



Spatial and temporal variability of CO₂ fluxes at the sediment–air interface in a tidal flat of a temperate lagoon (Arcachon Bay, France)



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ABSTRACT

This study aimed to explore the spatial and temporal variability of benthic metabolism in a temperate mesotidal lagoon. This was achieved by measuring fluxes of CO₂ in static chambers during emersion, both under light and dark conditions. Three sample sites were selected according to their tidal level (upper or mid), their sediment type (sand or mud) and the presence/absence of the seagrass *Zostera noltei*. The three sites were investigated at three seasons (end of winter, spring and beginning of autumn). At each site and each season, three benthic chambers were used simultaneously in successive incubations over the emersion period. The sediment chlorophyll-*a* content varied seasonally in the upper sands (reaching 283 mg·m⁻² in spring) but not in the mid muds (averaging 142 mg m⁻² in bare muds and 186 mg m⁻² in muds covered by seagrass). The maximum sediment CO₂-uptake under light was 9.89 mmol m⁻² h⁻¹ in the mid-bare muds, in early autumn. The maximum sediment CO₂-release under darkness was 6.97 mmol m⁻² h⁻¹ in the mid muds covered by seagrass, in spring. Both CO₂-fluxes measured in the light and in the dark increased over periods of emersion. This increase, not related to light nor temperature variations, could be explained by changes in the amount and chemistry of pore water during the air exposure of sediments. The benthic trophic state index, based on the maximum light CO₂-flux versus maximum dark CO₂-flux ratio, assigned to each site at each season indicated that the sediments were net autotrophic in spring in upper sands and in mid muds covered by seagrass and highly autotrophic in other cases. The most autotrophic sediments were the mid-level bare muds whatever the season. The relevance of this index is discussed compared to carbon annual budget.

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1. Introduction

The metabolic balance of the coastal ocean appears to be a key part of the global carbon budget (Muller-Karger et al., 2005). Within coastal areas, intertidal sediments inhabited by microalgae and seagrasses play an important role in both the production and the remineralization of organic matter (Cahoon, 1999; Duarte et al., 2005). The definition of the status of these intertidal ecosystems as source or sink of CO₂ for the atmosphere requires evaluating the balance between primary production and respiration at relevant spatial and temporal scales.

Factors affecting the biomass of primary producers in intertidal sediments, and thereafter the associated metabolic processes, are

numerous. Exposure to hydrodynamic energy (as indicated by sediment type) and tidal level have been recognized as significant factors affecting spatial variations of microphytobenthic biomass in intertidal flats. The biomass of microalgae is considered to be lower in sandy sediments than in muddy sediments (Mac Intyre et al., 1996), to peak between mid-tide level and mean high water neap tide level (Underwood and Kromkamp, 1999) and to show a high degree of heterogeneity at small spatial scale with a patchy distribution (Spilmont et al., 2011 and references therein). Seagrasses, such as *Zostera*, occur from the mid-intertidal to the immediate sublittoral on various sediments, and primary production has long been shown to be higher in sediment covered by seagrass than in unvegetated sediment (e.g. Asmus and Asmus, 1985). Seasonality in light availability and temperature is well recognized as exerting an important influence on primary production in temperate areas (e.g. Migné et al., 2004). Temporal variability of microphytobenthic biomass is however also dependent on local environmental changes at other temporal scales such as erosion and deposit events in muddy shores (Underwood and Kromkamp, 1999). In microalgae community (e.g. Migné et al., 2004) and seagrass meadows

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(e.g. Ouisse et al., 2011), gross primary production has been shown to vary over the emersion period, in response to natural light variations. Variation in community gross primary production is also expected to occur during the course of emersion due to vertical migrations of the microphytobenthos in the surface sediment (e.g. Spilmont et al., 2007).

Factors controlling intertidal sediment respiration have been less studied than the ones controlling primary production and no general relationship with the sediment type has been evidenced (Middelburg et al., 2005). Bacterial respiration is however suspected to be the highest contributor to benthic community respiration and granulometry could control the distribution of benthic compartments and thus the benthic respiration at an intertidal bay scale (Hubas et al., 2006). Sediment respiration is also known to be enhanced in seagrass meadows due to the stimulation of the bacterial activity around roots (Middelburg et al., 2005). Temporal variations in sediment respiration are expected to be mainly controlled by temperature both at seasonal and daily scales (van Es, 1982; Hancke and Glud, 2004).

