Regional Studies in Marine Science
March 2021, Volume 43, Pages 101668 (12p.)
https://doi.org/10.1016/j.rsma.2021.101668
https://archimer.ifremer.fr/doc/00679/79087/

Comparison of benthic oxygen exchange measured by aquatic Eddy Covariance and Benthic Chambers in two contrasting coastal biotopes (Bay of Brest, France)

Polsenaere Pierre [1, 2, 3, *], Deflandre Bruno [1, 2], Thouzeau Gerard [4], Rigaud Sylvain [1, 2, 5], Cox Tom [6], Amice Erwan [4], Bec Thierry Le [4], Bihannic Isabelle [7], Maire Olivier [1, 2]

[1] Université de Bordeaux, EPOC, UMR 5805, F-33400 Talence, France
[2] CNRS, EPOC, UMR 5805, F-33400 Talence, France
[3] IFREMER, Laboratoire Environnement et Ressources des Pertuis Charentais (LER-PC), BP133, 17390, La Tremblade, France
[4] LEMAR, UMR 6539 CNRS/UBO/Ifremer/IRD, Technopôle Brest-Iroise, Rue Dumont d'Urville, 29280 Plouzané, France
[5] Université de Nîmes, EA 7352 CHROME, Laboratoire de Géochimie Isotopique Environnementale (GIS), 30035 NIMES Cedex 1, France
[6] Royal Netherlands Institute for Sea Research (NIOZ), Ecosystem Studies Department, Korringaweg 7, 4401 NT Yerseke, The Netherlands
[7] LEMAR, UMR 6539 CNRS/UBO/Ifremer/IRD, Technopôle Brest-Iroise, Rue Dumont d'Urville, 29280 Plouzané, France

* Corresponding author : Pierre Polsenaere, email address : Pierre.Polsenaere@Ifremer.fr

Abstract :

To the best of our knowledge, the understanding of benthic metabolism of coastal sedimentary areas is still limited due to the complexity of determining their true in situ dynamics over large spatial and temporal scales. Multidisciplinary methodological approaches are then necessary to increase our comprehension of factors controlling benthic processes and fluxes. An aquatic Eddy Covariance (EC) system and Benthic Chambers (BC) were simultaneously deployed during the winter of 2013 in the Bay of Brest within a Maerl bed and a bare mudflat to quantify and compare exchange at the sediment-water interface. Environmental abiotic parameters (i.e., light, temperature, salinity, current velocity and water depth) were additionally monitored to better understand the mechanisms driving benthic exchange. At both sites, EC measurements showed short-term variations (i.e. 15 min) in benthic fluxes according to environmental conditions. At the Maerl station, EC fluxes ranged from -21.0 mmol m−2 d−1 to 71.3 mmol m−2 d−1 and averaged 22.0 ± 32.7 mmol m−2 d−1 (mean SD), whilst at the bare muddy station, EC fluxes ranged from -43.1 mmol m−2 d−1 to 12.1 mmol m−2 d−1 and averaged -15.9 ± 14.0 mmol m−2 d−1 (mean SD) during the total deployment. Eddy Covariance and Benthic Chambers measurements showed similar patterns of temporal flux changes at both sites. However, at the Maerl station, BC may have underestimated community respiration. This may be due to the relative large size of the EC footprint (compared to BC), which takes into account the mesoscale spatial heterogeneity (e.g. may have included contributions from bare sediment patches). Also, we hypothesize that the influence of bioturbation induced by large-sized mobile benthic fauna on sediment oxygen consumption was not fully captured by BC compared to EC. Overall, the results of the present study highlight the importance of taking into account specific

methodology limitations with respect to sediment spatial macro-heterogeneity and short-term variations of environmental parameters to accurately assess benthic exchange in the various benthic ecosystems of the coastal zone.

Highlights

► Benthic O_2 exchange was monitored in a temperate bay in winter. ► The aquatic Eddy Covariance and benthic chambers were deployed over two stations. ► Maerl beds and muddy sediments generally released and consumed O_2. ► Techniques showed similar patterns of temporal O_2 flux changes at both sites. ► Benthic chambers may have underestimated Maerl community respiration.

Keywords : benthic O2 fluxes, aquatic Eddy Covariance, benthic chambers, Maerl bed, bare mudflat, Bay of Brest

