>2.63 <math>\pm</math> 0.19</b>
	Z2	21.5	34.6	0.7	0.31 $\pm$ 0.06	2.86 $\pm$ 0.47
Oct 2011	N	14.5	33.4	0.78	0.29 $\pm$ 0.04	2.68 $\pm$ 0.35
	Z2	14.5	33.4	0.84	0.23 $\pm$ 0.02*	2.08 $\pm$ 0.07*

ranged from 0.67 to 0.83 (Table 1). The PON and POC contents did not differ between vegetated and bare sediments except in October 2011 (Table 1). The mean POC and PON contents were 2.2  $\pm$  0.53% DW (mean  $\pm$  SD) and 0.22  $\pm$  0.05% DW, respectively.

## Seagrass and benthic macrofauna

*Zostera noltei* was the only macrophyte colonizing vegetated stations, and no significant amounts of epiphytes were observed on its leaves during the entire period under study. Conversely, benthic microalgae formed a brown biofilm at the surface sediment that was clearly visible in February 2011 at Stn N. At Stn Z2, the aboveground (AG) *Zostera* sp. biomass exhibited strong seasonal changes (Table 2), with a minimum in February (9.8  $\pm$  1.9 g DW m<sup>-2</sup>) and a maximum in July and October (38.2  $\pm$  2 g DW m<sup>-2</sup>, mean of the 2 mo  $\pm$  SD). The AG *Z. noltei* biomass at Stn Z2 correlated positively with temperature (r = 0.73, p < 0.001; Table 3). At this station, the belowground (BG) *Z. noltei* biomass and shoot density did not vary significantly between sampling periods. All seagrass parameters increased significantly along the leaf density gradient (Table 2). The mean AG *Z. noltei* biomass was lower at Stn Z1 (11.3  $\pm$  3.6 and 15.8  $\pm$  5.4 g DW m<sup>-2</sup>

Table 2. Seagrass and macrofauna parameters measured in bare (N) and vegetated (Z1, Z2 and Z3) sediments: mean  $\pm$  SD (n = 4 to 6) shoot density, above- (AG) and belowground (BG) biomass, abundance and biomass of epi- and infauna. **Bold:** significant difference between dates (n vs. n - 1) within the station (N or Z2). In October 2010 and July 2011, stations (N, Z1, Z2, Z3) not connected by the same letter are significantly different (p < 0.05). \*significant difference (p < 0.05) between N and Z2 within the same date. Letters refer to the results of the pairwise tests associated with PERMANOVA regarding the effect of the factor 'station' in each season. AFDW: ash-free dry weight; x: Stn N not colonised by *Z. noltei*

<i>Zostera noltei</i>			Epifauna		Infauna	
AG biomass (g DW m <sup>-2</sup> )	BG biomass (g DW m <sup>-2</sup> )	Shoot density (shoots m <sup>-2</sup> )	Biomass (g AFDW m <sup>-2</sup> )	Abundance (ind. m <sup>-2</sup> )	Biomass (g AFDW m <sup>-2</sup> )	Abundance (ind. m <sup>-2</sup> )
<b>Oct 2010</b>						
N	x	x	0.3 $\pm$ 0.3	362 $\pm$ 187	4.2 $\pm$ 2.4	2645 $\pm$ 1402
Z1	11.3 $\pm$ 3.6	5101 $\pm$ 2476	7.9 $\pm$ 5.7	2203 $\pm$ 1791	14.8 $\pm$ 11.4	6580 $\pm$ 1722
Z2	<b>36.2 <math>\pm</math> 7.8</b>	10339 $\pm$ 987	10.8 $\pm$ 6.0	7283 $\pm$ 3426	6.6 $\pm$ 6.4	906 $\pm$ 381
Z3	89.0 $\pm$ 21.1	17032 $\pm$ 2985	20.4 $\pm$ 10.1	11536 $\pm$ 3965	8.0 $\pm$ 9.0	2000 $\pm$ 1082
<b>Feb 2011</b>						
N	x	x	0.2 $\pm$ 0.1	145 $\pm$ 130	3.8 $\pm$ 1.8	2681 $\pm$ 1249
Z2	<b>9.8 <math>\pm</math> 1.9</b>	12560 $\pm$ 2644	7.7 $\pm$ 2.6	6667 $\pm$ 1746	25.1 $\pm$ 18.8	8551 $\pm$ 2626
<b>Apr 2011</b>						
N	x	x	0.1 $\pm$ 0.1	48 $\pm$ 75	4.6 $\pm$ 2.3	3285 $\pm$ 2069
Z2	<b>22.1 <math>\pm</math> 6.3</b>	14362 $\pm$ 3903	4.0 $\pm$ 2.5	4758 $\pm$ 3120	20.8 $\pm$ 16.5	8961 $\pm$ 3357
<b>Jul 2011</b>						
N	x	x	0.1 $\pm$ 0.1	174 $\pm$ 189	3.6 $\pm$ 1.4	2870 $\pm$ 1072
Z1	15.8 $\pm$ 5.4	5130 $\pm$ 898	4.5 $\pm$ 2.3	12203 $\pm$ 4660	6.1 $\pm$ 4.8	3333 $\pm$ 845
Z2	<b>40.3 <math>\pm</math> 4.9</b>	12536 $\pm$ 2229	10.5 $\pm$ 4.7	6580 $\pm$ 2666	8.8 $\pm$ 4.5	7217 $\pm$ 1443
Z3	63.2 $\pm$ 7.4	18214 $\pm$ 2351	15.9 $\pm$ 5.9	7739 $\pm$ 2800	8.2 $\pm$ 5.3	7478 $\pm$ 1777
<b>Oct 2011</b>						
N	x	x	0.1 $\pm$ 0.1	531 $\pm$ 270	6.5 $\pm$ 3.0	4058 $\pm$ 1230
Z2	38.1 $\pm$ 7.3	6052 $\pm$ 1318	5.4 $\pm$ 6.6	870 $\pm$ 367	8.4 $\pm$ 2.8	<b>6304 <math>\pm</math> 2076</b>

Table 3. Pairwise correlation coefficients relating the aboveground *Z. noltei* biomass (AG biom.), community respiration (CR) and gross primary production (GPP) to temperature (temp.), seagrass (above- and belowground *Z. noltei* biomass and shoot density) and macrofaunal (biomass, abundance of epi- and infauna) parameters. Only correlation coefficients associated with  $p < 0.05$  are shown.  $-p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . Shoot den.: shoot density; BG: belowground; abund.: abundance. x: non-tested correlations; see 'Materials and methods: statistical analysis'

	Temp.	<i>Zostera noltei</i>			Epifauna		Infauna	
		AG biom.	BG biom.	Shoot den.	Biom.	Abund.	Biom.	Abund.
<b>AG biomass</b>								
Z2	0.73***	1	–	–	–	–	–0.47*	–0.44*
Z1/Z2/Z3 Oct 2010	x	1	0.88***	0.94***	0.74**	0.85***	–	–0.63*
Z1/Z2/Z3 Jul 2011	x	1	0.97***	0.85***	0.78**	–	–	0.77***
<b>CR</b>								
N	–	x	x	x	–	–	–	0.45*
Z2	0.93***	0.75***	–0.44*	–	–	–	–	–
Z1/Z2/Z3 Oct 2010	x	0.98***	0.87***	0.90***	0.69**	0.83***	–	–0.57*
Z1/Z2/Z3 Jul 2011	x	0.83***	0.83***	0.80***	0.56*	–0.53*	–	0.78***
<b>GPP</b>								
N	–0.57**	x	x	x	x	x	x	x
Z2	0.78***	0.67***	–	–	x	x	x	x
Z1/Z2/Z3 Oct 2010	x	0.98***	0.81**	0.95***	x	x	x	x
Z1/Z2/Z3 Jul 2011	x	0.83**	0.83**	0.83**	x	x	x	x

in October and July, respectively) than at Stn Z3 ( $89.0 \pm 21.1$  and  $63.2 \pm 7.4$  g DW  $m^{-2}$  in October and July, respectively). During these 2 sampling periods, both the shoot density and BG *Z. noltei* biomass showed a positive, significant relationship with the AG *Z. noltei* biomass (Table 3).