The aim of this study was to explore the spatial and temporal variability of benthic primary production and benthic respiration in a temperate mesotidal lagoon. Sample sites varied according to their tidal level, their sediment type and the presence/absence of the seagrass *Zostera noltei*. Primary production and respiration were measured in situ as CO₂-exchange rates between the sediment and the atmosphere at low tide, using static benthic chambers under both light and dark conditions. Small spatial scale variability was considered at each site using three benthic chambers simultaneously. Measurements were performed at three seasons and the small temporal scale variability was considered performing successive incubations over the emersion period.

2. Materials and methods

2.1. Study site

The Arcachon Bay is a mesotidal shallow lagoon on the French Atlantic coast with a semidiurnal tide. The studied tidal flat is located in the eastern part of the lagoon, near Cassy harbour (44°43' N, 1°03' W, Fig. 1). Three sites were investigated; site S1 was in the upper beach sandy area (covered with water 1 to 2 h per tide, grain size \approx 250 μ m, porosity \approx 0.4) and sites S2 and S3 were in the mid-muddy area (covered with water 3 to 4 h per tide, grain size \approx 15–40 μ m, porosity \approx 0.8). Sites S1 and S2 were free of macrophytes while S3 was covered by the seagrass *Zostera noltei*, which biomass varied seasonally, from 23 to 377 g_{DW} m⁻² in March and September 2006 respectively (Deborde et al., 2008a).

2.2. CO₂ flux measurements

Fluxes of CO₂ were measured at the sediment-air interface at low tide using the closed-chamber method described in Migné et al. (2002). A sediment area of 0.071 m² was enclosed down to a 10-cm depth. Changes in air CO₂ concentration (ppm) in the benthic chamber (10.5 L) were measured with an infrared gas analyser (LiCor Li-800) for 10–20 min. CO₂ concentrations were recorded in a data logger (LiCor Li-1400) with a 15 s frequency. CO₂ flux was calculated as the slope of the linear regression of CO₂ concentration (μ mol mol⁻¹) against time (min) and expressed in mmol C m⁻² h⁻¹ assuming a molar volume of 22.4 L at standard temperature and pressure.

Transparent chambers were used to estimate the net benthic community production (NCP, the balance between the community gross