1. Introduction

Coastal soft-bottom substrates represent active sites of biogeochemical cycling where benthic communities of microbes and fauna deeply influence the fate (i.e. recycling, burial, resuspension) of sedimented organic matter (Middelburg et al. 2004). Shallow marine sediments can also support intense autotrophic production, thus controlling the metabolic status (i.e. source or sink of carbon) of coastal marine systems (Jahnke et al. 2000). The sediment oxygen consumption, assessed through the measurement of the total O_2 influx across the sediment-water interface, provides an overall estimate of the total carbon turnover rate (Glud 2008). In permeable sediments, physical processes, such as advective porewater transport driven by current and wave actions strongly influence benthic O_2 exchange (Berg et al. 2003, Reimers et al. 2012, Huettel et al. 2013, Berg et al. 2013). Conversely, in cohesive sediments inhabited by diverse macrofaunal communities, benthic O_2 fluxes are predominantly controlled by the biological mixing of the surficial sediment layer (i.e. bioturbation), which encompasses both sediment reworking (i.e. particle transport) and bio-irrigation (i.e. enhanced exchange of porewater and dissolved solutes across the sediment-water interface) processes (Kristensen at al. 2012). However, the influence of bioturbation activities on sedimentary biogeochemical processes is particularly difficult to accurately assess at the scale of the whole habitat. Indeed, key processes (biological activities vs. chemical redox reactions) typically occur at different spatial and temporal scales, which cannot be simultaneously fully captured using classical methodologies. For instance, total benthic O_2 exchange is typically quantified using incubation techniques either *in situ* or in sediment cores incubated at the laboratory (McGlathery et al. 2001, Berg et al. 2003, Martin et al. 2005, Huettel et al. 2007, Thouzeau et al. 2007, Khalil et al. 2013). Although fundamental insights into the role of benthic fauna on biogeochemical processes have been gained using both methodologies, benthic chambers (BC) have significant limitations. Firstly, they most often consider small (or very small) sediment areas (i.e. a few tenths of m^2 in the very best case) whereas large-sized bioturbating macrofauna often exhibits relatively low densities and patchy distributions over much larger spatial scales. Moreover, the time required to deploy BC or a sediment corer onto the seafloor, without disturbing the sediment-water interface, does not allow for capturing the impact on solute exchanges of highly mobile (e.g. flat fishes) or deep burrowing (e.g. thalassinid crustaceans) species, which can easily escape from experimental enclosures before measurements are made. Yet, it is acknowledged that *in situ* BC may significantly affect active transport processes and associated natural

hydrodynamic forcing at the sediment-water interface (Berg and Huettel 2008). Light penetration can also be substantially reduced in BC compared to natural *in situ* conditions (Tengberg et al. 2004).

The aquatic Eddy Covariance (EC) technique, developed by Berg et al. (2003), is expected to solve such limitations. It allows the measurement of benthic O_2 exchange in a continuous fashion and without being intrusive or disturbing the flow field over the sediment (Berg et Huettel 2008). Furthermore, the sediment surface that contributes to the measured fluxes is very large (10 to 100 m^2, Berg et al. 2007) in comparison to traditional incubation techniques. Eddy Covariance measurements thus allow for taking into account the bioturbation activities and the respiration of large mobile benthic fauna and overall to integrate the strong spatial heterogeneity of complex coastal benthic systems. To date, this new alternative technique was used to assess benthic metabolisms of various aquatic soft-bottom habitats, i.e. from lakes (Brand et al. 2008, McGinnis et al. 2008, Lorrai et al. 2010), sandy-bottom river and sea sediments (Berg et al. 2003, Chipman et al. 2012, Berg et al. 2013, Koopmans and Berg 2015, Rovelli et al. 2017, Attard et al. 2019), vegetated and muddy lagoon sediments (Berg et al. 2003, Hume et al. 2011, Rheuban et al. 2014), vegetated and shallow sandy sea sediments (Attard et al. 2019), sandy intertidal bays (Kuwae et al. 2006, Berg et al. 2013), continental shelf (Reimers et al. 2012) to deeper oceanic realms (Berg et al. 2009, Donis et al. 2016, Attard et al. 2019). The use of the EC technique is particularly suitable over hard-bottom substrates such as coral reefs (Long et al. 2013, Rovelli et al. 2015), Maerl beds (Attard et al. 2015), macroalgal and mussel reefs (Attard et al. 2019) and rocky embayments (Glud et al. 2010). In these latter rocky systems, incubation methods, which require a perfect sealing between the chamber walls and the substratum, can be hardly deployed.

Maerl beds (i.e. unattached calcareous red algae communities developing at the surface of shallow coastal sediments) are unique and complex habitats, somehow intermediate between hard- and soft-bottom substrates. Accordingly, they host highly diverse biocenoses with abundant autotrophic and heterotrophic organisms living within either the lattice of algae thalli or the underlying sediment (Grall 2002, Barbera et al. 2003, Grall et al. 2006). Maerl beds are considered among the most diversified and productive benthic ecosystems in the world. However only few studies based on *in situ* incubation measurements, investigated their biogeochemical functioning (Martin et al. 2005, 2007). Attard et al. (2015) have investigated the biogeochemical functioning of a live Maerl bed community using an EC system, thus

showing that in the Scottish Loch Sween (1) O_2 exchange at the benthic interface are highly dynamic, mainly driven by light availability and tidal flow, and (2) the benthic O_2 consumption exceeds O_2 production over a diel period. In the Bay of Brest, these complex biogenic structures are particularly threatened by various human activities (mainly bivalve dredging) (Hall-Spencer et al. 2003). To better predict the consequences of the accelerated degradation of Maerl beds in the biogeochemical functioning of the whole Bay of Brest ecosystem, similar studies investigating benthic organic matter remineralisation processes and carbon cycling at large spatial scales are required.

In the present study, O_2 exchange was investigated at the sediment-water interface of two contrasted biotopes, a Maerl bed and a bare muddy sediment, through simultaneous deployments of an aquatic EC system and BC. The objectives were (1) to compare O_2 fluxes measured at different spatial and temporal scales with EC and BC, (2) to assess short-term dynamic in benthic O_2 exchange and to identify environmental controlling factors at the two stations, and (3) to accurately quantify the benthic metabolism of the two studied biotopes in the Bay of Brest.

