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Tidal controls on trace gas dynamics in a seagrass meadow of the Ria Formosa lagoon (southern Portugal)

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Abstract

Coastal zones are important source regions for a variety of trace gases including halocarbons and sulphur-bearing species. While salt-marshes, macroalgae and phytoplankton communities have been intensively studied, little is known about trace gas fluxes in seagrass meadows. Here we report results of a newly developed dynamic flux chamber system that can be deployed in intertidal areas over full tidal cycles allowing for high time resolved measurements. The trace gases measured in this study included carbon dioxide (CO₂), methane (CH₄) and a variety of hydrocarbons, halocarbons and sulphur-bearing compounds. The high time resolved CO₂ and CH₄ flux measurements revealed a complex dynamic mediated by tide and light. In contrast to most previous studies our data indicate significantly enhanced fluxes during tidal immersion relative to periods of air exposure. Short emission peaks occurred with onset of the feeder current at the sampling site.

We suggest an overall strong effect of advective transport processes to explain the elevated fluxes during tidal immersion. Many emission estimates from tidally influenced coastal areas still rely on measurements carried out during low tide only. Hence, our results may have significant implications for budgeting trace gases in coastal areas. This dynamic flux chamber system provides intensive time series data of community respiration (at night) and net community production (during the day) of shallow coastal systems.

1 Introduction

Coastal zones are hot spots for a variety of volatile organic compounds (VOC's) including halogenated compounds (Gschwend et al., 1985; Baker et al., 1999; Rhew et al., 2000; Christoph et al., 2002; Manley et al., 2006; Valtanen et al., 2009; Moore et al., 1995) and sulphur bearing compounds (Leck and Rhode, 1990; Dacey et al., 1987; Cooper et al., 1987a, b; De Mello et al., 1987; Baker et al., 1992; Turner

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et al., 1989), but a minor source for hydrocarbons such as CH₄ (Van der Nat and Middelburg, 2000; Middelburg et al., 2002). While coastal ecosystems, such as salt-marshes, macroalgae and phytoplankton communities have been intensively studied, little is known about trace gas fluxes from seagrass meadows. Seagrass meadows are amongst the most productive coastal ecosystems with an average net primary production of 817 g carbon m⁻² yr⁻¹ (Mateo et al., 2006). They cover a considerable portion of global coastal zones with estimates ranging from 300 000 km² (Duarte et al., 2005) to 600 000 km² Mateo et al. (2006). Most previous studies in seagrass meadows have focussed on carbon dynamics (e.g. Migné et al., 2004; Davoult et al., 2004; Spilmont et al., 2005; Silva et al., 2005; Hubas et al., 2006) and were often restricted to periods of air exposure. More recently, benthic chambers for underwater incubations were developed (Silva et al., 2008; Barron et al., 2006). There is some evidence that seagrass meadows (*Zostera spec.*) are capable to form a variety of trace gases (Urhahn, 2003; Weinberg et al., 2013). Furthermore, seagrass meadows may foster dimethyl sulfide (DMS) emissions (Jonkers et al., 2000; López and Duarte, 2004).

As other higher plants rooting in anoxic soils and sediments, seagrasses have an aerenchymatic tissue for supplying oxygen to their root system. This aerenchymatic tissue may also provide an effective transport pathway for trace gases from the sediment to the atmosphere. The importance of this transport pathway has been shown for CH₄ emissions from a variety of vegetation types (Laanbroek, 2010). However, early incubation experiments have indicated fairly low emission rates from *Thalassia testudinum* beds (Oremland et al., 1975). More recently Deborde et al. (2010) reported CH₄ fluxes from *Z. noltii* meadows in the Arcachon lagoon (SW France) being below 1.6 μmol m⁻² h⁻¹, which was the detection limit of the instrumentation used for the experiment.

So far, the fluxes of trace gases in coastal environments, mainly CH₄ and CO₂, have been measured in most cases using static chambers (e.g. Van der Nat and Middelburg, 2000; Delaune et al., 1983; Bartlett et al., 1987; Migné et al., 2002, 2004; Davoult et al., 2004; Spilmont et al., 2005; Silva et al., 2005; Hubas et al., 2006). There are several

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problems arising from chamber based flux measurements such as perturbations of the turbulent fields on both air and water side, introduction of artificial gradients, perturbations of the thermal environment and the gas composition inside the chamber. In particular solid static chambers will most likely introduce stagnant conditions and thus suppress advective exchange (Cook et al., 2007). For this study we used a dynamic chamber modified to enable flux measurements over full tidal cycles. During tidal immersion the chamber is continuously purged whereby the purging introduces an advective flow inside the chamber. Though artificial, this turbulent motion inside the chamber may to some extent mimic the turbulent flow outside the chamber. The system allows continuous CH_4 and CO_2 flux measurements with a time resolution of 10 min as well as the determination of VOC fluxes by discrete sampling. Here we provide a detailed description of the flux chamber system and first results of a field study conducted in a seagrass meadow of the Ria Formosa lagoon, southern Portugal. We report tidal-cycle fluxes of CO_2 , CH_4 , propane, butane, propene, chloromethane (CH_3Cl), bromomethane (CH_3Br), iodomethane (CH_3I), chloroform (CHCl_3), Bromoform (CHBr_3), carbondisulfide (CS_2), carbonylsulfide (COS), as well as dimethyl sulfide (DMS) and discuss them in terms of the factors controlling trace gas dynamics in intertidal seagrass meadows.