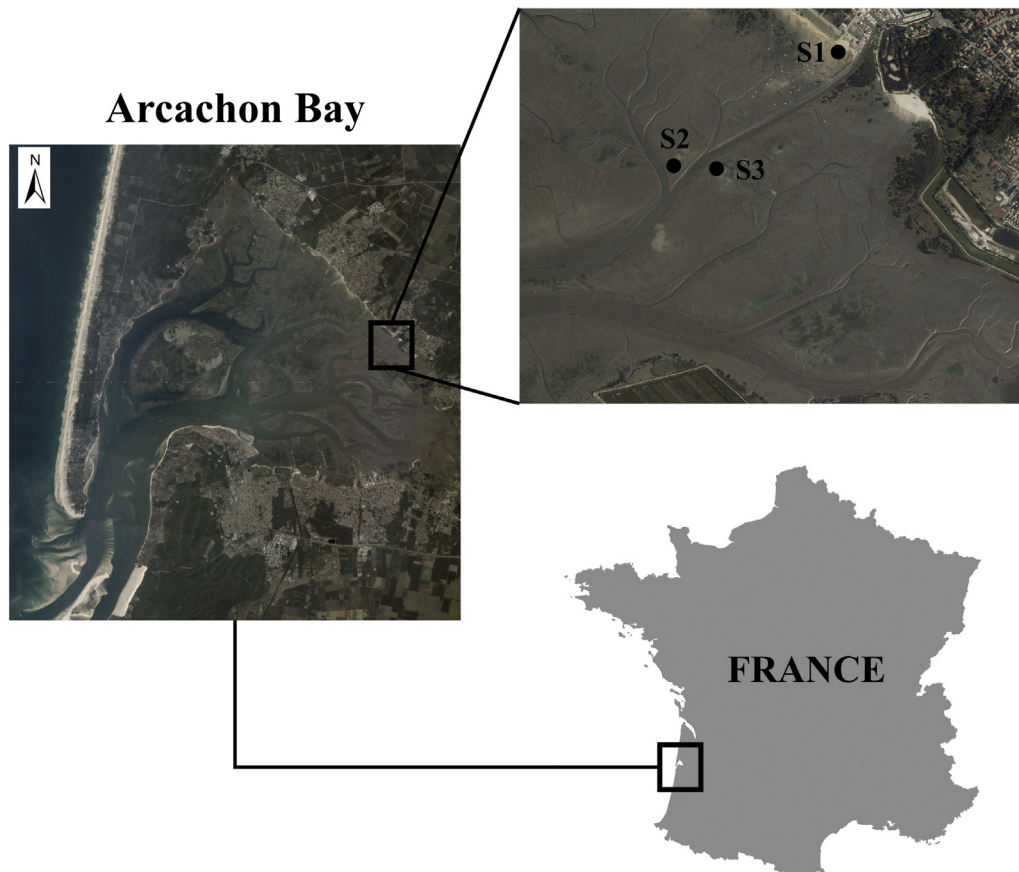


Fig. 1. Detailed map of the study site and sampling stations in the Arcachon Bay (SW France). S1: upper tidal level, sand; S2: mid-tidal level, bare mud; S3: mid-tidal level, mud + *Z. noltei*. © Ortho littorale 2008.

primary production and the community respiration). Opaque chambers were used to estimate the community respiration (CR). During light incubations, incident photosynthetically available radiation (PAR 400–700 nm) was monitored with a LiCor SA-190 quantum sensor. During dark incubations, the temperature of the top layer of the sediment was measured using a digital pen thermometer (0.1 °C accuracy).

2.3. Sampling strategy

Measurements were performed during spring tides, at the end of winter (March 2005), in spring (May 2006) and beginning of autumn (September 2007). Three benthic chambers were positioned about 10 m apart to take into account the small spatial scale variability at each site. Successive triplicate incubations were performed to take into account the small temporal scale variability at each occasion.

The number of successive triplicate incubations varied according to the date, the site and the light or dark condition, from 3 to 7 (but only one under darkness at S2 in March). In May 2006, a fourth chamber was used for monitoring dark fluxes over the low tide period at S1 (15 incubations from about 3 h after high tide to about 10 h after high tide).

After CO₂ flux measurements, three sediment cores (16-mm diameter, 10-mm depth) were collected inside each chamber to determine the Chlorophyll-*a* content (spectrophotometry method, Jeffrey and Humphrey, 1975).

2.4. Benthic trophic state index

The benthic trophic state index (BTSI) proposed by Rizzo et al. (1996) was calculated at each site at each season. The BTSI was assigned to sediments based on the relative magnitude of maximum hourly rates of net community production (NCP) and community respiration (CR). The classification given by Cook et al. (2004) for CO₂ fluxes was applied on the NCP versus CR values (NCP:CR < 0, BTSI 1, net heterotrophic; 0 < NCP:CR < 1, BTSI 2, net autotrophic; NCP:CR > 1, BTSI 3, highly autotrophic).

2.5. Statistical analyses

ANOVA (or its non-parametric equivalent if necessary) was used to test the effect of site, season and their interaction on the sediment chlorophyll-*a* content. The normality of data was checked using the Shapiro test ($P > 0.05$) and the homogeneity of variances was checked using the Bartlett test ($P > 0.05$). Pairwise comparisons were made using t-tests with the Bonferroni correction.

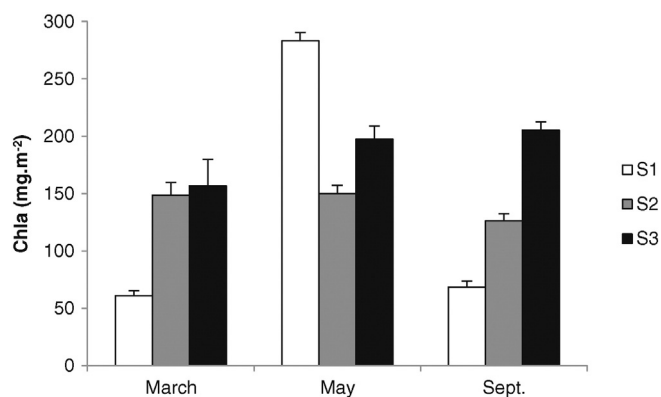


Fig. 2. Sediment chlorophyll-*a* content (Chla in mg m⁻²) in upper sandy site (S1) and mid-muddy (S2) and seagrass (S3) sites in March 2005, May 2006 and September 2007 (mean ± se, n = 9, except for S1 in March n = 8).

3. Results

The sediment chlorophyll-*a* content ranged from 61 to 283 mg·m⁻² (Fig. 2). The Scheirer–Ray–Hare H-test (non-parametric 2-way ANOVA) showed significant effects of season ($H = 21.169$, $P < 0.001$), site ($H = 9.205$, $P = 0.010$) and their interaction ($H = 28.217$, $P < 0.001$). The sediment chlorophyll-*a* content increased in May at site 1 (ANOVA, $F_{2,23} = 504.17$, $P < 0.001$) while it did not vary significantly between the three months at S2 (ANOVA, $F_{2,24} = 2.553$, $P = 0.099$) and S3 (ANOVA, $F_{2,14.02} = 1.950$, $P = 0.179$).