Overall, we collected 18 epifaunal and 35 infaunal species (see the Appendix; full data set available on request). At both vegetated and bare stations, in terms of abundance and biomass, epifauna and infauna were highly dominated by the gastropod *Peringia ulvae* and the polychaete *Melinna palmata*, respectively. The other 5 dominant epifaunal species were the gastropods *Bittium reticulatum*, *Littorina littorea*, *Gibbula umbilicalis* and *Rissoa membranacea*, and the amphipod *Ampithoe rubricata*. The other 4 dominant infaunal species were the oligochaete *Tubificoides benedii*, the polychaetes *Aphelocheata marioni* and *Heteromastus filiformis*, and the bivalve *Abra segmentum*. For both epi- and infauna, seasonal changes in abundance and biomass tended to be much less important than spatial changes in these parameters. Infauna abundance and biomass were higher in vegetated than in bare sediments (overall means  $\pm$  SD of  $5703 \pm 3211$  vs.  $3107 \pm 1428$  ind.  $m^{-2}$  and  $11.9 \pm 11.8$  vs.  $4.5 \pm 2.3$  g AFDW  $m^{-2}$ , respectively). This trend was even more pronounced for epifauna (overall means  $\pm$  SD of  $6649 \pm 4430$  vs.  $252 \pm 242$  ind.  $m^{-2}$  and  $9.7 \pm 7.2$  vs.  $0.2 \pm 0.2$  g AFDW  $m^{-2}$ , respectively). In October 2010 and July 2011, epifaunal parameters (except for the abundance in July

2011) consistently increased from Stns N to Z3 and correlated positively with the AG *Z. noltei* biomass (Table 3). Spatial changes in infaunal characteristics were not as clear and only the infauna abundance measured in July 2011 correlated positively with the AG *Z. noltei* biomass (Table 3).

### Diffusive O<sub>2</sub> uptake

The mean DOU ranged from  $0.37 \pm 0.18$  to  $0.93 \pm 0.15$  mmol  $m^{-2} h^{-1}$  (Fig. 2). Significant changes were observed both between seasons and stations ( $p < 0.001$  in both cases), with a significant interaction between these 2 factors ( $p < 0.001$ ). In both February and April 2011, the DOU was significantly higher at Stn N. Conversely, in July 2011, the DOU was significantly higher at Stn Z2. However, the DOU did not significantly differ at Stns N and Z2 during October 2011. Overall, there was no clear effect of the presence of *Z. noltei* on DOU.

### Community respiration

CR (Fig. 3) showed significant differences both between stations and seasons ( $p < 0.001$  in both cases), with a significant interaction between these 2 factors ( $p < 0.001$ ). At Stn N, the CR ranged from  $1.15 \pm 0.21$  to  $2.05 \pm 0.15$  mmol  $m^{-2} h^{-1}$  and exhibited only weak seasonal changes. Except in February 2011, CR was

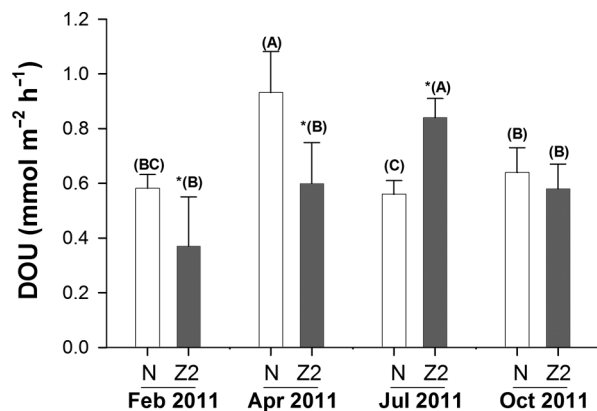


Fig. 2. Mean + SD ( $n = 5$  to  $10$ ) diffusive  $O_2$  uptake (DOU) measured on each sampling date at bare (N) and vegetated (Z2) stations between February and October 2011. Letters refer to the results of the pairwise tests associated with PERMANOVA regarding the effect of the factor 'season' at each station. \*significant difference between N and Z2 within the same season ( $p < 0.05$ )

higher in vegetated sediments compared to bare sediments. The CR at Stn Z2 exhibited stronger seasonal changes, with a minimum in February 2011 ( $0.84 \pm 0.12 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) and a maximum in July 2011 ( $5.83 \pm 0.84 \text{ mmol m}^{-2} \text{ h}^{-1}$ ). The CR measured along the whole leaf cover gradient also significantly differed between stations ( $p < 0.001$ ) and sampling dates ( $p < 0.001$ ). Here again, there was a significant interaction effect between these 2 factors ( $p = 0.023$ ). In October 2010, the CR significantly increased along the leaf density gradient from  $1.83 \pm 0.30 \text{ mmol m}^{-2} \text{ h}^{-1}$  at Stn Z1 to  $5.89 \pm 1.68 \text{ mmol m}^{-2} \text{ h}^{-1}$  at Stn Z3. The same

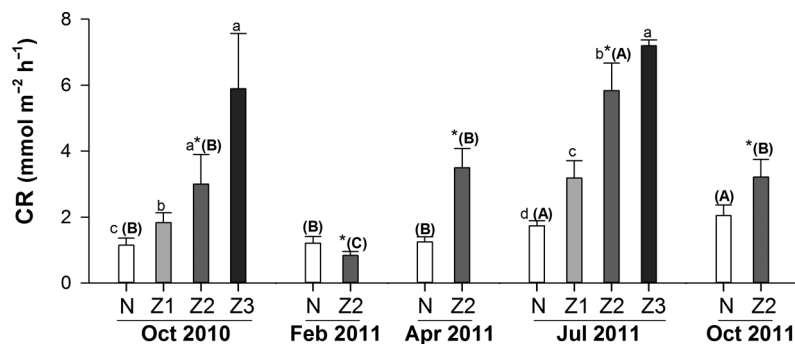


Fig. 3. Mean + SD ( $n = 4$  to  $6$ ) community respiration (CR) measured at bare (N) and vegetated (Z1, Z2, Z3) stations between October 2010 and October 2011. Lowercase letters refer to the results of the pairwise tests associated with the PERMANOVAs regarding the effect of the factor 'season' at each station (N, Z1, Z2 and Z3). Uppercase letters refer to the results of the pairwise tests associated with the PERMANOVAs regarding the effect of the factor 'season' at each station (N and Z2). \*significant difference between N and Z2 within the same season ( $p < 0.05$ )

trend was observed in July 2011, with an increase from  $3.18 \pm 0.52 \text{ mmol m}^{-2} \text{ h}^{-1}$  at Stn Z1 to  $7.19 \pm 0.17 \text{ mmol m}^{-2} \text{ h}^{-1}$  at Stn Z3. The main difference between the 2 sampling dates was the occurrence of much higher CR at Stn Z2 during July 2011.

### Gross primary production

GPP (Fig. 4) varied significantly between both stations and seasons ( $p < 0.001$  in both cases), with a significant interaction between these 2 factors ( $p < 0.001$ ). The GPP at Stn N exhibited strong seasonal changes, with a minimal value close to zero in October 2010 and a maximum of  $2.49 \pm 0.87 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  in February 2011. Conversely, the GPP at Stn Z2 was minimal ( $0.47 \pm 0.28 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) in February 2011 and maximal in July 2011 ( $4.78 \pm 0.54 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ). Except in February 2011, the GPP at Stn N was significantly lower than that measured in the vegetated sediment cores. In October 2010 and July 2011, the GPP significantly increased along the leaf density gradient to  $8.77 \pm 1.38 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  at Stn Z3 in October 2010.