2 Methods

2.1 Flux chamber design

Dynamic flux chambers have been widely used in trace gas studies in terrestrial systems (Gao et al., 1997; Gao and Yates, 1998; Kim and Lindberg, 1995; Pape et al., 2009; Zhang et al., 2002). Details on the theory of dynamic flux chamber measurements are given in Gao et al. (1997) and Meixner et al. (1997). Briefly, the surface of interest is enclosed with a chamber and air is drawn through the chamber at a predefined flow rate. Net fluxes above the covered surface are commonly calculated from the

2.2 Sampling site

The sampling was conducted in an intertidal seagrass meadow of *Zostera noltii* (Hornem) of Ria Formosa lagoon, a mesotidal system located in southern Portugal. The lagoon has a surface area of 84 km² with about 80 % of it being intertidal. It is separated from the open ocean by a system of sand barrier islands. Six inlets allow exchanges of water with the Atlantic Ocean. The tidal amplitude ranges from 3.50 m on spring tides to 1.30 m on neap tides. In each tidal cycle about 50 % to 75 % of the water in the lagoon is renewed. Except during sporadic periods of heavy rainfall salinity ranges from 35.5 to 36.0 PSU throughout the year; water temperature varies between 12 and 27 °C in winter and summer, respectively.

Z. noltii is the most abundant seagrass species in the Ria Formosa, covering about 45 % of the intertidal area (Guimarães et al., 2012). The species plays a major role in the whole ecosystem metabolism of the lagoon (Santos et al., 2004). The range of *Z. noltii* biomass variation at the sampling site is 229–310 g DW m⁻² (Cabaço et al., 2008).

2.3 Sampling and measurement

The CO₂ and CH₄ flux measurements were performed between 23 April and 27 April 2012. VOC fluxes were measured between 17 April and 28 April 2012. Therefore, the time base of the VOC sampling does not fully overlap the time base of the CO₂ and CH₄ sampling. The sampled seagrass patches (*Z. noltii*) were free of visible epiphytes and macroalgae. The canopy coverage was estimated to be higher than 95 %.

CO₂ and CH₄ were measured on site with a Picarro 1301 cavity ring down spectrometer. A six port Valco valve was used to switch between three different sampling lines. The first sampling line was directly connected to the dynamic flux chamber and the two other sampling lines were used to sample ambient air from two different heights above the ground (2 m and 4 m). The sampling lines were consecutively sampled for 5 min and each line was connected to an additional membrane pump for continuously

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more pronounced emission fluxes generally occurring during tidal inundation. At daytime, CO₂ assimilation dominated over benthic respiration resulting in a net uptake, regardless of the tidal state. Elevated fluxes during tidal immersion were also observed for all non-CH₄ VOC's studied here.

3.1 Methane

During air exposure at low tide CH₄ fluxes averaged 4.4 μmol m⁻² h⁻¹ at night and 6.9 μmol m⁻² h⁻¹ at day. With the flood current just arriving at the sampling site the fluxes dropped almost to zero for 5 to 10 min. A sharp emission peak was observed for 15 min followed this drop. Accounting for the integration time and the response time of the chamber system we deduce that these events may have actually lasted for 2 to 5 min. During these peak events the fluxes averaged 71 μmol m⁻² h⁻¹. The peaks were more pronounced during the night (76 and 123 μmol m⁻² h⁻¹) than during daytime (38 and 51 μmol m⁻² h⁻¹). After the peak events, the fluxes rapidly decreased to values below 9 ± 1 μmol m⁻² h⁻¹.

During tidal immersion the CH₄ fluxes increased with rising height of the water and showed a second maximum of 30 ± 1 μmol m⁻² h⁻¹ at high tide. With the ebb flow the CH₄ fluxes decreased constantly to values about 9 ± 1 μmol m⁻² h⁻¹ at water levels below 10 cm. The change from tidal immersion to air exposure was marked by slightly elevated fluxes observed for about 15 min followed by a drop close to zero before the flux stabilized on the low tide level again.

The circadian flux cycles observed above the sediment (Fig. 3) were similar to the diurnal cycles above the seagrass but, with much lower values (Table 1 and Fig. 2). The CH₄ fluxes averaged 0.3 μmol m⁻² h⁻¹ during low tide, and 6 μmol m⁻² h⁻¹ (5.2 μmol m⁻² h⁻¹ at daytime and 6.6 μmol m⁻² h⁻¹ at night time) during tidal inundation.