Light incubations were performed under incident photosynthetically available radiation varying from 185 to 1650 μmol m⁻² s⁻¹ (Fig. 3). Mean light CO₂-fluxes ranged from -9.89 to +0.41 mmol m⁻² h⁻¹ (Fig. 3). Except for the first incubation performed at S3 in May, the light fluxes always corresponded to a sediment CO₂-uptake. The sediment CO₂-uptake increased with the time of exposure at each site and season, independently of light variations.

During dark incubations, the temperature of the top layer of the sediment varied from 8.4 to 29.0 °C (Fig. 4). Mean dark CO₂-fluxes ranged from +0.06 to +6.97 mmol m⁻² h⁻¹ (Fig. 4). The sediment CO₂-release increased with the time of exposure at each site and season, independently of temperature variations. At S1 in May, fluxes measured in the supplementary chamber reached a plateau about 8 h after high tide.

The benthic trophic state index, based on the relative magnitude of maximum hourly rates under light (NCPmax) and darkness (CRmax) measured at each site at each season, indicated that sediments were net autotrophic (BTSI 2) in spring at S1 and S3 and highly autotrophic (BTSI 3) in other cases (Fig. 5).

4. Discussion

The sediment chlorophyll-*a* contents measured during this survey indicated that the microphytobenthic biomass was seasonally influenced, with a peak in spring at the sandy site but not at the muddy sites. This is consistent with previous surveys of annual variations of sediment chlorophyll-*a* content in sands (Migné et al., 2004, 2011) and muds (Spilmont et al., 2006; Davout et al., 2009) of various intertidal flats of the French coast of the English Channel. Temporal variations of microphytobenthic biomass are not only regulated by light and temperature at seasonal scale but are also dependent on local environmental changes at other temporal scales. In muddy shores, erosion and deposit due to particular weather events can lead to sudden decrease in microphytobenthos biomass compensated by rapid growth during favorable conditions (Underwood and Kromkamp, 1999). Nevertheless, our samplings were performed during three seasons of three consecutive years and the present observation might also result from an inter-annual variability of microphytobenthos development. Indeed, monthly monitoring of tidal flats over a four to five year period allowed to highlight an inter-annual variability in the peaks of microphytobenthos biomass in the Dutch Wadden Sea (Cadée and Hegeman, 1974) and in the Seto Inland Sea of South West Japan (Montani et al., 2003).

Both light and dark CO₂-fluxes tended to increase over the emersion period whatever the season, the sediment type and the presence or not of seagrasses. These increases, not related to light nor temperature variations, should result from non-biological processes occurring in the sediment during emersion. Discrepancies between instantaneous soil respiration and CO₂ efflux have been shown and attributed to a temporary storage of CO₂ in the soil pore water after rainfalls (Maier et al., 2011). In intertidal sediments, photosynthesis and respiration gradually change the amount of dissolved inorganic carbon in pore water, slowly changing the partial pressure of CO₂ and then the flux of CO₂ between the sediment and the atmosphere. This uncoupling between metabolism and CO₂ flux should result in an only slight delay of CO₂ uptake or emission relative to photosynthesis or respiration (Middelburg