2. Methods

2.1. Study site

The Bay of Brest is a semi-enclosed macrotidal marine ecosystem of about 180 km^2 located in the West of France (Fig. 1). This coastal bay exchanges shelf waters with the Iroise Sea through a narrow (2 km wide) and deep (40 m) strait. It receives moderate inputs of freshwater from the Elorn and Aulne rivers that represent 80 % of the total freshwater inputs (Chauvaud et al. 2000). The Bay is a shallow basin with more than 50 % of its surface shallower than 5 meters (average depth 8 m). Tidal action induces short-term variability in hydrological parameters and enhances mixing of the water masses (Chauvaud et al. 1998, Thouzeau 2003). Maximal tidal range is 7.3 meters during spring tides. In the Bay of Brest, Maerl beds cover more than one third of the benthic substrate (~ 60 km^2) and develop from the limit of spring low tides to a depth of 15 meters. They consist of cohesive muddy sediments covered by a dense community of free-living coralline red algae, *Lithothamnion corallioides* being the dominant species (Grall 2002). Though Maerl beds in the Bay of Brest are of importance to sustainable fisheries, providing nursery grounds for commercial species

of fish and shellfish (i.e. scallops *Pecten maximus*, Hall-Spencer et al. 2003), the studied Maerl bed was chosen because it had no anthropogenic disturbances during measurements. Finally, the American slipper limpet *Crepidula fornicata* is also largely found in the Bay, covering more than half of its benthic surface whilst seagrass meadows represent a much smaller percentage of the area compared to Maerl beds in the Bay of Brest (Martin et al. 2007b, Ni Longphuirt et al. 2007). *In situ* measurements were carried out during wintertime of 2013, under anticyclonic conditions with cold and sunny weather and negligible surface waves. Eddy Covariance and Benthic Chambers were simultaneously deployed within two contrasted biotopes: a Maerl bed station located in the Northwest of the bay (48°21.916'N 04°26.006'W) and a bare muddy sediment station located in the South of the bay (48°17.358'N 04°28.267'W) at five and ten meters deep, respectively (Fig. 1, Table 1).

2.2. Field measurements

2.2.1. Aquatic Eddy Covariance deployments

The different components of the EC system (Unisense A/S, version EC^2) were mounted on a custom-made stainless steel tripod frame specially designed to avoid, as far as possible, hydrodynamic perturbation around sensors but able to sustain the natural hydrodynamic forces in the Bay (Fig. 2A). Current velocity was measured by an acoustic Doppler velocimeter (ADV with a fixed probe, Nortek vector) in a cylindrical measurement volume (14 mm height and 14 mm in diameter) situated at 157 mm below the base of the three transducers (Fig. 2B). The velocity was corrected against the speed of sound with water temperature and salinity from the sampled station using the Vector software (1.34 version). Oxygen concentration was measured by a Clark-type microelectrode from Unisense (< 25 µm tip diameter) (Fig. 2B). All O_2 sensors used in this study had a 90 % response time below 0.3 seconds and a stirring sensitivity close to 2 %. The O_2 sensor was polarized at -0.8 volts for 24 hours before each deployment. An *in situ* eddy amplifier (ISA-Eddy, Unisense A/S) was coupled to the microelectrode to amplify the total O_2 signal from the microelectrode and to maximize signal-to-noise ratio, sensitivity and signal speed. The O_2 microelectrode was positioned so that its tip was located as close as possible (< 1 cm) to the ADV measurement volume (Fig. 2B). The signals generated by both the *in situ* eddy amplifier and the Nortek vector were logged by the Unisense EC system controller unit (Fig. 2A). The EC controller

unit allowed deployment programming, storage (8 GB data capacity), power supply (internal Li-ion batteries, approximately 34 hours at 25 °C of autonomy) and other unit interface connections.

Water current velocity and O_2 concentration measurements were performed at 40 cm above the substrate surface in continuous mode at 64 Hz. Additional sensors were set up on the EC frame for measurement of environmental parameters. Oxygen concentrations were recorded every ten seconds with an optode (4330F, Aanderaa) directly connected to the EC controller unit. Another O_2 probe (SDOT300, NKE Instrumentation) equipped with a 3835 optode (Aanderaa) was also used to monitor in parallel the O_2 in the bottom water and to calibrate the microelectrode (see 2.3.1. section) (Fig. 2A). Both optodes were positioned at the same distance above the substrate surface as the EC microelectrode tip. The optode signal was checked by collecting triplicate samples of bottom water, in which the O_2 concentration was analysed by Winkler titration. Temperature, salinity, pressure (water height) and photosynthetically active radiation (PAR) were measured every two minutes by a STPS probe (NKE Instrumentation) and a SPAR probe (NKE Instrumentation) equipped with a LI-COR sensor, respectively (Fig. 2A).

At the two studied stations, the EC system was deployed from the boat but supervised by IUEM SCUBA divers who (1) oriented the frame so that sensors were most of the time downstream according to the main flow direction (negative x-current velocity), (2) ensured that perturbation (i.e. frame position) and sediment re-suspension were the lowest possible, and (3) removed potential obstructions such as rock, macro-algae, or maerl accumulations close to the sensor axis that could lead to possible sensor damage or breaking.