### Relationship between benthic metabolic fluxes and environmental parameters

CR positively correlated with temperature at Stn Z2 ( $r = 0.93$ ,  $p < 0.001$ ) but not at Stn N (Table 3). At both stations, the CR did not (or only weakly) correlate with benthic macrofauna parameters. Conversely, highly significant correlations were found between the measured CR and AG *Z. noltei* biomass during the seasonal monitoring at Stn Z2 ( $r = 0.75$ ,  $p < 0.001$ ) and along the leaf density gradients in October 2010 and July 2011 (Table 3;  $r = 0.98$  and  $0.83$ , respectively,  $p < 0.001$  in both cases). During these 2 sampling periods, significant positive correlations were also found between CR and several macrofaunal parameters. GPP significantly correlated with temperature, with negative coefficients at Stn N and positive coefficients at Stn Z2. The GPP measured in vegetated cores during the seasonal monitoring and along the leaf density gradients correlated positively with the AG biomass.



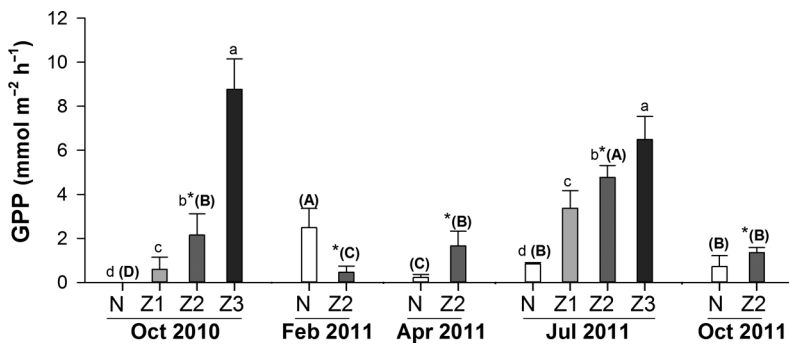


Fig. 4. Mean + SD (4 to 6 replicates) gross primary production (GPP) measured at bare (N) and vegetated (Z1, Z2, and Z3) stations between October 2010 and October 2011. Lowercase letters refer to the results of the pairwise tests associated with the PERMANOVAs regarding the effect of the factor 'season' at each station (N, Z1, Z2 and Z3). Uppercase letters refer to the results of the pairwise tests associated with the PERMANOVAs regarding the effect of the factor 'season' at each station (N and Z2). \*significant difference between N and Z2 within the same season ( $p < 0.05$ )

The best stepwise regression model describing the temporal changes in CR at Stn N was obtained for infauna and epifauna abundances. However, the corresponding multiple  $r^2$  was only 30% (with relative contributions of 17 and 13% for infauna and epifauna, respectively; Table 4). At Stn Z2, the best stepwise regression model showed a multiple  $r^2$  of 89%, with a major contribution from temperature (86.5%) and a small contribution from epifauna biomass (2.5%). The macrofauna parameters did not (or only

Table 4. Main characteristics of the best models of stepwise regression describing community respiration (CR) and gross primary production (GPP). The percentage of additional variance explained when a variable is added to the regression model is shown in parenthesis after the variable name. Abund.: abundance; biom.: biomass; temp.: temperature; AG biom.: aboveground *Zostera noltei* biomass

	n	$r^2$	Stepwise regression
<b>CR</b>			
N	26	0.30	a + b × infauna abund. (17.0) + c × epifauna abund. (13.0)
Z2	27	0.89	a + b × temp. (86.6) + c × epifauna biom. (2.4)
Z1/Z2/Z3 Oct 10	13	0.95	a + b × AG biom. (95)
Z1/Z2/Z3 Jul 11	15	0.90	a + b × AG biom. (86.5) + b × infauna abund. (3.5)
<b>GPP</b>			
N	26	0.29	a + b × temp. (29.3)
Z2	26	0.69	a + b × temp. (68.8)
Z1/Z2/Z3 Oct 10	13	0.94	a + b × AG biom. (94)
Z1/Z2/Z3 Jul 11	15	0.70	a + b × AG biom. (70)

poorly, i.e. 3.5% for infauna abundance in July 2011), explain the spatial changes in CR measured along the leaf cover gradient. Conversely, the AG *Z. noltei* biomass strongly contributed to CR models in both July 2011 and October 2010 (95.0 and 86.5%, respectively). The best stepwise regression models for temporal changes in GPP at Stns N and Z2 included only temperature (Table 4). As observed for CR, the  $r^2$  was much lower at Stn N (29%) than at Stn Z2 (69%). Changes in GPP along the leaf density gradient during October 2010 and July 2011 were best explained by the AG *Z. noltei* biomass, and the corresponding regression models were not improved by adding any other parameters.

#### Upscaling of benthic metabolism to the entire intertidal area

Upscaling to the entire intertidal area of Arcachon Bay showed that, during 2005 and 2007, CR was maximal in summer and minimal in winter, whereas GPP was maximal in summer but minimal in spring (Fig. 5). The *Z. noltei* meadow contributed more than bare sediments to CR and GPP during spring, summer and autumn. The contribution of bare sediments was high in winter. From spring to autumn, the contributions of the *Z. noltei* meadow to GPP were higher than their contributions to CR. The CR and GPP of the surface covered by *Z. noltei* decreased, respectively, by 42 and 51% between autumn 2005 and autumn 2007. When computed for the entire intertidal area during autumn, this induced a decrease in CR and GPP from  $359 \pm 70$  to  $253 \pm 36$   $\text{kmol O}_2 \text{ h}^{-1}$  and from  $390 \pm 58$  to  $192 \pm 31$   $\text{kmol O}_2 \text{ h}^{-1}$ , respectively. On an annual basis, the decline of *Z. noltei* meadows by 25% between 2005 and 2007 resulted in a decrease of 20 and 28% in CR and GPP, respectively.

## DISCUSSION

### Seagrass and benthic macrofauna

During the present study, we measured  $\text{O}_2$  fluxes and seagrass and benthic macrofauna within the same cores to generate sound correlations between