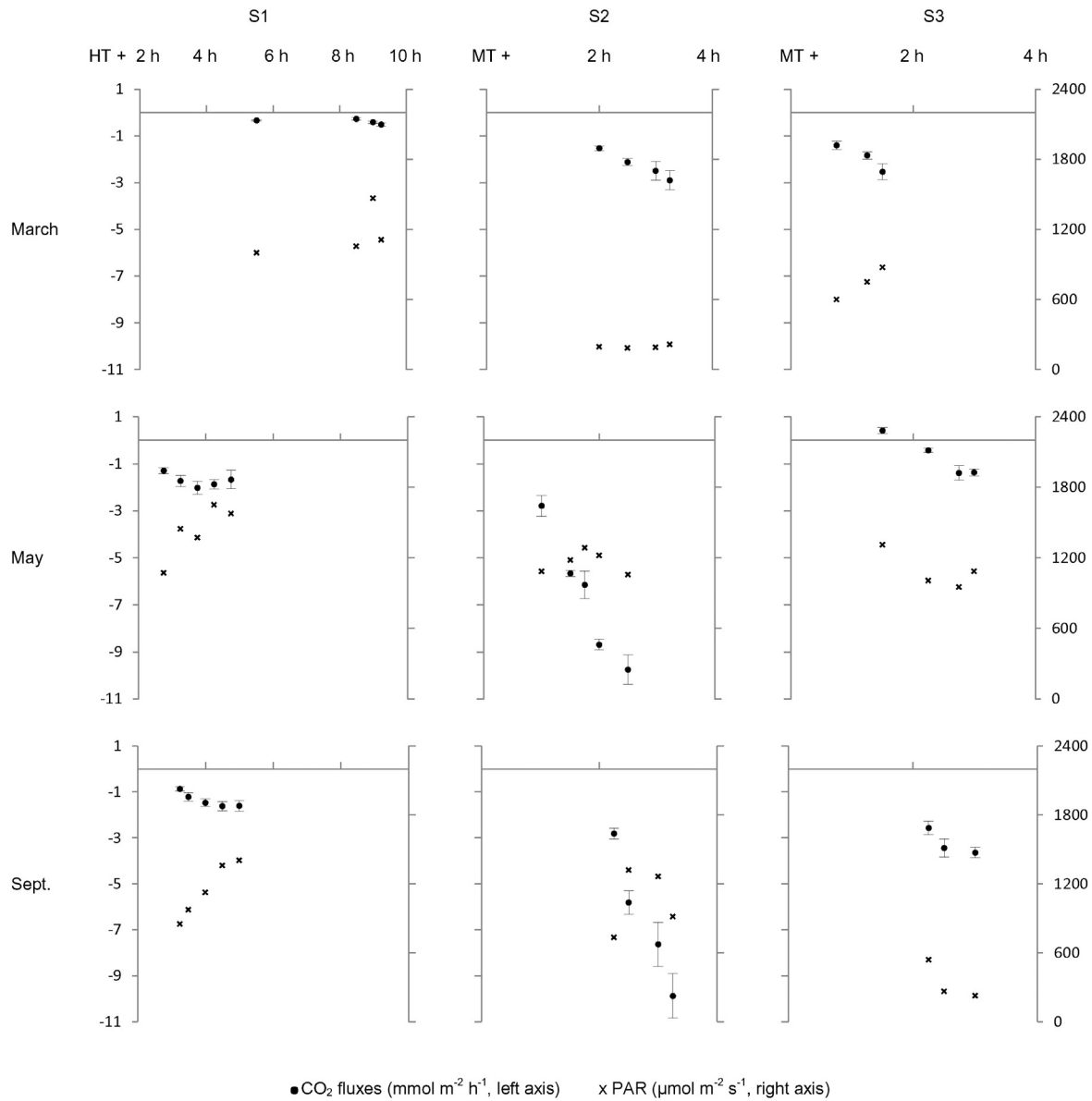


Fig. 3. Sediment-air CO₂ fluxes (mean \pm se, $n = 3$) measured under ambient light (PAR) at different moments after high tide (HT) at the upper sandy site (S1) and after mid-tide (MT) at the mid-muddy (S2) and seagrass (S3) sites in March 2005, May 2006 and September 2007.

et al., 1996). During exposure, however, changes in the amount of pore water could occur, due to advection and evaporation, and drive variations of CO₂ exchanges at the sediment-air interface. Variations of CO₂ exchanges at the sediment-air interface during exposure could also be driven by changes in the chemistry of pore water. In the sandy sediments of the Kurose River Estuary (Japan), Sasaki et al. (2009) measured a rapid increase in the rates of CO₂ emission in the first hour of ebbing tide and thereafter fairly stable rates until the end of the period of emersion. The initial phase of rapid increase in the CO₂ emission rates was supposed to correspond to the time when seawater drained rapidly in surface sediments. In a muddy tidal flat of the Wadden Sea, Klaassen and Spilmont (2012) observed negligible light and dark CO₂ fluxes at the start of the emersion, followed by slow increases until maximum values were reached after 3 h of emersion. Fluxes did not show any sign of change near the end of the period of emersion and maximum values were supposed to be reached and maintained after the pore water has been evaporated in the surface sediment. In the tidal flat of the Arcachon bay, the permeability of upper sands allows the advective transport of pore waters and the vertical distribution of reduced species (Mn, Fe, S) has been shown to vary during ebbing and rising tide

(Delgard et al., 2012). Lower cohesive muds remain saturated with seawater at low tide, evaporation occurs however, and annelids and bivalves burrows act as ducts for pore water seeping (Deborde et al., 2008b). Furthermore, strong anaerobic organic matter mineralization has been evidenced in both vegetated and unvegetated muds (Deborde et al., 2008a, 2008b, 2010), which should generate alkalinity changes leading to shifts in the equilibrium between the forms of dissolved inorganic carbon in pore water and hence in gaseous CO₂ flux (Faber et al., 2012).