3.2 CO₂

In contrast to CH₄, the CO₂ flux was strongly influenced by both, the time of day and the tidal cycle. Deposition fluxes were observed during the day resulting from photosynthetic carbon uptake while positive fluxes were observed during the night due to respiratory release of CO₂. During air exposure at night, the emissions were relatively constant and averaged $8.4 \pm 0.5 \text{ mmol m}^{-2} \text{ h}^{-1}$. As observed for CH₄, the flux dropped to zero for about 10 min with the incoming tide and then rapidly increased to highest CO₂ emissions of up to $62 \text{ mmol m}^{-2} \text{ h}^{-1}$. Thereafter, the CO₂ flux decreased rapidly to $38 \pm 4 \text{ mmol m}^{-2} \text{ h}^{-1}$ and then further declined slowly over the period of tidal inundation. After sunrise, roughly coinciding with high tide during our measurements, the CO₂ fluxes declined more rapidly due to the beginning of photosynthetic CO₂ assimilation. During the daylight period, CO₂ assimilation dominated over benthic CO₂ respiration resulting in a net uptake of CO₂ with average fluxes of $-9.1 \text{ mmol m}^{-2} \text{ h}^{-1}$ during air exposure and of $-16.4 \text{ mmol m}^{-2} \text{ h}^{-1}$ during immersion.

At night, the average sedimentary CO₂ fluxes were $1.0 \text{ mmol m}^{-2} \text{ h}^{-1}$ during air exposure and $6.4 \text{ mmol m}^{-2} \text{ h}^{-1}$ during tidal inundation. The CO₂ night time flux during inundation decreased until high tide and increased again with the onset of ebb flow indicating an inverse relation with the height of the water table. The daytime average CO₂ fluxes from sediment were $-1 \text{ mmol m}^{-2} \text{ h}^{-1}$ during low tide and $-2 \text{ mmol m}^{-2} \text{ h}^{-1}$ during tidal inundation.

3.3 VOC's

Relative fluxes of COS, CS₂, DMS, CH₃Cl, CH₃Br, CH₃I, CHCl₃, CHBr₃, propane, butane and propene are shown in Fig. 4. For those, which have been quantified against the Scott TOC 15/17 standard, mean fluxes and ranges are provided in Table 2. It has to be noted that for most of the VOC flux data the sampling time does not coincide with the sampling time for the CO₂ and CH₄ data shown above. As observed for CO₂

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and CH₄, the emission rates during tidal immersion significantly exceeded those measured during air exposure. The average enhancement during tidal immersion ranged from 4–12 for CS₂, COS and propane and the halocarbons CH₃Br, CH₃I, CHCl₃ and CHBr₃. A higher enhancement was observed for CH₃Cl. A less pronounced enhancement ranging from 1 to 3 was observed for DMS, propene and butane. Among the analysed VOC's, only CH₃Cl fluxes increase similarly drastically as the CH₄ with the feeder current arriving at the sampling site. In this context it is important to note that the sampling time for the VOC's was 30 min followed by a break of 15 min required to change the cryo traps. Hence, it is possible that peak flux, lasting 3 to 5 min for CH₄, is missed or not fully captured by our VOC sampling protocol. For propane, CHBr₃, and butane our data also show a small enhancement when the water just starts receding from the sampling site.

The temporal flux patterns show some remarkable differences between individual VOCs during tidal immersion. Strongly enhanced fluxes during high tide were observed for propane, COS and CS₂, showing a similar pattern as for CH₄. The fluxes of the other monitored compounds decreased or even turned from emission to uptake during high and thus acted more similar as CO₂.

4 Discussion

4.1 Temporal flux patterns

The most striking feature of our results is the pronounced effect of the tidal cycle on the fluxes of all trace gases, which were significantly enhanced during immersion compared to air exposure periods. Additionally, strong emission peaks of CH₄, among other VOCs, and particularly of CO₂ occurred during a short transition period from air exposure to immersion.

We are aware of only one study reporting a positive correlation of CO₂ and CH₄ fluxes with the height of the water table from a brackish coastal lagoon in Japan (Ya-

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mamoto et al., 2009). The authors of this study did not come up with a conclusive explanation for this observation but suggested either lateral transport in the sediment in combination with salinity gradients affecting the source strength and/or enhanced gas ebullition due to increased pressure from the water column. In the case of the Ria Formosa lagoon, there is a negligible inflow of freshwater and thus significant salinity driven lateral changes in methanogenesis and benthic respiration are implausible. Spatial variations in the source strength that might occur due to variations in the benthic communities and in the supply of substrate by litter production and root exudates are also not plausible as the benthic vegetation around the sampling site consisted almost exclusively of *Z. noltii* and was quite homogeneous. Variations in the above ground biomass were clearly below a factor of 2 and thus do not support a change in the source strength by a factor of 6 as observed for CH₄ during tidal immersion. On the other hand, a negative relation between bubble ebullition and water pressure has been reported in other studies (Baird et al., 2004; Glaser et al., 2004), including the only study we are aware of that was carried out in a tidally influenced system (Chanton et al., 1989).

Most previous studies on trace gas fluxes in tidally influenced systems have reported higher fluxes during low tide than during high tide. These higher emissions during low tide were attributed to reduced gas diffusion during inundation (Heyer and Berger, 2000; Van der Nat and Middelburg, 2000) or to deep pore water circulation in tidal flats. Since the pioneering work of Riedl et al. (1972) there is rising evidence that advective exchange processes at the sediment-water interface strongly affect the fluxes and concentrations of trace constituents. Billerbeck et al. (2006) proposed two different pathways for pore water circulation in intertidal sediments. The first pathway, called “body circulation”, is generated by the hydraulic gradient between sea water and pore water levels in the sediment, and leads to seepage of pore water close to the low water line at low tide. Several studies have attributed elevated levels of $p\text{CO}_2$ (Barnes et al., 2006; De La Paz et al., 2008) and $p\text{CH}_4$ (Grunwald et al., 2009; Deborde et al., 2010) during low tide to this kind of deep pore water advection.