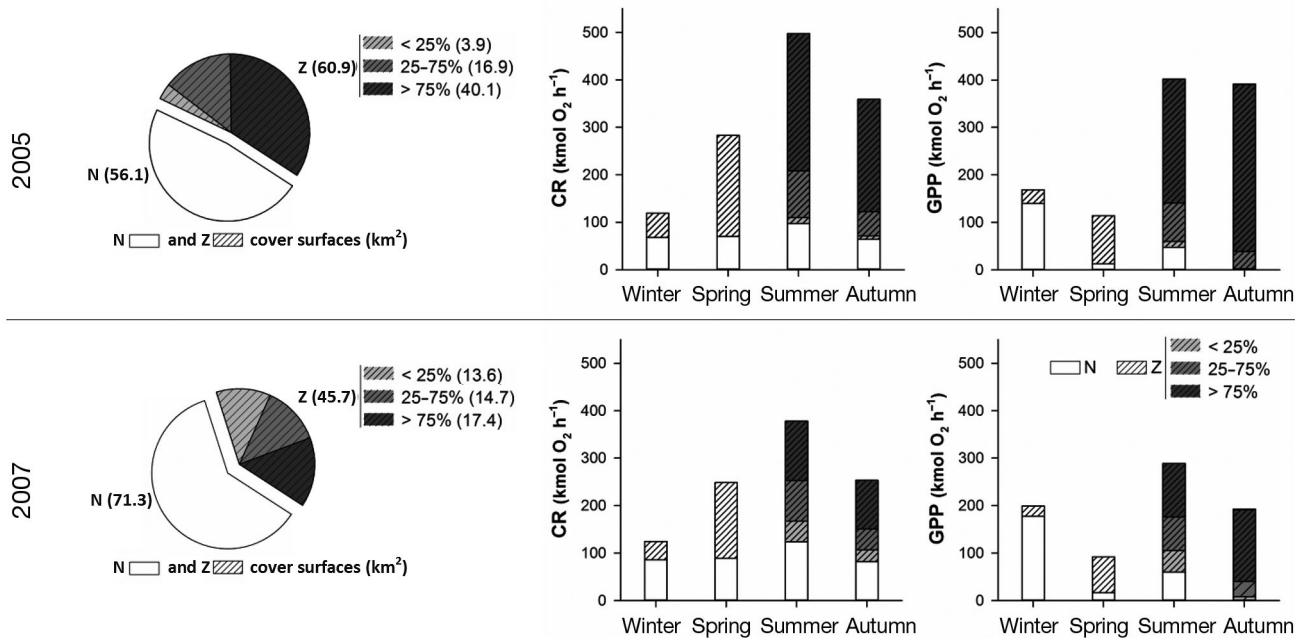


Fig. 5. Left: proportion of the intertidal area (117 km<sup>2</sup> as a whole) colonized (Z) or not (N) by *Zostera noltei* during the summers of 2005 and 2007. The spatial heterogeneity in *Z. noltei* cover during summer and autumn is taken into account by considering 3 different coverage classes: <25%, 25–75% and >75%. Respective surfaces (km<sup>2</sup>) are indicated in brackets. Data from Plus et al. (2010) and Auby et al. (2011). Right: seasonal estimates of community respiration (CR) and gross primary production (GPP) resulting from the upscaling of our measurements to the entire intertidal bay for 2005 (top) and 2007 (bottom)

these 2 sets of parameters. This resulted in a possible undersampling of both *Zostera noltei* and macrofauna. It was therefore essential to compare our results with literature data to verify that our flux values were representative of both the seagrasses and macrofauna present in the field, and that they adequately described the spatiotemporal changes in these characteristics and were therefore suitable for the upscaling of O<sub>2</sub> fluxes to the intertidal area of the entire bay. In the case of *Z. noltei*, these conditions were warranted because our sampling design was itself stratified relative to the seagrass abundance.

Bernard et al. (2014) and G. Bernard (unpubl.) sampled Stns N and Z2 for infauna and epifauna, respectively, during the same dates as our study but using a much larger sampling area. We therefore compared our own macrofauna data with theirs. During the present study, the infauna was dominated by the polychaete *Melinna palmata*; the 4 other dominant species were the oligochaete *Tubificoides benedii*, the polychaetes *Aphelochaeta marioni* and *Heteromastus filiformis*, and the bivalve *Abra segmentum*. This list is in good agreement with Bernard et al. (2014), who reported that *M. palmata* and *H. filiformis* contributed most to the similarity of the infauna composition at Stn Z2, whereas *M. palmata*, *H. filiformis*, *T. benedii*, *A. marioni* and *A. segmentum* contributed most to the

similarity in infauna composition at Stn N. Similarly, there was good agreement between the mean infauna abundances and biomasses recorded at Stns N and Z2 during the present study and in Bernard et al. (2014). During the present study, we collected only 18 epifaunal taxa versus 37 in G. Bernard (unpubl.). Nevertheless, the 2 dominant species in terms of abundance (i.e. the gastropods *Peringia ulvae* and *Bittium reticulatum*) and the 3 dominant species in terms of biomass (i.e. the gastropods *P. ulvae*, *Littorina littorea* and *Nassarius reticulatus*) were similar between the 2 studies. Accordingly, there was a reasonable agreement between the mean abundance and biomass recorded at Stns N and Z2 during the 2 studies. Overall, considering there was only a small effect of macrofauna characteristics on both CR and GPP (see Table 4 and the discussion below), the macrofaunal data collected during the present study allows for sound upscaling of CR and GPP to the entire intertidal area of Arcachon Bay.

### Spatiotemporal changes in DOU

DOU in vegetated sediments has been poorly studied to date. The present study provides the first computations of diffusive O<sub>2</sub> uptake derived from O<sub>2</sub>

microprofiles measured in a temperate *Z. noltei* meadow. The diffusive O<sub>2</sub> uptake measured in the present study (0.37 to 0.93 mmol m<sup>-2</sup> h<sup>-1</sup>; Fig. 2) was similar to literature data collected within other shallow coastal unvegetated areas such as the Thau Lagoon (Dedieu et al. 2007), the Berre Lagoon (Rigaud et al. 2013), the Gulf of Fos (Rabouille et al. 2003), Brest Bay (Khalil et al. 2013) and Aarhus Bay (Glud et al. 2003). There was no significant difference between the DOU in vegetated and bare sediments, suggesting that the influence of *Z. noltei* on the diffusive contribution of sediment O<sub>2</sub> exchanges was low. Given the high hydrodynamics at the study site (Ganthy et al. 2013), the repetition of deposition and resuspension cycles affecting particles and associated organic matter may homogenize the spatial distributions of organic matter, as indicated by the lack of consistent differences in both POC and PON contents within bare and vegetated sediments (Table 1). Moreover, the impact of seagrasses on O<sub>2</sub> dynamics is often associated with O<sub>2</sub> leakage at root extremities within sediments, which typically represents a small contribution to DOU across the sediment–water interface (Jensen et al. 2005, Frederiksen & Glud 2006). In addition, O<sub>2</sub> leakage is a process occurring on a very small scale and can thus be easily missed when obtaining a limited number of O<sub>2</sub> vertical microprofiles using microelectrodes. Nevertheless, because the O<sub>2</sub> depth profiles were performed only in sediments with low leaf cover, one cannot exclude a more significant effect of *Z. noltei* on the DOU in denser patches, as previously reported by Burdige & Zimmerman (2002) in the presence of *Thalassia testudinum*.

### Spatiotemporal changes in CR

The CR values measured during the present study were within the range of those recorded in other *Z. noltei* meadows within Arcachon Bay (Table 5), in addition to other coastal areas such as the northwest coast of Mauritania (Clavier et al. 2014) and the western English Channel (Ouisse et al. 2011). Similarly to what Stutes et al. (2007) suggested when studying a patchy shoalgrass *Halodule wrightii* meadow in the north central Gulf of Mexico, the present study provides several lines of evidence that CR tends to be higher in vegetated versus bare sediments. First, except for in February 2011, when we compared the fluxes at Stns Z2 and N, the CR was significantly higher (4-fold) at Stn Z2 (Fig. 3). Second, during our 2 gradient surveys (October 2010 and July 2011), we found positive correlations between seagrass cover and CR (Fig. 3). Third, the CR measured in Arcachon Bay before 2005 tended to be higher than more recent measurements (Table 5), which is likely related to the global decrease of seagrass biomass that occurred in 2005 (Plus et al. 2010, Auby et al. 2011), and is thus also indirectly indicative of a positive effect of the seagrass meadows on CR.