EC deployments over Maerl bed and muddy sediment stations were carried out sequentially during a two-day period in February 2013 and lasted from 11:30 to 17:30 (TU+1) (2013/02/20) and from 11:30 to 18:30 (TU+1) (2013/02/21), respectively. Unfortunately, no longer diurnal cycle deployments could be done at that time due to logistical reasons.

2.2.2. Benthic chamber deployments

Oxygen fluxes were simultaneously monitored using *in situ* large-sized benthic chambers (see Thouzeau et al. 2007 for review). Three replicate enclosures made of 0.196 m^2 cylindrical acrylic tubes (ca. 15 cm in height) were gently pushed into the substratum (Maerl bed and bare muddy sediments) by SCUBA divers. The total enclosed volume was around 36 L slightly varying depending on the depth of insertion. A submersible pump connected to the

chamber and to waterproof batteries was adjusted to a fixed flow rate of 2 L min^{-1} to homogenize the water inside the enclosures, corresponding roughly with the average hydrodynamics of the surrounding free-flowing water (Thouzeau et al. 2007). Transparent and dark chambers were used to determine net community production (NCP) and community respiration (CR), respectively. For each station, a set of three chambers (two transparent and one darkened) was simultaneously deployed for at least one hour. This procedure was repeated three times over the course of the daylight period from 11:00 to 15:00 (2013/02/20) and from 11:55 to 16:30 (2013/02/21) (TU+1) at the Maerl bed and bare muddy sediment stations, respectively. Each enclosure was opened for 30 minutes at least between each successive set of incubations to restore *in situ* conditions. Multiparameter probes (YSI 6920v2) were used to continuously measure the oxygen concentrations, salinity, temperature and depth inside the chambers every minute. A LI-COR sensor (LI-192SA) was deployed near one of the clear BC to measure the light (PAR, 400-700 nm). Irradiance (µmol m^{-2} s^{-1}) was averaged every minute.

2.3. Data processing

2.3.1. EC data processing

The O_2 signal from the microelectrode was a millivolt reading (mv_μ) stored by time that linearly corresponds to the O_2 concentration. The O_2 microelectrode calibration was done from raw reading (mv_μ) converted to O_2 concentration ($[O_2]_\mu$, µmol L^{-1}) according to Eq (1).

$$[O_2]_\mu = [O_2]_{sdot} \times (mv_\mu - mv_0) / (mv_{sdot} \times mv_0) \quad (1)$$

where $[O_2]_{sdot}$ is the O_2 concentration (µmol L^{-1}) of the bottom water measured by the autonomous SDOT optode averaged over thirty minutes and corrected from water solubility, salinity and atmospheric pressure (Garcia and Gordon 1992, Hushida et al. 2008). The mv_{sdot} is the averaged O_2 signal in millivolt measured by the microelectrode over the same 30 min. averaging period, and mv_0 is the O_2 signal in millivolt that corresponded to the zero calibration obtained by immersing the microlectrode tip into an anoxic solution of sodium ascorbate and soda (2 g $C_6H_8O_6$ and 10 ml of 1 mol L^{-1} NaOH completed to 100 ml with distilled water) before deployment.

Sediment-water O_2 fluxes, one for each 15 min. averaging time period or burst, were extracted from the high-resolution (64 Hz) raw data. The vertical turbulent eddy flux is defined as (2) (Berg et al. 2003).

$$\overline{FO_2} = \overline{u_z' C'} \quad (2)$$

where FO_2 is O_2 flux at the sediment-water interface measured by the aquatic EC technique, u_z' is the vertical turbulent fluctuating velocity and C' is the turbulent fluctuating O_2 concentration. The overbar represents a temporal average (i.e. 15 min. during this study), and primes denote the instantaneous turbulent fluctuations relative to their temporal average (e.g. $u_z' = u_z - \overline{u_z}$ and $C' = C - \bar{C}$, Reynolds 1895). Data were processed using the EC R-package (open source R software) developed by the NIOZ Institute (The Netherlands) (see Cathalot et al. 2015). Fluxes were then obtained from these raw EC data with a procedure involving several steps: (1) spike removal in vector and microelectrode O_2 data; (2) unit modifications and statistical operations on velocity and O_2 concentration; (3) coordinating rotation (two-axis rotation) on 3D velocity to align coordinate system with the stream lines of the 15 min. averages; (4) moving average filtering (window length of 100 seconds) to remove the mean (non-turbulent part of the covariance) from raw EC data; (5) determining and applying time shift correction for velocity and O_2 data using a cross-correlation procedure (shift window of ± 2 seconds); and (6) computing mean values, turbulent fluxes and characteristic parameters (i.e. noise analysis with standard deviation of first difference of v_z and O_2, σ_{vz} and σ_{O2}, respectively). In parallel, a (co)-spectral (variance preserving power spectra, average cumulative (co)-spectra ogive) analysis was carried out for each burst to quantify the distribution by frequency of the covariance of the raw measured signals. The sampling frequency (64 Hz), the short response time of the microelectrode (< 0.3 s) and the time averaging period (15 min.) allowed catching all contributing eddies (high and low frequency) to O_2 fluxes measured by EC. For more details on EC data processing, refer to Berg et al. (2003, 2009, 2013), Kuwae et al. (2006), McGinnis et al. (2008) and Lorrai et al. (2010).