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The second pathway, called “Skin circulation” (Billerbeck et al., 2006), refers to the advective exchange in surface sediments and is driven by bottom current induced pressure gradients at the sediment surface. Several studies have shown a prominent effect of advective transport processes on the exchange of organic matter and nutrients in tidal sand flats (Werner et al., 2006; Billerbeck et al., 2006; Huettel et al., 1996; Precht et al., 2004). Werner et al. (2006) found a more intense and deeper transport of oxygen into the sediment due to advective exchange during tidal immersion than during air exposure, when the exchange is presumably driven by gas diffusion. This is also supported by a study of Kim and Kim (2007), who reported total oxygen fluxes exceeding diffusive fluxes by a factor of 2 to 3 for intertidal sediments from Taean Bay located in the Midwestern part of the Korean peninsula. Cook et al. (2007) reported a concurrent increase of total oxygen and TIC fluxes at the sediment surface by a factor of up to 2.5 under turbulent conditions relative to stagnant (diffusive) conditions. During measurements carried out in the back barrier area of the island of Spiekeroog (Billerbeck et al., 2006; Jansen et al., 2009), the highest oxygen penetration rates were observed immediately after high tide.

The CH₄ fluxes observed in the Ria Formosa lagoon provide a mirror image of these oxygen dynamics, in accordance with Yamamoto et al. (2009), who noted a concurrent increase of the redox potential of the sediment with increasing CH₄ and CO₂ fluxes during tidal inundation. Given this, we deduce an overall strong effect of advective solute transport at the sediment water interface on trace gas fluxes to explain the elevated fluxes during tidal immersion. Both, the observed similarities between the flux patterns among all trace gases and the relatively constant CO₂/CH₄ ratios observed at night time, when photosynthesis was not confounding flux patterns, suggest physical forcing as the major driver of trace gas fluxes rather than the biogeochemical processes controlling their formation.

It is commonly thought that the fluxes during air exposure are most likely driven by gas evasion across the sediment-air and plant-air interface, respectively, and are hence controlled by the transfer resistance across these interfaces (Yamamoto et al.,

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2009 and references therein). However, this model cannot explain the observed drop to zero of CO₂ and CH₄ fluxes for about 15 min when the incoming tide reached the sampling site. In waterlogged sediments trace gases have to be transported to the sites of gas diffusion, such as to a water gas interface or to the root systems of higher plants.

5 Werner et al. (2006) observed a constant flow velocity of pore water over the entire period of air exposure and noted a decreasing flow velocity in the top 2 cm shortly before the flood current reached the sampling site and flow direction reversed. This decrease may explain the observed drop in the emission fluxes.

The drop in the fluxes was followed by a dramatic peak in both, CO₂ and methane emissions, when floodwater reached the chamber. Thereafter, CH₄ fluxes dropped to increase again with tidal height whereas the respiratory CO₂ night flux showed a gradual decline. Similar flux peaks at incoming floodwater have been previously reported for biogenic sulphur compounds (Aneja et al., 1986; Cooper et al., 1987a, b) and ammonia (Falcão and Vale, 2003), being attributed to increased hydrodynamic pressure. In contrast to these observations, we did not observe a pronounced peak for any of the VOC's other than CH₄. However, it is possible that the peak events were not captured due to our discrete VOC sampling method.

We speculate that the peaks are caused by the sudden release of the air trapped in the sediment pore space that becomes enriched in CH₄ and CO₂ during air exposure. The release of trapped air from the sediment may be fostered by the aforementioned reversal of flow direction in tidal surface sediments reported by Werner et al. (2006). Such an emission mechanism is further supported by the fact that a similar drop in the CH₄ emission is also observed for the change from tidal immersion to air exposure, but not followed by an emission peak, which is simply due to the lack of air bubbles in the sediment at this stage of the tidal cycle. Furthermore, the higher fluxes during tidal inundation may impede the enrichment of trace gases in the surface sediment. The short and sharp emission peak for CH₄ suggests that the CH₄ has been accumulated close to the sediment surface or close to the roots of the seagrass from where it can be readily transferred into the atmosphere. In agreement with this, our data clearly show

higher CH₄ emission peaks during night time than daytime, when sediment oxygenation resulting from photosynthesis favours CH₄ oxidation.

During night time, the respiratory CO₂ flux and the CH₄ flux show a fairly constant ratio during air exposure but evolve differently during tidal immersion. In contrast to the gradual decline of CO₂ after the peak at incoming tide, CH₄ dropped sharply after this peak to increase again with tidal height. Methane originating from deeper sediment layers has a fairly low water solubility and thus becomes strongly enriched in the entrapped gas. Hence, the transition from a bubble ebullition driven emission as suggested for the “methane peak” to an advective transport of pore water as suggested for the period of tidal immersion results in a sharp decrease of the methane flux. The following increase in CH₄ may reflect the increasing penetration depth of the advective flow with the rising water table. CO₂ is always close to equilibrium with the much larger pore water DIC pool. After the transition from bubble ebullition to advective transport the CO₂ flux is driven by the exchange of enriched pore water DIC and the observed gradual decline in the CO₂ flux reflects the dilution of the pore water with the overlying seawater.