As mentioned in the introduction, such an effect could be direct and/or indirect. Indirect effects can result from the benthic macrofauna associated with seagrasses and also known to control CR through respiration and bioturbation. Our study provides several lines of evidence suggesting that direct effects are much more important than indirect ones in controlling CR. First, benthic macrofauna characteristics accounted for only 30% of temporal changes in CR at

Table 5. Benthic metabolic fluxes (mean ± SD) of tidal flats colonized (Z) or not (N) by *Zostera noltei* (% coverage by *Z. noltei*) in Arcachon Bay. CO<sub>2</sub> fluxes measured by eddy covariance at low tide were converted into O<sub>2</sub> fluxes assuming a molar ratio of 1:1. GPP: gross primary production; CR: community respiration

		Benthic GPP (mmol O <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup> )				Benthic CR (mmol O <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup> )				Reference
		Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	
Benthic chamber (around noon)	Z		8.8	14.8		2.5 ± 0.8	7.9 ± 1.9			Viaroli et al. (1996)
Core incubation ( <i>ex situ</i> , natural light)	Z	9.5	40.1		28.5	3.6 ± 1	10.5 ± 1.0		≈9	Welsh et al. (2000)
Benthic chamber	N	5.3				3.4	3.1			Deborde (2007)
	Z	2.8	1.6			1.9	3.1			
Eddy covariance	Z (22%)				15.8 ± 14.8				9.7 ± 13.3	Polsenaere et al. (2012)
	Z (90%)			9.5 ± 5.4	4.0 ± 7.2			3.6 ± 3.20	8 ± 4.0	
Core incubation ( <i>ex situ</i> , artificial light)	N	2.5 ± 0.9	0.2 ± 0.1	0.8 ± 0.0	0 ± 0.1	1.2 ± 0.2	1.2 ± 0.2	1.7 ± 0.2	1.1 ± 0.2	This study
	Z1			3.4 ± 0.8	0.6 ± 0.6			3.2 ± 0.5	1.8 ± 0.3	
	Z2	0.5 ± 0.3	1.7 ± 0.7	4.8 ± 0.5	2.9 ± 1.7	0.8 ± 0.1	3.5 ± 0.6	5.8 ± 0.8	3.0 ± 0.9	
	Z3			6.0 ± 1.2	8.8 ± 1.4			6.7 ± 0.9	5.9 ± 1.7	

Stn N, which suggests that, even in the absence of seagrasses, benthic macrofauna only loosely control CR. Second, the proportions of the explained spatial/temporal variances in CR were always much higher (i.e. >89%) when seagrasses were present. Third, considering the seasonal changes at Stn Z2, temperature was the parameter best correlated with CR (Table 5), as previously observed by Plus et al. (2001) and Ouisse et al. (2010). This suggests that any co-correlation effect is likely to involve quantitative seagrass characteristics and temperature rather than quantitative seagrass and benthic macrofauna characteristics. Indeed, the AG *Z. noltei* biomass positively correlated with temperature (Table 4), as previously reported for other temperate seagrasses (e.g. Marbà et al. 1996). Fourth, considering only spatial changes in CR along the seagrass cover gradient in October 2010 and July 2011, the AG *Zostera* biomass clearly contributed the most to the description of those changes (95 and 90%, respectively), whereas infauna abundance was the only macrofauna characteristic included (only in July 2011 and representing only 3.5%).

In bare sediments, the CR was twice as large as the DOU, indicating that approximately half of the O<sub>2</sub> uptake was due to biotic processes mainly cued by the activities of benthic macrofauna (Figs. 1 & 2). In spite of this potential control, temporal changes in infauna and epifauna abundances accounted for only 30% of the temporal changes in CR. However, it should be noted that this last result does not necessarily imply a lack of control of CR by the macrofauna parameters. The ranges of variations of macrofauna characteristics (Table 2; and as previously observed by Bachelet et al. 2000 in Arcachon Bay) and CR (Fig. 3) were indeed limited. Therefore, one cannot exclude the possibility that the (limited) changes recorded during the present study were mainly (i.e. for 70%) cued by factors other than the quantitative characteristics of benthic macrofauna, whereas the main component of CR was conversely largely seasonally invariant (and yet possibly cued by quantitative macrofauna characteristics).

### Spatiotemporal changes in GPP

As observed for CR, the GPP values measured during the present study were within the range of those recorded in other *Z. noltei* meadows and within Arcachon Bay after 2005 (Table 5), when seagrass biomass was in the same low range as during the

present study due to its global decline. Our data provide the same lines of evidence as for CR, indicating that GPP tends to be higher in vegetated versus bare sediments: higher GPP at Stn Z2 than at Stn N for 4 of the 5 sampling dates (Fig. 4); and positive correlations between seagrass cover and GPP during both gradient surveys (October 2010 and July 2011; Fig. 4). This is also in good agreement with a previous study performed in a patchy shoalgrass *H. wrightii* meadow of the north central Gulf of Mexico (Stutes et al. 2007). Similar to CR, our results strongly support a direct effect of seagrasses on GPP because: (1) the proportions of the explained spatial/temporal variances of GPP were always much higher (i.e. >69%) when seagrasses were present; (2) considering seasonal changes at Stn Z2, temperature correlated best with GPP, possibly partly due to co-correlation with quantitative seagrass characteristics (Table 5); and (3) in October 2010 and July 2011, the AG *Z. noltei* biomass was clearly contributing most (i.e. for 94 and 70%, respectively; Table 5) to the description of changes in GPP along the seagrass cover gradients. Overall, our results suggest that *Z. noltei* was the main primary producer in the studied meadow (Table 4), which is in good agreement with the fact that no significant amounts of epiphytes were visually observed during the study period, even though these organisms have been shown to significantly contribute to community production in other *Z. noltei* meadows (Ouisse et al. 2010).

The GPP measured at Stn N, particularly the maximum value measured in February 2011, was likely supported by microphytobenthos, although our data provide no evidence regarding the nature of the primary producer(s). This biological compartment is indeed known to play a key role in controlling the benthic metabolism of intertidal mudflats within the Arcachon Bay (Delgard et al. 2012, Polsenaere et al. 2012) as well as in other coastal systems (e.g. Guarini et al. 1997, Bartoli et al. 2003, Spilmont et al. 2006). Winter maxima in the concentration of chl *a* in surface sediments have been reported in many coastal areas (e.g. Magni & Montani 1997, Montani et al. 2003, Koh et al. 2007). To our knowledge, there has been no specific study on the seasonal dynamics of microphytobenthos in Arcachon Bay. However, Glé et al. (2007) observed recurring phytoplankton blooms in February, suggesting that anticyclonic weather conditions in winter may initiate winter blooms when incident irradiance reaches a threshold value. Such favorable light conditions could benefit the microphytobenthos as well, especially when grazing pressure is low (Koh et al. 2007).

### Effect of *Z. noltei* on temporal changes in the benthic metabolism of Arcachon Bay

The metabolic rates measured during the present study were assessed *ex situ* under constant immersion and with a light intensity representative of mean *in situ* irradiances under immersed conditions. However, it is well established that the benthic metabolism of intertidal flats varies with the light and tidal conditions. The tidal variation of benthic metabolism has been previously described within 2 other *Z. noltei* meadows located in tropical (Clavier et al. 2011, Clavier et al. 2014) and temperate areas (Ouisse et al. 2011). These 3 studies recorded CR and GPP that were at least 3-fold higher during immersion than during emersion. A higher CR rate during immersion has also been reported in bare temperate mudflats (Cook et al. 2004, Migné et al. 2009). The effect of light on the photosynthetic rate has been described for several temperate *Z. noltei* meadows, demonstrating a saturation effect at various irradiance levels. For instance, Plus et al. (2005) estimated that the photosynthesis rates measured in a *Z. noltei* meadow of a Mediterranean coastal lagoon reached saturation at irradiances varying from 174 to 305  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  under immersion. In bare sediments, microalgal primary production is negatively affected by high irradiance levels under emerged conditions (Seródio et al. 2008).

Our experimental plan was set to isolate the effects of seasonal changes in temperature, and both seasonal and spatial changes in seagrass cover. Conversely, it did not account for temporal changes in light intensity, temporal changes in tidal conditions and spatiotemporal changes in bathymetry, which also contribute to controlling emersion/immersion cycles. Regarding this last point, the study site was located mid-distance from the Leyre River and the ocean at a medium bathymetry level relative to the whole intertidal area of the bay. It may therefore be considered representative of mean bathymetrical conditions and also mean tidal conditions. Indeed, *Z. noltei* meadows are typically found in the intertidal areas of Arcachon Bay with daily emersion periods of between 3 and 15.5 h (Auby 1991), whereas the studied flat was exposed for 6 h  $\text{d}^{-1}$ . Shallower areas with longer emersion times are more likely to be exposed to extreme temperatures that can negatively affect *Z. noltei* metabolism (Massa et al. 2009). The interpretation of our upscaling could also be limited by the spatial heterogeneity of sedimentary organics. But Dubois et al. (2012) recently demonstrated that sedimented POM tends to be homogeneously spatially

distributed in Arcachon Bay due to the strong hydrodynamics and shallow depth. Nevertheless, the above-mentioned limitations restrict the significance of the upscaling of our results to the whole intertidal area of the bay. We thus limit the hereafter discussion to the assessment of the contribution of the *Z. noltei* meadow to seasonal changes in the benthic metabolism of the whole bay, and the changes in this metabolism between 2005 and 2007.