According to data quality control protocols, incorrect processed data have to be removed to obtain reliable O_2 fluxes. Several factors can lead to bias or errors, i.e. instrument malfunctioning, data processing artefacts, and natural *in situ* conditions not satisfying the assumptions of the EC methodology, i.e. non-stationary time series, convergence, divergence (Brand et al. 2008, Berg et al. 2009, Hume et al. 2011, Holtappels et al. 2013, Attard et al. 2014, Donis et al. 2015). Therefore, each 15 min. burst was carefully checked and we removed bursts that showed (1) ADV velocity data with a beam correlation threshold lower than 70 %, (2) standard deviations of first difference of v_z and O_2, σ_{vz} and σ_{O2} larger than 0.01 m s^{-1} and 0.1 µmol L^{-1}, respectively, (3) deviations from the linearity of cumulative O_2 fluxes and (4) non steady-state conditions: the steady-state test was applied to pairs of specified signals, particularly to u_z and C in this study. Standard deviations and covariance of u_z and C

were computed on short time intervals of 1 min. and these values were compared to those computed on the chosen time run of 15 min. following Foken and Wichura (1996). Only data corresponding to a difference lower than 30 % (periods defined as steady-state conditions) were retained. A clear linear trend within each burst indicates quasi-steady state conditions with a constant O_2 flux and a statistically good representation of all eddy sizes that contribute to the flux. In the end, 66 % and 54 % of the EC bursts were retained for further analysis in the Maerl bed and the bare muddy sediments, respectively.

In order to estimate the surface area that contributes to EC O_2 flux (i.e. the footprint), footprint calculations were done according to equations from Berg et al. (2007). The footprint length (l), the upstream distance (x_{max}) and the footprint width (w) were computed from measurement heights (h) and the roughness length (z_0) at each burst. The latter parameter was obtained from the law of the wall from the measurement height (h), the mean current velocity ($\overline{ux}$), the von Karman's constant (k = 0.41) and the friction velocity (u_*) defined by Stull (1988) (see Attard et al. 2015 for more details).

2.3.2. Benthic chamber data processing

Oxygen fluxes in the benthic chambers (BC) were calculated from the continuous O_2 concentrations during BC measurements in the overlying water as defined in Eq. 3.

$$FO_2 = (\Delta[O_2] \times V) / (A \times \Delta t) \quad (3)$$

where FO_2 is O_2 flux at the sediment-water interface (mmol m^{-2} h^{-1}), $\Delta[O_2]$ is the variation in the O_2 concentration during the incubation (mmol L^{-1}), V is the chamber volume (L), A is the enclosed surface area (m^2) and Δt is the incubation time duration (hour). Net community production (NCP) and community respiration (CR) were computed as mean O_2 fluxes averaged over flux values measured during each sampling day by transparent and dark BC, respectively.

2.3.3. Statistical tools

Post-processing (graphs and statistics) was performed using the GraphPad Prism version 6.00 software (La Jolla California USA, www.graphpad.com). The Shapiro-Wilk test was used to test the normality of the data (with a p value below 0.05). The non-parametric test of Mann-Whitney (with a p value below 0.01) was applied to distinguish significant differences in benthic O_2 fluxes between stations and methodologies.

3. Results

3.1. Benthic O_2 exchange and associated environmental parameters at the Maerl station

Environmental parameters showed large variations during the 6.5 h deployment of the EC system at the Maerl station (Fig. 3 and Table 1). Water height decreased from 6.3 m to 4.9 m. High PAR values were recorded from 11:30 to 15:00 and reached values of up to 112 µmol m^{-2} s^{-1} around 14:00. PAR values suddenly dropped at 15:15 down to low values of ~2 µmol m^{-2} s^{-1} during the rest of deployment due to turbid riverine inputs into sub-surface water bodies of the Bay with the ebbing tide (Fig. 3A). This sudden drop was not seen in any of the other recorded environmental parameters. Water temperature and salinity at the sediment-water interface increased steadily over the first two hours (from 8.9 to 9.7 °C and from 32.1 to 33.0, respectively), suggesting that warmer and saltier waters arrived with the flooding tide (Fig. 3B). Water temperature and salinity then remained constant thereafter during the early ebb tidal phase in the afternoon. Current velocities were in general low at the Maerl station (from 1.0 to 7.4 cm s^{-1}) although short-term temporal variations were noticed. In particular, at the beginning of the deployment the current first decreased from 5.1 to 1.0 cm s^{-1} over thirty minutes and then increased to 6.9 cm s^{-1} one hour later (Fig. 3C). Oxygen concentrations measured by the microelectrode and the SDOT optode (273 ± 3 µmol L^{-1} on average) showed weak variations during the deployment with values ranging from 269 to 279 µmol L^{-1} (Fig. 3D and Table 1).