While the seagrass incubations showed a continuous decline of the CO₂ flux during tidal immersion, the incubations at the non-vegetated sediment showed a partial recovery of the CO₂ flux after high tide and thus an inverse correlation with the height of the water table. As outlined before, this difference may result from the onset of photosynthetic CO₂ assimilation at the end of the tidal cycle at sunrise, which had a more pronounced impact within the seagrass incubations.

4.2 Magnitude of methane fluxes

CH₄ emissions of *Z. noltii* community averaged 0.31 mol m⁻² d⁻¹ with ~76% being released during tidal immersion. They are about 4 fold higher than CH₄ fluxes from the non-vegetated sediment community (0.07 mmol m⁻² d⁻¹ with ~93% being released during tidal immersion).

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Bartlett et al. (1987) and Delaune et al. (1983) reported decreasing CH_4 fluxes with increasing salinity. CH_4 fluxes decreased from 17 to $34.2 \text{ mmol m}^{-2} \text{ d}^{-1}$ at salinities around 1 PSU to 0.17 to $0.85 \text{ mmol m}^{-2} \text{ d}^{-1}$ at salinities above 18 PSU. Hence a direct comparison of these values with our data is difficult due to the differences in salinity. However, our CH_4 fluxes from the unvegetated sediment agree well with those reported by Deborde et al. (2010) for the Arcachon lagoon, which were generally below the detection limit ($0.04 \text{ mmol m}^{-2} \text{ d}^{-1}$) during air exposure and ranged from below the detection limit to $0.24 \text{ mmol m}^{-2} \text{ d}^{-1}$. Middelburg et al. (2002) have estimated the average CH_4 flux from European estuarine waters to be $0.13 \text{ mmol m}^{-2} \text{ d}^{-1}$, which is about twice the fluxes of the non-vegetated sediments of the Ria Formosa lagoon. Hence our data suggest that apart from body circulation (Jansen et al., 2009; Grunwald et al., 2009) skin circulation may substantially contribute to CH_4 fluxes in tidal flats.

Somehow in contrast to Deborde et al. (2010), who reported substantially lower CH_4 production rates for sites covered by *Z. noltii* as compared to unvegetated sites in the Arcachon lagoon with the CH_4 production rates at the *Z. noltii* sites being mostly below the detection limits of their method, we observed 4 times higher fluxes above the seagrass site as above the bare sediment.

Anyhow, a tentative upscaling using our flux data and a global seagrass coverage area of $300\,000 \text{ km}^2$ (Duarte et al., 2005) reveals a global CH_4 flux of $\sim 0.5 \text{ Tg CH}_4 \text{ yr}^{-1}$ from seagrass meadows. The world's ocean including the productive coastal ecosystems are a minor source for atmospheric CH_4 contributing about 10% to the global emissions (Wuebbles and Hayhoe, 2002). Emissions including productive coastal areas have been estimated to be in the range of 11 to 18 Tg yr^{-1} (Bange et al., 1994). Hence we suppose seagrass meadows being a minor global source of CH_4 .

4.3 Magnitude of CO_2 fluxes

During our experiment, the overall net community production of *Z. noltii* (NCP) was $101 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and that of unvegetated sediments was $50 \text{ mmol C m}^{-2} \text{ d}^{-1}$, show-

ing that heterotrophic metabolism was dominating in the intertidal of Ria Formosa lagoon. Santos et al. (2004) found that in July 2002, the intertidal was marginally autotrophic as the *Z. noltii* NCP was $-5.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and the unvegetated sediment NCP was $-21.2 \text{ mmol C m}^{-2} \text{ d}^{-1}$.

To the best of our knowledge, we present here the first assessment of how the respiration of a seagrass community varies over night along with the tidal cycle. In order to estimate the daily metabolic budgets of seagrass communities, authors have considered that community respiration does not vary during the night, using only one point estimate, or measure it during the day using dark chambers and assume that daytime respiration rates can be applied over a 24 h period (Duarte et al., 2010). Our data show that this practice may seriously affect the estimation of the metabolic daily budgets of seagrass communities, particularly in the intertidal. The average net CO_2 emissions (community respiration, CR) of *Z. noltii* during night were $10.2 \text{ mmol m}^{-2} \text{ h}^{-1}$ (air exposure), $23.2 \text{ mmol m}^{-2} \text{ h}^{-1}$ (tidal immersion) and $55.0 \text{ mmol m}^{-2} \text{ h}^{-1}$ (peak event) (Table 1). With an average daylight period of 12 h and an average period of tidal inundation of 15.30 h d^{-1} , the community respiration is estimated to 233 mmol m^{-2} during night time.