In 2005 and 2007, the *Z. noltei* meadow occupied 52% (i.e. 60.8  $\text{km}^2$ ) and 39% (i.e. 45.7  $\text{km}^2$ ), respectively, of the intertidal area of Arcachon Bay (Fig. 5). Our study clearly indicates higher contributions from the *Z. noltei* meadow than from bare sediments to CR and GPP (>64 and >79%, respectively; Fig. 5) during spring, summer and autumn but not during winter (<43% for CR and <17% for GPP). Our hypothesis is that the benthic primary production supported by the microphytobenthos probably helped maintain high photosynthetic activity during winter in bare sediments while the seagrass contribution was much lower. However, this trend may change from year to year due to the typical occurrence of strong inter-annual changes in the benthic metabolism of coastal bare sediments (e.g. Eyre & Ferguson 2005).

This study shows that seasonal changes in the benthic metabolism of the whole intertidal area of Arcachon Bay were only poorly explained by the studied environmental variables in bare sediments, but were strongly correlated with temperature in the presence of *Z. noltei*. Additional studies are thus necessary to better assess how the environmental factors affect the variability of benthic metabolic rates estimated in the present work. Overall, our study suggests that the characteristics of the benthic macrofauna living within a seagrass meadow would only weakly affect the seasonal changes of benthic metabolism. The use of the leaf cover gradient allowed a first estimation of the contribution of *Z. noltei* meadows to the benthic metabolism of the whole intertidal area of Arcachon Bay. Spatial changes in both GPP and CR were rather high and were mainly driven by the AG *Z. noltei* biomass. This implies that the leaf cover variable can be a key driver of the spatial variability of the benthic metabolism in coastal bays. The present work also highlights the global decline in benthic metabolism between 2005 and 2007 in the intertidal area of Arcachon Bay, resulting from the 25% decline in the *Z. noltei* cover during the same period (Fig. 5). Our results are similar to those reported by 2 previous studies performed in threatened seagrass meadows, where both GPP and CR were negatively affected by the decrease of seagrass biomass and density (Stutes

et al. 2007, Antón et al. 2011). Interestingly, the present work points out a marked seasonality in the magnitude of the decline in benthic metabolism in relation to the seasonal dynamics of *Z. noltei*. In the context of the worldwide decline of seagrasses, this study emphasizes that the spatial heterogeneity and seasonal changes of threatened meadows should be carefully considered and incorporated into the global carbon budget of seagrass meadows (Duarte et al. 2010, Kennedy et al. 2010, Duarte et al. 2013).

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#### LITERATURE CITED

- Aller RC (2014) Sedimentary diagenesis, depositional environments, and benthic fluxes. In: Holland HD, Turekian KK (eds) Treatise on geochemistry, Vol 8, 2nd edn. Elsevier, Oxford, p 293–334
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci* 58:626–639
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Antón A, Cebrian J, Heck K, Duarte C, Sheehan K, Miller M, Foster C (2011) Decoupled effects (positive to negative) of nutrient enrichment on ecosystem services. *Ecol Appl* 21:991–1009
- Auby I (1991) Contribution à l'étude des herbiers de *Zostera noltii* dans le bassin d'Arcachon: dynamique, production et dégradation, macrofaune associée. PhD dissertation, University of Bordeaux I
- Auby I, Labourg PJ (1996) Seasonal dynamics of *Zostera noltii* Hornem. in the Bay of Arcachon (France). *J Sea Res* 35:269–277
- Auby I, Bost CA, Budzinski H, Dalloyau S and others (2011) Decline of eelgrass beds in the Arcachon Bay: present state and research for causes. IFREMER Report RST/LER/AR/11.007
- Bachelet G, De Montaudouin X, Auby I, Labourg PJ (2000) Seasonal changes in macrophyte and macrozoobenthos assemblages in three coastal lagoons under varying degrees of eutrophication. *ICES J Mar Sci* 57:1495–1506
- Bartoli M, Nizzoli D, Viaroli P (2003) Microphytobenthos activity and fluxes at the sediment-water interface: interactions and spatial variability. *Aquat Ecol* 37:341–349
- Bernard G, Delgard ML, Maire O, Ciuat A and others (2014) Comparative study of sediment particle mixing in a *Zostera noltei* meadow and a bare sediment mudflat. *Mar Ecol Prog Ser* 514:71–86
- Berner RA (1980) Early diagenesis: a theoretical approach. Princeton University Press, Princeton, NJ
- Boström C, Bonsdorff E (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *J Sea Res* 37:153–166
- Bouma TJ, Ortells V, Ysebaert T (2009) Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. *Helgoland Mar Res* 63:3–18
- Braeckman U, Foshtomi MY, Van Gansbeke D, Meysman F, Soetaert K, Vincx M, Vanaverbeke J (2014) Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17:720–737
- Broecker WS, Peng TH (1974) Gas exchange rates between air and sea. *Tellus* 26:21–35
- Burdige DJ (2006) Geochemistry of marine sediments. Princeton University Press, Princeton, NJ
- Burdige DJ, Zimmerman RC (2002) Impact of seagrass density on carbonate dissolution in Bahamian sediments. *Limnol Oceanogr* 47:1751–1763
- Champerois W, Borges AV (2012) Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnol Oceanogr* 57:347–361
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth
- Clavier J, Chauvaud L, Carlier A, Amice E and others (2011) Aerial and underwater carbon metabolism of a *Zostera noltii* seagrass bed in the Banc d'Arguin, Mauritania. *Aquat Bot* 95:24–30
- Clavier J, Chauvaud L, Amice E, Lazure P and others (2014) Benthic metabolism in shallow coastal ecosystems of the Banc d'Arguin, Mauritania. *Mar Ecol Prog Ser* 501:11–23
- Cook PLM, Butler ECV, Eyre BD (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. I. Benthic metabolism. *Mar Ecol Prog Ser* 280:25–38
- De Wit R (1995) Measurements of sedimentary gradients of pore water species by use of microelectrodes. Calculations of microbial metabolic processes in the sediments. *Oceanis* 21:287–297
- De Wit R, Relexans JC, Bouvier T, Moriarty DJW (1997) Microbial respiration and diffusive oxygen uptake of deep-sea sediments in the Southern Ocean (ANTARES-I cruise). *Deep-Sea Res II* 44:1053–1068
- De Wit R, Stal LJ, Lomstein BA, Herbert RA and others (2001) ROBUST: the role of buffering capacities in stabilising coastal lagoon ecosystems. *Cont Shelf Res* 21:2021–2041
- Deborde J (2007) Biogeochemical processes of intertidal zones of lagoon systems: Arcachon Bay (SW, France). PhD thesis, Université Bordeaux 1, Bordeaux
- Deborde J, Abril G, Mouret A, Jézéquel D and others (2008) Effects of seasonal dynamics in a *Zostera noltii* meadow on phosphorus and iron cycles in a tidal mudflat (Arcachon Bay, France). *Mar Ecol Prog Ser* 355:59–71
- Dedieu K, Rabouille C, Thouzeau G, Jean F and others (2007) Benthic O<sub>2</sub> distribution and dynamics in a Medi-