A seasonal trend appeared in dark CO₂ fluxes at each site, with highest rates measured in spring when sediment temperature was the highest. Pooling data, but excluding the particularly high value measured in the *Zostera* site in May, there was a significant exponential relationship between maximum dark CO₂ fluxes and sediment temperature ($R^2 = 0.920$, $n = 8$, $P < 0.001$). This confirms the control of sediment respiration by temperature variations at a seasonal scale. The particularly high dark CO₂ fluxes measured in the *Zostera* site in May could result from the increase of anoxic respiration processes at the periphery of the rhizosphere which has been suggested to occur during the growth phase of seagrasses in the Arcachon bay (Deborde et al., 2008a).

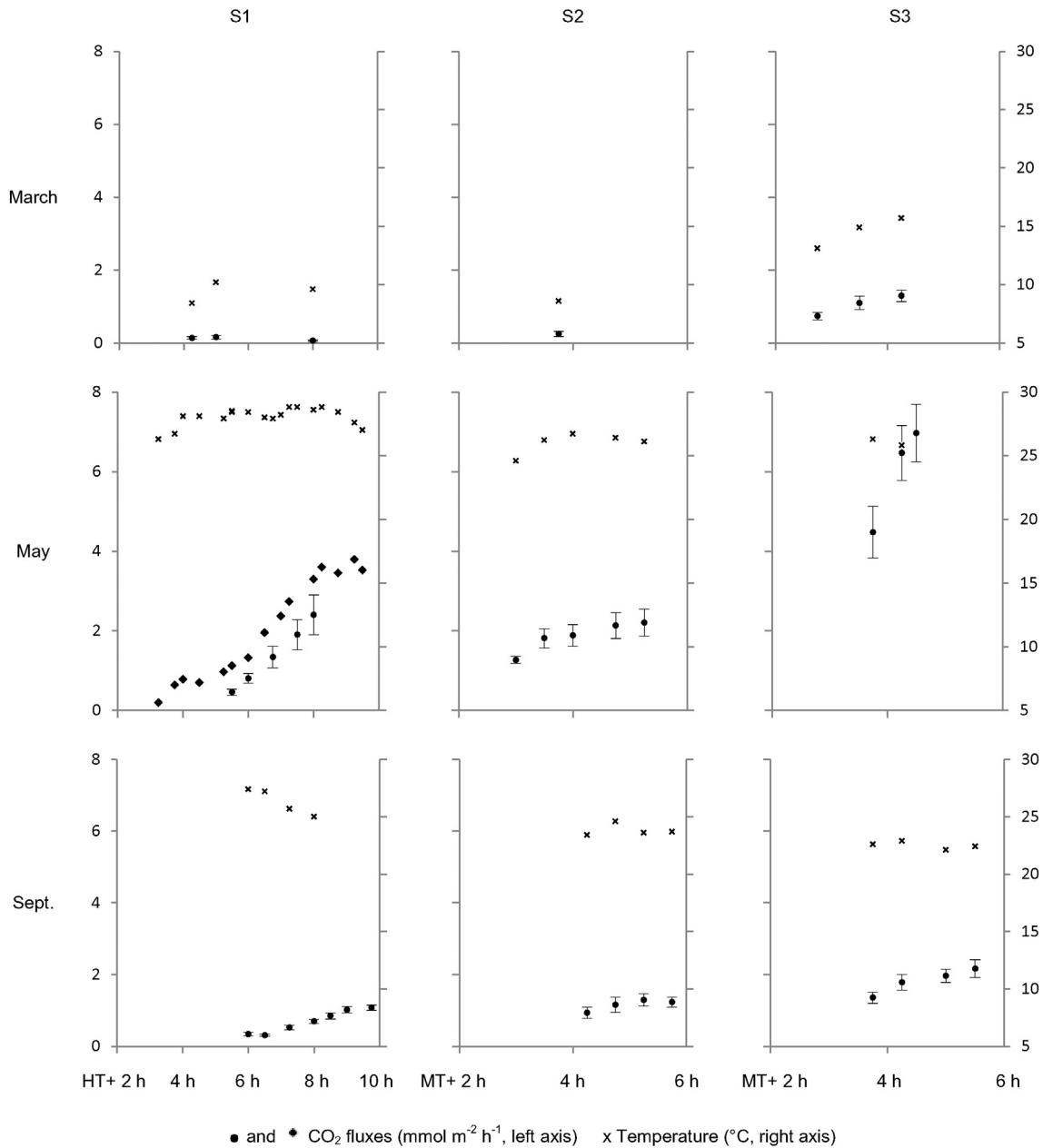


Fig. 4. Sediment-air CO₂ fluxes (mean ± se, n = 3) measured under dark conditions and sediment temperature at different moments after high tide (HT) at the upper sandy site (S1) and after mid-tide (MT) at the mid-muddy (S2) and seagrass (S3) sites in March 2005, May 2006 and September 2007. Sediment-air CO₂ fluxes were also measured from 3 h 15 after HT to 9 h after HT at S1 in May using a supplementary benthic chamber.