The respiratory CO_2 production peaks during incoming flood tide are immediately recycled, i.e assimilated by the seagrass community, during the day. The observed accelerated decreases in the CO_2 flux coinciding with sunrise and the much lower CO_2 peaks observed during the day at the transition from air exposure to inundation provide evidence for this. Over the course of the experiment a net CO_2 assimilation occurred roughly between 9.00 a.m. and 6.00 p.m. with average assimilation rates of $9.1 \text{ mmol m}^{-2} \text{ h}^{-1}$ during air exposure and $16.4 \text{ mmol m}^{-2} \text{ h}^{-1}$ during immersion summing up to a net CO_2 assimilation of $125 \text{ mmol m}^{-2} \text{ d}^{-1}$. The NCP of *Z. noltii* during air exposure estimated here compares well to the previous reported rates ranging from 10 to $15 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Silva et al., 2005), whereas NCP during tidal immersion significantly exceeds previously reported rates of less than $5 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Santos et al., 2004; Silva et al., 2005, 2008). These earlier studies used static chambers prone to

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introduce stagnant condition. In contrast, the bubbling in our chamber introduces turbulent mixing and hence may facilitate the transport of CO₂ across the water leaf interface. In conclusion, these differences can be mainly attributed to the introduction of advection in our chamber system. In this context it should be noted that, as already outlined in Silva et al. (2005), the available data on the aerial vs. submerged photosynthesis of *Z. noltii* are not consistent. While Leuschner and Rees (1993) and Leuschner et al. (1998) measured comparable rates of CO₂ assimilation in air and water, Perez-Llorens and Niell (1994) found CO₂ uptake rates in air 10 to 20 times lower than in water. As the strength of advection in our chamber system relative to ambient conditions is unknown we can currently not appraise the quality and reliability of the difference chamber systems. However these differences highlight the importance of accurately addressing the perturbations of turbulent flows in benthic flux chambers.

4.4 VOC's

The overall focus of this section is the temporal evolution of the VOC fluxes over a tidal cycle. A quantitative discussion of the VOC data and an assessment of potential intrinsic sources are beyond the scope of this paper. For the halocarbons this will be done elsewhere (Weinberg et al., 2014). COS, CS₂, and propane having a known sedimentary source (Claypool and Kvenvolden, 1983; Bodenbender et al., 1999) show a similar temporal pattern as CH₄ during high tide. Thus, we conclude that the emission of these compounds is in analogy to CH₄ mainly controlled by advective transport across the sediment water interface.

Halocarbon production in the marine environment is generally attributed to photoautotrophic sources (Gschwend et al., 1985; Manley et al., 2006; Moore et al., 1995) though there is some evidence of a sedimentary bacterial source for iodomethane (Amachi et al., 2001). In the seagrass meadows halocarbons are presumably produced by the seagrass or by the microphytobenthos. Only in the latter case porewater flow across the sedimentary interface can directly affect the emission. However, the elevated halocarbon fluxes during tidal immersion may reflect an enhanced transport

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accurately addressing the perturbations of turbulent flows in flux chamber studies. If the observed flux enhancements are more than just episodic events this may have fundamental implications for our understanding of the carbon and trace gas cycling in coastal environments.

5 *Acknowledgements.* The authors thank the German Federal Ministry of Education and Research (BMBF) for funding (grants 03F0611E and 03F0662E). This work was partly supported by the EU FP7 Assemble research infrastructure initiative and the project “Whole-system metabolism and CO₂ fluxes in a coastal lagoon dominated by saltmarsh and seagrass meadows”, PTDC/AAC-CLI/103348/2008. João Reis, and Bruno Fragoso (CCMAR, Universidade do
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Table 1. Averaged CO₂ and CH₄ fluxes above seagrass for different periods of the tidal cycle. The fluxes were calculated from the measurements of day 2 and 3. By definition emission fluxes are positive and deposition fluxes are negative.

tidal stage	CO ₂ (mmol m ⁻² h ⁻¹)		CH ₄ (μmol m ⁻² h ⁻¹)	
	sediment	seagrass	sediment	seegrass
air exposure (day)	-1.1	-9.1	0.4	6.9
air exposure (night)	1.0	8.4	0.2	4.4
tidal inundation (day)	-2.0	-16.4	6.6	14.3
tidal inundation (night)	6.4	20.1	5.2	16.6
peak (water just arriving)	14.8	55.0	10.8	71.0
mean (time averaged)	2.1	4.2	3.0	12.8

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Table 2. Mean trace gas fluxes (bold) obtained from seagrass meadows along the tidal cycle. Fluxes are given in $\text{nmol m}^{-2} \text{h}^{-1}$. Numbers in parenthesis are the range of fluxes. Fluxes during high tide are given as single values. Further details on CH_3Cl , CH_3Br , CH_3I , and CHBr_3 are given in Weinberg et al. (2014). By definition emission fluxes are positive and deposition fluxes are negative.