- terranean lagoon (Thau, France): an *in situ* microelectrode study. *Estuar Coast Shelf Sci* 72:393–405
- Deflandre B (2001) Biogeochemical heterogeneity of marine coastal sediments: from microenvironments to Saguenay Fjord sediments. PhD dissertation, University of Rimouski
- Deflandre B, Duchêne JC (2010) PRO<sub>2</sub>FLUX: a software for profile quantification and diffusive O<sub>2</sub> flux calculations. *Environ Model Softw* 25:1059–1061
- Delgard ML, Deflandre B, Metzger E, Nuzzio D, Capo S, Mouret A, Anschutz P (2012) *In situ* study of short-term variations of redox species chemistry in intertidal permeable sediments of the Arcachon lagoon. *Hydrobiologia* 699:69–84
- Delgard ML, Deflandre B, Deborde J, Richard M, Charbonnier C, Anschutz P (2013) Changes in nutrient biogeochemistry in response to the regression of *Zostera noltii* meadows in the Arcachon Bay (France). *Aquat Geochem* 19:241–259
- Delgard ML, Deflandre B, Kochoni E, Avaro J and others (2016) Biogeochemistry of dissolved inorganic carbon and nutrients in seagrass (*Zostera noltii*) sediments at high and low biomass. *Estuar Coast Shelf Sci* in press, doi:10.1016/j.ecss.2016.01.012
- Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2:1–8
- Duarte CM, Marbà N, Gacia E, Fourqurean JW, Beggins J, Barrón C, Apostolaki ET (2010) Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. *Global Biogeochem Cycles* 24:GB4032, doi:10.1029/2010GB003793
- Duarte CM, Kennedy CH, Marbà N, Hendriks I (2013) Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean Coast Manag* 83:32–38
- Dubois S, Savoye N, Grémare A, Plus M, Charlier K, Beltoise A, Blanchet H (2012) Origin and composition of sediment organic matter in a coastal semi-enclosed ecosystem: an elemental and isotopic study at the ecosystem space scale. *J Mar Syst* 94:64–73
- Eyre BD, Ferguson AJP (2005) Benthic metabolism and nitrogen cycling in a subtropical east Australian estuary (Brunswick): temporal variability and controlling factors. *Limnol Oceanogr* 50:81–96
- Fourqurean JW, Duarte CM, Kennedy H, Marbà N and others (2012) Seagrass ecosystems as a globally significant carbon stock. *Nat Geosci* 5:505–509
- Frederiksen MS, Glud RN (2006) Oxygen dynamics in the rhizosphere of *Zostera marina*: a two-dimensional planar optode study. *Limnol Oceanogr* 51:1072–1083
- Fredriksen S, De Backer A, Boström C, Christie H (2010) Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Mar Biol Res* 6:189–200
- Ganthy F, Sottolichio A, Verney R (2013) Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). *J Mar Syst* 109–110:S233–S240
- Glé C, Del Amo Y, Bec B, Sautour B and others (2007) Typology of environmental conditions at the onset of winter phytoplankton blooms in a shallow macrotidal coastal ecosystem, Arcachon Bay (France). *J Plankton Res* 29:999–1014
- Glud NR (2008) Oxygen dynamics of marine sediments. *Mar Biol Res* 4:243–289
- Glud NR, Gundersen JK, Røy H, Jørgensen BB (2003) Seasonal dynamics of benthic O<sub>2</sub> uptake in a semienclosed bay: importance of diffusion and faunal activity. *Limnol Oceanogr* 48:1265–1276
- Grasshoff K, Kremling K, Ehrhardt M (1983) Methods of seawater analysis. Wiley-VCH, Weinheim
- Guarini JM, Blanchard GF, Gros P, Harrison SJ (1997) Modelling the mud surface temperature on intertidal flats to investigate the spatio-temporal dynamics of the benthic microalgal photosynthetic capacity. *Mar Ecol Prog Ser* 153:25–36
- Hansen JW, Pedersen AGU, Berntsen J, Rønbøg IS, Hansen LS, Lomstein BA (2000) Photosynthesis, respiration, and nitrogen uptake by different compartments of a *Zostera marina* community. *Aquat Bot* 66:281–295
- Hasegawa N, Hori M, Mukai H (2007) Seasonal shifts in seagrass bed primary producers in a cold-temperate estuary: dynamics of eelgrass *Zostera marina* and associated epiphytic algae. *Aquat Bot* 86:337–345
- Holmer M, Andersen FO, Nielsen SL, Bøschker HTS (2001) The importance of mineralization based on sulfate reduction for nutrient regeneration in tropical seagrass sediments. *Aquat Bot* 71:1–17
- Hume AC, Berg P, McGlathery KJ (2011) Dissolved oxygen fluxes and ecosystem metabolism in an eelgrass (*Zostera marina*) meadow measured with the eddy correlation technique. *Limnol Oceanogr* 56:86–96
- Isaksen MF, Finster K (1996) Sulphate reduction in the root zone of the seagrass *Zostera noltii* on the intertidal flats of a coastal lagoon (Arcachon, France). *Mar Ecol Prog Ser* 137:187–194
- Iversen N, Jørgensen BB (1993) Diffusion coefficients of sulfate and methane in marine sediments: influence of porosity. *Geochim Cosmochim Acta* 57:571–578
- Jensen SI, Köhl M, Glud RN, Jørgensen LB, Priemé A (2005) Oxidic microzones and radial oxygen loss from roots of *Zostera marina*. *Mar Ecol Prog Ser* 293:49–58
- Kennedy H, Beggins J, Duarte CM, Fourqurean JW, Holmer M, Marbà N, Middelburg JJ (2010) Seagrass sediments as a global carbon sink: isotopic constraints. *Global Biogeochem Cycles* 24:GB4026, doi:10.1029/2010GB003848
- Khalil K, Raimonet M, Laverman AM, Yan C and others (2013) Spatial and temporal variability of sediment organic matter recycling in two temperate eutrophicated estuaries. *Aquat Geochem* 19:517–542
- Koh CH, Khim JS, Araki H, Yamanishi H, Koga K (2007) Within-day and seasonal patterns of microphytobenthos biomass determined by co-measurement of sediment and water column chlorophylls in the intertidal mudflat of Nanaura, Saga, Ariake Sea, Japan. *Estuar Coast Shelf Sci* 72:42–52
- Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426:1–24
- Li YH, Gregory S (1974) Diffusion of ions in sea water and in deep-sea sediments. *Geochim Cosmochim Acta* 38:703–714
- Magni P, Montani S (1997) Development of benthic microalgal assemblages on an intertidal flat in the Seto Inland Sea, Japan: effects of environmental variability. *Mer* 35:137–148
- Marbà N, Duarte CM, Cebrián J, Gallegos ME, Olesen B, Sand-Jensen K (1996) Growth and population dynamics of *Posidonia oceanica* in the Spanish Mediterranean coast: elucidating seagrass decline. *Mar Ecol Prog Ser* 137:203–213
- Massa SI, Arnaud-Haond S, Pearson GA, Serrão EA (2009)