Large temporal changes in benthic O_2 fluxes were observed over the Maerl bed. EC fluxes ranged from an uptake of -21.0 mmol m^{-2} d^{-1} to a release of 71.3 mmol m^{-2} d^{-1} and averaged 22.0 ± 32.7 mmol m^{-2} d^{-1} during the total duration of the deployment (Fig. 3E, Table 1). Until the observed sudden drop in PAR (i.e. 60 % of the time of the EC deployment), the Maerl community showed a net O_2 production (47.2 ± 13.7 mmol m^{-2} d^{-1} on average) associated with the high PAR period (Fig. 3E). Benthic O_2 fluxes dropped suddenly in thirty minutes concomitantly with the PAR decrease during the second half part of the deployment when a net mean O_2 uptake of -13.9 ± 5.7 mmol m^{-2} d^{-1} was measured (Fig. 3E). The footprint length, the upstream distance to the location and the footprint width associated to EC fluxes over the Maerl station were estimated to be between 63 and 257 m (mean of 171 ± 64 m), 2 and 10 m (mean of 7 ± 3 m), and at 2.6 m, respectively (Table 1).

Transparent BC were deployed between 11:00 and 15:00 corresponding to the high PAR period. They revealed high positive O_2 fluxes across the benthic interface. Oxygen fluxes

ranged from 64.8 to 105.7 mmol m^{-2} d^{-1} and averaged 87.4 ± 14.5 mmol m^{-2} d^{-1} (Table 1, Fig. 3E). In contrast, dark chamber incubations measured a community respiration (CR) ranged between -44.0 and -33.3 mmol m^{-2} d^{-1} with a mean value of -38.6 ± 7.6 mmol m^{-2} d^{-1}.

3.2. Benthic Oxygen exchange and associated environmental parameters at the bare muddy sediment station

Large variations also occurred during the 7 h EC deployment at the bare muddy station (Fig. 4, Table 1). Water height was higher and ranged from 9.1 m to 11.0 m (Fig. 4A, Table 1). PAR values were low during the whole duration of the deployment, decreasing from 17 µmol m^{-2} s^{-1} at the beginning of the deployment (11:30) to 2 µmol m^{-2} s^{-1} afterwards (Fig. 4A). Water temperature and salinity were steady with mean values of 9.6 ± 0.1 °C and 33.5 ± 0.1 (N=28), respectively (Table 1, Fig. 4B). Mean current velocity showed small variations from 2.4 to 5.8 cm s^{-1} with a slight current decrease with the ebbing tide between 15:00 and 18:30 (Fig. 4C). Oxygen concentrations recorded by the EC microelectrode and the SDOT optode showed weak temporal changes from 239 to 265 µmol L^{-1} and averaged 248 ± 5 µmol L^{-1} (Table 1, Fig. 4D).

Overall, sediment-water O_2 exchange measured by EC was negative and variable at the bare muddy station, ranging from -43.1 to 12.1 mmol m^{-2} d^{-1}, with a mean value of -15.9 ± 14.0 mmol m^{-2} d^{-1} (Table 1, Fig. 4E). A net O_2 uptake (-19.4 ± 11.3 mmol m^{-2} d^{-1} on average) was measured during 88 % of the time. Large short-term variations in this O_2 uptake were observed over short time scales (fifteen minutes at maximum) as for instance at the beginning of the deployment with an O_2 uptake decrease from -28.0 to -6.7 mmol m^{-2} d^{-1} between 11:37 and 11:52 (Fig. 4E). O_2 flux shifts from negative to positive values also occurred (i.e. from -43.1 to 12.1 between 14:52 and 15:22, Fig. 4E) although most of them were removed with our data quality procedure (i.e. stationary test). The footprint length, the upstream distance to the location and the footprint width associated to these fluxes at the mud station were comparable to footprint characteristics computed at the Maerl station, and were estimated to be between 57 and 195 m (mean of 115 ± 35 m), 2 and 10 m (mean of 5 ± 2 m), and at 2.6 m, respectively (Table 1).

An O_2 uptake (net negative NCP) of -9.1 ± 4.2 mmol m^{-2} d^{-1} on average (ranging from -14.6 to -2.4 mmol m^{-2} d^{-1}, Table 1) was measured by clear BC incubations deployed from 11:55 to 16:30 under similar PAR values (2.1-7.1 µmol m^{-2} s^{-1}) (Fig. 4D). Community Respiration

values measured by dark benthic chambers were between -27.0 and -7.6 mmol m^{-2} d^{-1} with a mean of -18.7 ± 10.0 mmol m^{-2} d^{-1}.

3.3. Comparison of aquatic Eddy Covariance and Benthic Chamber techniques

During the present study, benthic O_2 exchange was investigated in both biotopes using two different and complementary approaches for the measurement of benthic O_2 fluxes (Fig. 5, Table 1). At the Maerl station, significant differences were found between benthic O_2 fluxes measured by BC and EC averaged over the same time period (EC_n) (87.4 ± 14.5 and 44.5 ± 11.0 mmol m^{-2} d^{-1}, respectively; Mann-Whitney test, p = 0.0004) (Fig. 5, Table 1). At the bare muddy sediment station, no significant differences were noticed between BC (-9.1 ± 4.2 mmol m^{-2} d^{-1}) and EC fluxes averaged over the same time period (EC_n), with -16.5 ± 8.5 mmol m^{-2} d^{-1} (Mann-Whitney test, p = 0.1276).