Compound	low tide ($n = 17$) ($\text{nmol m}^{-2} \text{h}^{-1}$)	CH_4 peak ($n = 5$) ($\text{nmol m}^{-2} \text{h}^{-1}$)	feeder current ($n = 6$) ($\text{nmol m}^{-2} \text{h}^{-1}$)	high tide ($n = 2$) ($\text{nmol m}^{-2} \text{h}^{-1}$)	ebb flow ($n = 5$) ($\text{nmol m}^{-2} \text{h}^{-1}$)
Halocarbons					
CH_3Cl	1.0 (-29.6–69.0)	40.1 (-14.2–99.7)	11.4 (-14.7–36.6)	-18.1, -58.3	21.3 (-13.5–46.2)
CH_3Br	0.4 (-0.8–3.9)	2.7 (0.1–8.3)	1.8 (0.2–3.3)	-0.5, -1.6	2.1 (0.1–4.4)
CH_3I	0.6 (-0.6–2.6)	3.3 (0.1–8.0)	1.6 (0.1–2.9)	0.1, 0.1	1.5 (0.2–3.0)
CHCl_3	0.3 (-0.8–2.8)	2.4 (0.1–6.6)	2.0 (0.5–3.0)	-0.1, -2.0	2.0 (-0.6–3.7)
CHBr_3	0.4 (-0.5–1.3)	2.9 (0.2–10.6)	2.8 (0.2–5.1)	0.5, -0.1	4.5 (-0.4–8.6)
S-Compounds					
CS_2	52 (-34–192)	216 (22–544)	135 (-5.5–200.0)	420, 398	129 (-13.4–230)
COS^1	–	3.8 (0.1–7.1)	2.1 (0.3–5.1)	22, 21	4.5 (1.0–10.5)
DMS^1	–	2 (0.1–3.0)	1.5 (0.7–1.9)	0.2, 0.2	1.3 (0.1–3.2)
Hydrocarbons					
propene	56 (-26–377)	167 (91–331)	91 (-5.1–170)	33, 27	182 (3.4–407)
propane ¹	–	6.0 (-0.2–14)	3.6 (-2.7–7.8)	48, 44	16.6 (5.7–37)
butane ¹	–	0.9 (-0.5–3.4)	1.5 (-0.2–2.8)	3.5, 2.3	5.7 (2.6–12)

¹ Fluxes are expressed as relative enhancement to the average flux during low tide experiments.

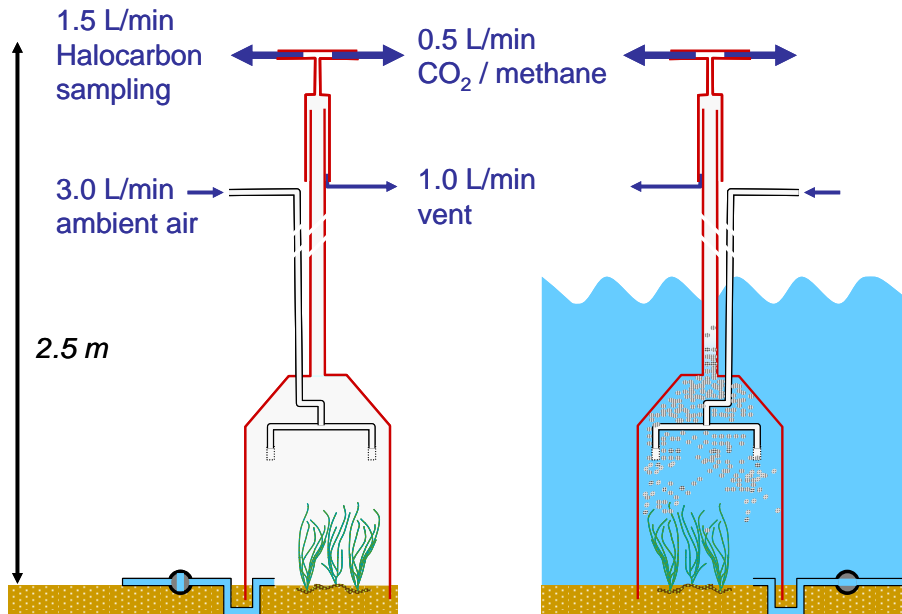


Figure 1. Scheme of the dynamic flux chamber system. During air exposure the chamber acts as a conventional dynamic flux chamber. During tidal immersion the enclosed water is continuously purged with ambient air.