- Temperature tolerance and survival of intertidal populations of the seagrass *Zostera noltii* (Hornemann) in southern Europe (Ria Formosa, Portugal). *Hydrobiologia* 619: 195–201
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
  - McGlathery KJ, Sundbäck K, Anderson IC (2007) Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Mar Ecol Prog Ser* 348:1–18
  - McGlathery KJ, Reidenbach MA, D'Odorico P, Fagherazzi S, Pace ML, Porter JH (2013) Nonlinear dynamics and alternative stable states in shallow coastal systems. *Oceanography* 26:220–231
  - McLeod E, Chmura GL, Bouillon S, Salm R and others (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Front Ecol Environ* 9:552–560
  - McRoy CP, McMillan C (1977) Seagrass ecosystems: a scientific perspective. In: McRoy CP, Helfferich C (eds) *Ecology and physiology of seagrass*. Marcel Dekker, New York, NY, p 65–87
  - Migné A, Spilmont N, Boucher G, Denis L and others (2009) Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness, microphytobenthos migration, and variability of respiration rates with tidal conditions. *Cont Shelf Res* 29:2280–2285
  - Montani S, Magni P, Abe N (2003) Seasonal and interannual patterns of intertidal microphytobenthos in combination with laboratory and areal production estimates. *Mar Ecol Prog Ser* 249:79–91
  - Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. *BioScience* 56:987–996
  - Ouisse V, Migné A, Davoult D (2010) Seasonal variations of community production, respiration and biomass of different primary producers in an intertidal *Zostera noltei* bed (western English Channel, France). *Hydrobiologia* 649: 3–11
  - Ouisse V, Migné A, Davoult D (2011) Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Z. noltii* beds. *Mar Ecol Prog Ser* 437:79–87
  - Plus M, Deslous-Paoli JM, Auby I, Dagault F (2001) Factors influencing primary production of seagrass beds (*Zostera noltei* Hornem.) in the Thau lagoon (French Mediterranean coast). *J Exp Mar Biol Ecol* 259:63–84
  - Plus M, Auby I, Verlaque M, Levavasseur G (2005) Seasonal variations in photosynthetic irradiance response curves of macrophytes from a Mediterranean coastal lagoon. *Aquat Bot* 81:157–173
  - Plus M, Sébastien D, Trut G, Auby I and others (2010) Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuar Coast Shelf Sci* 87: 357–366
  - Polsenaere P, Lamaud E, Lafon V, Bonnefond JM and others (2012) Spatial and temporal CO<sub>2</sub> exchanges measured by eddy covariance over a temperate intertidal flat and their relationships to net ecosystem production. *Biogeosciences* 9:249–268
  - Rabouille C, Denis L, Dedieu K, Stora G, Lansard B, Grenz C (2003) Oxygen demand in coastal marine sediments: comparing *in situ* microelectrodes and laboratory core incubations. *J Exp Mar Biol Ecol* 285–286:49–69
  - Rasmussen H, Jørgensen BB (1992) Microelectrode studies of seasonal oxygen uptake in a coastal sediment: role of molecular diffusion. *Mar Ecol Prog Ser* 81:289–303
  - Revsbech NP (1989) An oxygen microsensor with a guard cathode. *Limnol Oceanogr* 34:474–478
  - Rheuban JE, Berg P, McGlathery KJ (2014a) Multiple timescale processes drive ecosystem metabolism in eelgrass (*Zostera marina*) meadows. *Mar Ecol Prog Ser* 507: 1–13
  - Rheuban J, Berg P, McGlathery KJ (2014b) Ecosystem metabolism along a colonization gradient of eelgrass (*Zostera marina* L.) measured by eddy correlation. *Limnol Oceanogr* 59:1376–1387
  - Rigaud S, Radakovitch O, Couture RM, Deflandre B, Cossa D, Garnier C, Garnier JM (2013) Mobility and fluxes of trace elements and nutrients at the sediment–water interface of a lagoon under contrasting water column oxygenation conditions. *Appl Geochem* 31:35–51
  - Seródio J, Vieira S, Cruz S (2008) Photosynthetic activity, photoprotection and photoinhibition in intertidal microphytobenthos as studied *in situ* using variable chlorophyll fluorescence. *Cont Shelf Res* 28:1363–1375
  - Spilmont N, Davoult D, Migne A (2006) Benthic primary production during emersion: *in situ* measurements and potential primary production in the Seine Estuary (English Channel, France). *Mar Pollut Bull* 53:49–55
  - Stockdale A, Davison W, Zhang H (2009) Micro-scale biogeochemical heterogeneity in sediments: a review of available technology and observed evidence. *Earth Sci Rev* 92:81–97
  - Stutes J, Cebrian J, Stutes AL, Hunter A, Corcoran AA (2007) Benthic metabolism across a gradient of anthropogenic impact in three shallow coastal lagoons in NW Florida. *Mar Ecol Prog Ser* 348:55–70
  - Thouzeau G, Grall J, Clavier J, Chauvaud L and others (2007) Spatial and temporal variability of benthic biogeochemical fluxes associated with macrophytic and macrofaunal distributions in the Thau lagoon (France). *Estuar Coast Shelf Sci* 72:432–446
  - Tu Do V, De Montaudoin X, Lavesque N, Blanchet H, Guyard H (2011) Seagrass colonization: knock-on effects on zoobenthic community, populations and individual health. *Estuar Coast Shelf Sci* 95:458–469
  - Vafeiadou AM, Materatski P, Adão H, De Troch M, Moens T (2014) Resource utilization and trophic position of nematodes and harpacticoid copepods in and adjacent to *Zostera noltii* beds. *Biogeosciences* 11:4001–4014
  - Viaroli P, Bartoli M, Bondavalli C, Christian RR, Giordani G, Naldi M (1996) Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. *Hydrobiologia* 329:105–119
  - Ward LG, Michael Kemp W, Boynton WR (1984) The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar Geol* 59: 85–103
  - Waycott M, Duarte CM, Carruthers TJB, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106:12377–12381
  - Welsh DT, Bartoli M, Nizzoli D, Castaldelli G, Riou SA, Viaroli P (2000) Denitrification, nitrogen fixation, community primary productivity and inorganic-N and oxygen fluxes in an intertidal *Zostera noltii* meadow. *Mar Ecol Prog Ser* 208:65–77
  - Wilkie L, O'Hare MT, Davidson I, Dudley B, Paterson DM (2012) Particle trapping and retention by *Zostera noltei*: a flume and field study. *Aquat Bot* 102:15–22
  - Yarbro L, Carlson P Jr (2008) Community oxygen and nutrient fluxes in seagrass beds of Florida Bay, USA. *Estuaries Coasts* 31:877–897



**Appendix 1.** List of the epifaunal and infaunal species identified during the present study

Epifauna	Infauna
<i>Ampithoe rubricata</i>	<i>Abra segmentum</i>
Anthozoa sp.	<i>Abra tenuis</i>
<i>Bittium reticulatum</i>	<i>Ampelisca brevicornis</i>
<i>Carcinus maenas</i>	<i>Aphelochaeta marioni</i>
<i>Crangon crangon</i>	<i>Arabella iricolor</i>
<i>Diastylis</i> sp.	<i>Cerastoderma edule</i>
<i>Gibbula umbilicalis</i>	<i>Clymenura clypeata</i>
<i>Hippolyte longirostris</i>	<i>Corophium volutator</i>
<i>Idotea chelipes</i>	<i>Cyathura carinata</i>
<i>Leptochiton asellus</i>	<i>Diopatra</i> sp.
<i>Littorina littorea</i>	Dolichopodidae sp.
<i>Musculista senhousia</i>	<i>Eurydice affinis</i>
Mysida sp.	<i>Glycera convoluta</i>
<i>Mytilus edulis</i>	<i>Glycera</i> sp.
<i>Nassarius reticulatus</i>	<i>Haminea navicula</i>
<i>Peringia ulvae</i>	<i>Heteromastus filiformis</i>
<i>Rissoa membranacea</i>	<i>Loripes lacteus</i>
<i>Siphonoecoes sabatieri</i>	Maldanidae sp.
	<i>Mediomastus fragilis</i>
	<i>Melinna palmata</i>
	<i>Microdeutopus chelifer</i>
	Nemertinea sp.
	<i>Nephtys hombergii</i>
	<i>Notomastus latericeus</i>
	<i>Phyllodoce mucosa</i>
	<i>Pinnotheres pisum</i>
	<i>Pseudopolydora antennata</i>
	<i>Pseudopolydora pulchra</i>
	<i>Pygospio elegans</i>
	<i>Ruditapes decussatus</i>
	<i>Ruditapes philippinarum</i>
	<i>Scrobicularia plana</i>
	<i>Streblospio shrubsolii</i>
	<i>Tubificoides benedii</i>
	<i>Tubularius polymorphus</i>

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