Contrary to what was expected, higher net community production rates were measured in the unvegetated mud than in the seagrass meadow. Adding maximum dark and light fluxes led to estimate gross community production (GCP) to be 3, 12 and 11 mmol C m⁻² h⁻¹, in March, May and September respectively, in the unvegetated mud and 4, 8 and 6 mmol C m⁻² h⁻¹ in the *Zostera* meadow. This is in accordance with results of Polsenaeere et al. (2012) in the same bay. Based on the micrometeorological Eddy Covariance technique, autumn GCP was estimated to be 16 and 4 mmol C m⁻² h⁻¹ in muds with 20 and 90% cover of *Zostera* respectively. This underlines the importance of microphytobenthic communities in the carbon cycle in the Arcachon flat.

The benthic trophic state index (BTSI) proposed by Rizzo et al. (1996) gives an indication of the balance between production and respiration using hourly rates. Applying this index to maximum CO₂ fluxes measured here indicated that sediments were net autotrophic in spring

at the sandy site and at the muddy site with seagrass and highly autotrophic at the other occasions. The lowest ratio of net community production to community respiration was obtained in the *Zostera* site in May, when the particularly high rate of respiration was measured. The most autotrophic sediments were the mid-level unvegetated muds, with maximum net community production more than 4 times higher than community respiration whatever the season. A previous study, based on oxygen fluxes measured at the sediment/water interface in laboratory incubations, already showed a persistent autotrophy in the *Z. noltei* meadow of the Arcachon Bay (de Wit et al., 2001). The present study reinforced and completed this result. Based on in situ measurements of CO₂ fluxes at the sediment/air interface, it showed persistent autotrophy not only in seagrass meadow but also in bare mud and sand.

Benthic trophic state indices were also calculated using rates obtained in various tidal sedimentary flats along the French coast of the English Channel with the same method as the one presented here

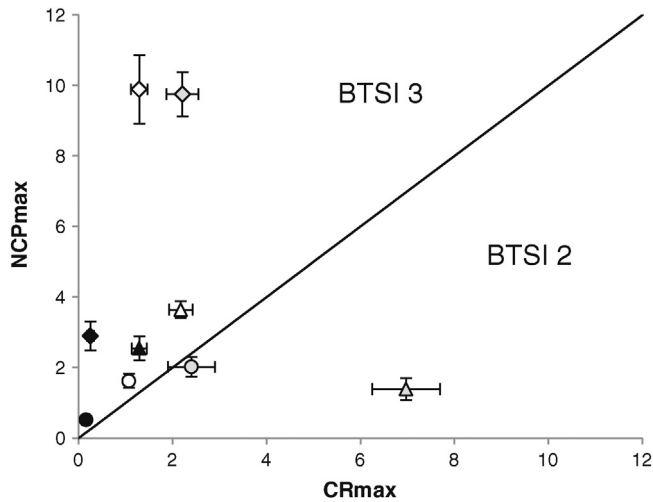


Fig. 5. Maximum CO_2 -fluxes (in $\text{mmol m}^{-2} \text{h}^{-1}$, mean \pm se, $n = 3$) under light (NCPmax) versus under darkness (CRmax) at the upper sandy (S1, circles), at the mid-muddy (S2, diamonds) and at the seagrass (S3, triangles) sites in March 2005 (dark), May 2006 (grey) and September 2007 (white) and corresponding benthic trophic state index according to Rizzo et al. (1996) (BTSI 2: net autotrophic, BTSI 3: highly autotrophic).

(Table 1). Net heterotrophy was observed only once, in the upper exposed sandy beach of Wimereux in winter. Net autotrophy was observed in the mid-level muddy sand flat of the Bay of Somme and high autotrophy in all the other cases. The investigation of Rizzo et al. (1996) of the variability of this index across a number of spatial and temporal scales showed a reduced autotrophy or enhanced heterotrophy associated with finer-grain sediment and a decline of autotrophy from winter to spring, particularly at sandy sites. In the study of Cook et al. (2004), however, the most autotrophic sediments were the finest ones in early spring. In the present investigation, no trend appeared according to the sediment type or to the tidal level but the ratio of net production to respiration was maximal in winter except in the upper sandy beaches of Wimereux and Roscoff Aber bay. No generalization can then be made about the effect of tidal-level, sediment type and season on the trophic status of the sediments assigned according to the BTSI.