Eddy Covariance O_2 exchange measured over the Maerl station (EC_N, 22.0 ± 32.7 mmol m^{-2} d^{-1}) was significantly different from those measured over the mud station (EC_N, -15.9 ± 14.0 mmol m^{-2} d^{-1}) (Mann-Whitney test, p = 0.0015) (Fig. 5, Table 1). Similarly significant differences were observed between O_2 exchange measured with BC over Maerl and mud stations (Mann-Whitney test, p = 0.0022) (Fig. 5, Table 1).

4. Discussion

4.1. Aquatic Eddy Covariance versus Benthic Chamber O_2 flux measurements

Benthic flux technique comparison over complex, heterogeneous and non-cohesive Maerl substrates

Biogeochemical fluxes can show strong spatial and temporal changes over complex substrates such as Maerl beds, characterized by a strong spatial heterogeneity and intense advective porewater transport and bio-irrigation due to large macrobenthic organisms (Glud et al. 2003, Rheuban and Berg 2013). In the present study, benthic O_2 fluxes measured by BC at the Maerl bed station were consistently higher than those measured with the EC technique (EC:BC ratio of 0.4-0.6; Figs. 3E and 5, Table 1).

Beyond potential hydrodynamic perturbations caused by BC deployments (Viollier et al. 2003), the larger sediment footprint covered by EC measurements may fundamentally

contribute to the difference between O_2 fluxes measured with the two methods. Indeed, at 40 cm above the Maerl bed, the footprint model gave an estimated area of ~ 350 m^2 (i.e. 171 m long for ca. 2.6 m wide) compared to ~ 0.2 m^2 with BC (Table 1). The larger EC footprint thus allows for a more accurate integration of the mesoscale spatial heterogeneity of sedimentary biotopes (e.g. taking into account the contribution of bare sediment patches in O_2 flux). However, it should be noticed that the station was specifically chosen in the middle of an extended Maerl bed covering several hectares to ensure that the footprint was consistently smaller than the bed edges.

Also, it is well known that Maerl beds shelter large macrobenthic organisms including worms, bivalves, crustaceans and echinoderms (Kamenos et al. 2004a, 2004b, Grall et al. 2006, Attard et al. 2015). They also represent nursery grounds for numerous species of demersal fish (Kamenos et al. 2004). The presence of large bio-irrigating animals enhances sediment reworking and bioirrigation processes, which in turn stimulates the microbial respiration, and leads to higher sediment O_2 uptakes. For instance, Yahel et al. (2008) estimated that silty sediment resuspension induced by benthic fish could increase benthic O_2 demand up to 3.5-fold. Due to patchy distributions of large benthic organisms, BC methodology tends to underestimate the effects of bioturbation processes and CR. It could thus partly explain the lower positive O_2 fluxes measured over the Maerl bed station by EC catching a more realistic *in situ* CR. Attard et al. (2015) also highlighted, over Maerl beds in Loch Sween, large variations between their BC replicates and indorsed the difficulty of the method to integrate larger spatial scales and resolve an O_2 uptake representative of the whole benthic community. In any case, our assumption (possible CR underestimation with BC) verified during daytime but not during nighttime periods would deserve longer deployments to address the influence of spatial heterogeneity on O_2 flux measurements along with methodological artifacts and temporal resolutions.

Benthic flux technique comparison over bare cohesive soft sediment substrates

Contrary to the non-cohesive Maerl bed site, an overall good agreement was found between EC and BC O_2 flux measurements over the cohesive bare muddy sediment site. Indeed, no significant differences in benthic O_2 fluxes were measured using simultaneously BC and EC methodologies suggesting that in homogeneous biotopes such as bare muddy sediments, the BC methodology allows for accurate benthic O_2 flux measurements (Fig. 5, Tables 1 and 2). Berg et al. (2003) also documented a great similarity in benthic O_2 fluxes measured by EC

and BC elsewhere in temperate bare muddy sediments (Table 2). Our results also suggest a good BC representation of *in situ* faunal activity (probably dominated by smaller animals) over homogeneous soft bottom cohesive sediments characterized by lower mesoscale heterogeneity. Additionally, the good correspondence between both techniques could reveal a weaker influence of environmental parameters, such as light or tidal currents on O_2 fluxes at the muddy station (Fig. 4, Table 1). Indeed, these parameters showed lower mean values and ranges of variations during the deployment compared to the Maerl site. In particular, the very low irradiance values did not allow recording NCP whatever the sampling technique and did rather correspond to CR (Tables 1 and 2). To the contrary, even in relatively homogeneous habitats, large benthic O_2 exchange differences could occur between the two techniques as soon as sporadic short-term events such as storms happen during measurements. Camillini et al. (in press) showed over a *Zostera marina* station in the Baltic Sea, the occurrence of elevated flow speeds and associated sediment resuspension could induce a 5-fold increase in the O_2 uptake rates measured by EC compared to BC due to reduced compound (FeSx) reoxidation during resuspension.