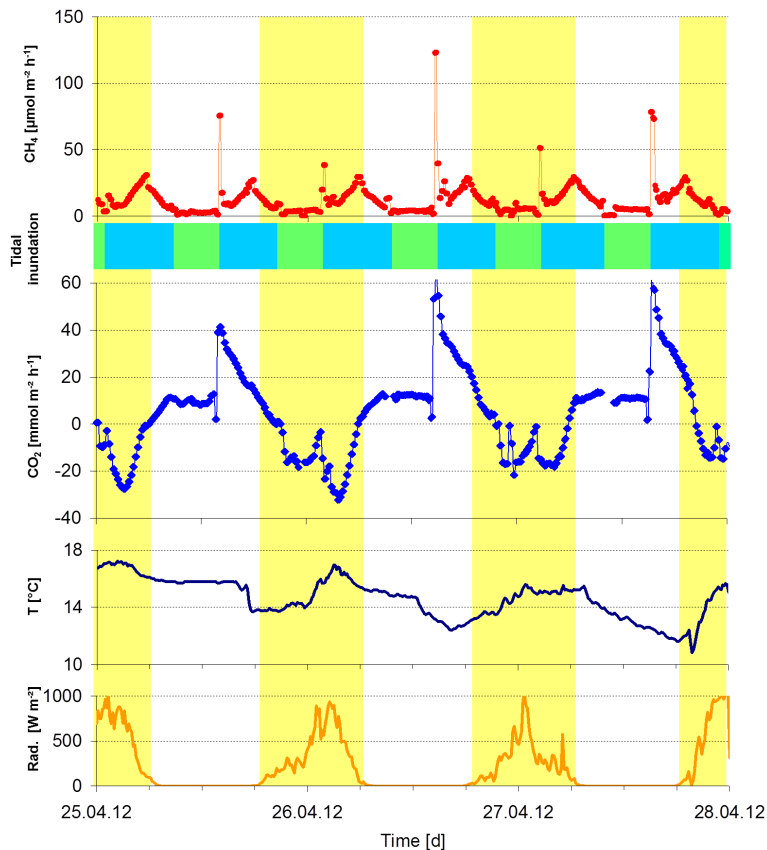


Figure 2. Circadian variations of the CH_4 and CO_2 fluxes above a meadow of the seagrass *Z. noltii*. Air temperature and light intensity are also shown. The measurements were carried out from 25 to 28 April 2012. Yellow bars indicate daylight periods, green bars indicate periods of air exposure, blue bars indicate periods of tidal immersion.

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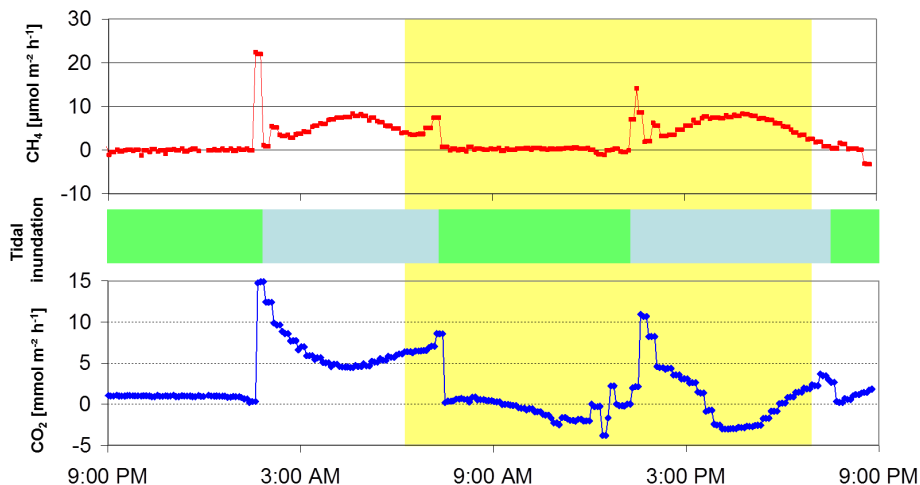


Figure 3. CH₄ and CO₂ fluxes above a bare sediment patch recorded on 23 April 2012. The upper graph in red shows the CH₄ fluxes in $\mu\text{mol m}^{-2} \text{h}^{-1}$ and the lower graph show the CO₂ fluxes in $\text{mmol m}^{-2} \text{h}^{-1}$. Yellow bars indicate daylight periods, green bars indicate periods of air exposure and blue bars indicate periods of tidal immersion respectively.

Tidal controls on trace gas dynamics in a seagrass meadow of the Ria Formosa lagoon

E. Bahlmann et al.

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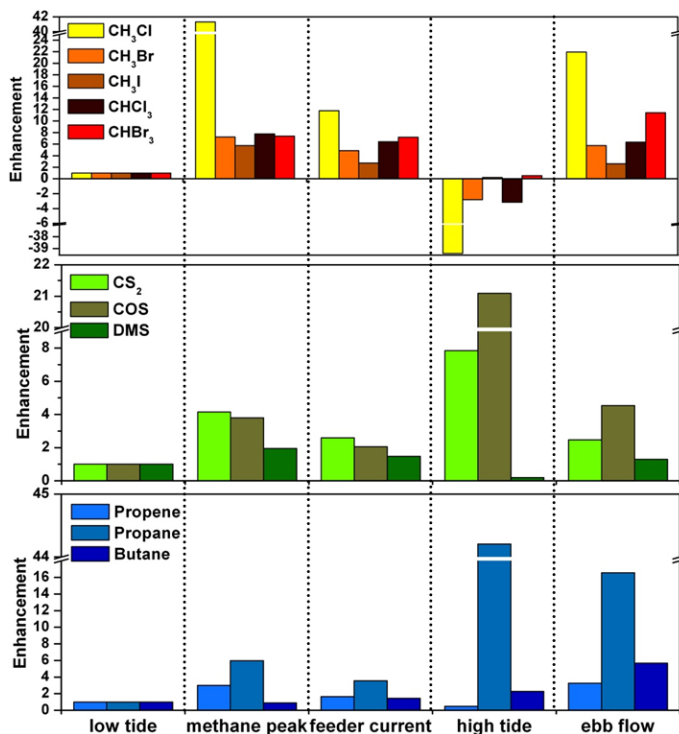


Figure 4. Relative enhancement of selected VOC fluxes from a tidally influenced seagrass bed. All fluxes were normalized to the respective mean fluxes during low tide. CS₂, CH₃Cl, CH₃Br, CH₃I, CHCl₃, CHBr₃, and propene were quantified against a Scott TOC 15/17 standard. Relative fluxes for COS, propane, butane and DMS were calculated from the measured intensities. For clarity the variability of the VOC fluxes is not shown. Mean and ranges are provided in Table 2.