The benthic trophic state index does not take into account the trophic status over a diurnal cycle which is considered in the more traditional and ecologically relevant ratio of gross primary production to

respiration. In intertidal unvegetated sedimentary flats where turbidity is likely to limit photosynthesis during immersion, the net primary production might be maximal during emersion but respiration might be enhanced during immersion. For example, Cook et al. (2004) measured inundated dark fluxes of dissolved inorganic carbon (TCO_2) 3 to 5 times higher than exposed fluxes of CO_2 in mudflats of a temperate Australian estuary. Net autotrophy assigned according to the BTSI means that the system is net autotrophic at saturating light during emersion but might present a net heterotrophy on a daily basis integrating the low/high tide cycle. The BTSI calculated on exposed CO_2 fluxes indicated that the muddy site of Cancale surveyed in the Bay of Mont St Michel was highly autotrophic at the 3 investigated seasons. This site was shown, however, to be net heterotrophic based on an annual budget taking into account the variability of fluxes with tidal, daily and seasonal cycles (Migné et al., 2009). This example highlights the need to incorporate the alternate periods of submersion and air exposure to determine the metabolic balance of intertidal sediments. The micrometeorological Eddy Covariance technique used by Polsemaere et al. (2012) over the intertidal mudflat of the Arcachon bay, provided net ecosystem exchange (NEE) at the air/sediment interface during emersion and at the air/water interface during immersion in the early autumn 2007. Strong CO_2 uptake was observed at low tide during the day but CO_2 degassing in all other cases. This suggests that the flat was autotrophic at low tide during the day but heterotrophic during the night and during the immersion. Nevertheless, NEE can differ from net ecosystem production due to the slow water–air diffusion. To determine the metabolic balance of the tidal sediments of the Arcachon bay, dissolved inorganic carbon fluxes measured at the sediment/water interface at high tide should also be considered.

Individual contribution of authors

AM, DD, GB: conceived the study.
 AM, DD, NS, VO, GB: performed the research.
 AM: analysed the data.
 AM, DD, NS, VO: prepared the article.

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Table 1
 Maximum net community production (NCPmax) and maximum community respiration (CRmax) measured in $\text{mmol C m}^{-2} \text{h}^{-1}$ and corresponding benthic trophic state index (BTSI 1, net heterotrophic; BTSI 2, net autotrophic; BTSI 3, highly autotrophic) in each site and season of the present study and in various tidal sedimentary flats along the French coast of the English Channel.

Site (Tidal level, sediment)	End of winter			Spring			End of summer			Reference
	NCPmax	CRmax	BTSI	NCPmax	CRmax	BTSI	NCPmax	CRmax	BTSI	
	(mmol C m ⁻² h ⁻¹)			(mmol C m ⁻² h ⁻¹)			(mmol C m ⁻² h ⁻¹)			
Arcachon bay S1 (upper, sand)	0.52	0.16	3	2.02	2.40	2	1.62	1.07	3	This study
Arcachon bay S2 (mid, mud)	2.90	0.25	3	9.75	2.21	3	9.89	1.29	3	This study
Arcachon bay S3 (mid, mud + <i>Z. noltei</i>)	2.54	1.29	3	1.39	6.97	2	3.64	2.17	3	This study
Wimereux beach (upper, sand)	-0.10	0.15	1	1.01	0.31	3	3.72	0.13	3	Spilmont et al. (2005)
Roscoff Aber bay C _E (upper, sand)	8.66	1.24	3	14.64	1.80	3	4.96	1.96	3	Migné et al. (2011)
Bay of Somme (mid, muddy sand)	10.17	0.98	3	3.58	2.77	3	1.75	3.94	2	Migné et al. (2004)
Bay of seine (mid, mud)	4.64	0.42	3	8.28	1.87	3	3.37	2.62	3	Spilmont et al. (2006)
Bay of Mt. St Michel Ca7m (mid, mud)	1.40	0.14	3	1.29	1.19	3	2.05	0.77	3	Davoult et al. (2009)
Bay of Morlaix (lower sand + <i>Z. noltei</i>)	6.75	1.04	3	5.23	3.62	3	5.94	4.09	3	Ouisse et al. (2010)

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