Another reason of this good matching relies on the EC data quality procedure we adopted during this study. One important assumption that must fulfill EC techniques is to measure vertical turbulent fluxes during stationary conditions. To our knowledge, although numerous studies have considered non-steady state conditions in their flux filtering protocol, it is the first time that an aquatic EC study applies robust stationary tests coming from the atmospheric EC technique to identify non-stationary conditions and remove it from the measured datasets (see M&M section 2.3.1 and associated references). Despite a smaller EC burst number retained, it results in robust and real EC flux variations that better match those measured with BC. For instance, at the muddy sediment station between 16:22 and 16:52, non-stationary conditions occurred with a mean velocity decreasing from 4.2 to 3 cm s^{-1} that led to an O_2 flux shift from -34.9 to 6.5 mmol m^{-2} d^{-1} (Fig. 4). This latter artificial positive flux value was identified and removed. Overall, the EC data quality procedure previously described allowed catching real EC O_2 flux variations (-43.1 to 12.1 mmol m^{-2} d^{-1} instead of -48.4 to 18.6 mmol m^{-2} d^{-1} without stationary tests) that better matched BC flux measurements (-14.6 to -2.4 mmol m^{-2} d^{-1}, Table 1).

4.2. Short-term variations in benthic O_2 exchange and associated flux controls

Environmental control of benthic fluxes over non-cohesive Maerl substrates

In the coastal ocean, larger amounts of light generally reach the bottom floor due to shallow depths particularly, which allows in turn benthic primary production. Several studies have quantified this light influence on benthic primary production. For instance, Attard et al. (2014, 2015) showed that light was the main driver of benthic O_2 production at a coralline red algae site in a Southwest Greenland fjord and at a Maerl site located in the Loch Sween. Over the Maerl bed station of the Bay of Brest, the highest NCP values were reached during the periods exhibiting highest PAR values and short temporal variations in O_2 fluxes driven by light were observed. The sudden PAR drop, due to possible turbid riverine inputs with the ebbing tide, led to an 8-fold decrease in benthic O_2 exchange within 30 minutes (Fig. 3A). This relationship resulted in a significant positive correlation between EC O_2 flux and PAR values (Fig. 6A). Martin et al. (2005) precisely showed from P-E curve calculations that available irradiance was the major factor influencing primary production of Maerl beds in the Bay of Brest, explaining up to 94 % of benthic exchange. EC studies carried out by Attard et al. (2014, 2015) showed that little light levels were sufficient to drive a net autotrophic status response with compensation irradiance (I_c) values (derived from simple linear fit models) of 6 and 16 µmol m^{-2} s^{-1}, respectively. These I_c values are in good agreement with the value of 22.7 µmol m^{-2} s^{-1} estimated in the present study but lower than the spring value calculated by Martin et al. (2005) of 107.5 µmol m^{-2} s^{-1} in a nearby Maerl bed in the Bay of Brest. This high value, in opposition to normal responses of communities dominated by red algae typically low light adapted, could be attributed according to authors, to a major photosynthetic contribution of epiphytic macro- and microalgae to the total community production.

Differences observed between EC and BC O_2 exchange at this station (Fig. 5) suggest the occurrence of other environmental parameters than PAR as controlling factors. Particularly, local hydrodynamics is expected to significantly influence benthic O_2 fluxes inducing short-term variability (Holtappels et al. 2013). Attard et al. (2015) computed EC O_2 exchange versus flow velocity in darkness at the Maerl station in Loch Sween, with a seasonal trend in the slope of the regression (i.e. smaller slope in winter). In the Bay of Brest, we had no correlation between the current velocity and O_2 flux since current velocity range was much lower at this station compared to Loch Sween. However, tidally driven water height significantly influenced O_2 fluxes with mostly positive values measured as soon as water

height was higher than 5.6 meters (Fig. 6B). Indeed, at the end of the flooding tide at this station, clearer waters with more available light would have allowed a higher photosynthetic activity of Maerl beds. In contrast to this, during the next part of the deployment, the presence of riverine turbid water bodies coming with the ebbing tide and more specifically current-induced turbidity generated a strong decrease in bottom PAR and could have led to the decrease observed in EC O_2 flux. Berg et al. (2013) discussed the sudden effect of light on O_2 production that is largely decoupled from current flow patterns, except in the case of current-induced turbidity. These results show that the aquatic EC technique, through high-resolution flux measurements, helps to resolve the strong dynamic of benthic O_2 exchange observed over such coastal systems. Further and longer EC deployments along with water turbidity measurements are however necessary and should allow decoupling the superimposition of environmental forcing to better understand their influence on benthic O_2 fluxes.

Environmental control of benthic fluxes over bare muddy sediments

Large variations in benthic O_2 exchange were recorded at the bare muddy station (Fig. 4). Light availability cannot explain these variations as suggested by PAR values below 10 µmol m^{-2} s^{-1} during most of the deployment time. This low light level at the sediment-water interface was likely due to higher water height and higher turbidity values compared to the Maerl station. Over shallower (4.2 ± 2.5 m) bare sediments in winter in the Bay of Brest, Ni Longphuirt et al. (2007) estimated from P-E curve calculations, minimum saturating irradiance values (E_k) of 57.8 ± 28.7 µmol m^{-2} s^{-1}. The microphytobenthic production was thus not light-limited at 4 m depth in the study of Ni Longphuirt et al. (2007), in contrast to our deeper (10.4 ± 0.5 m) muddy site (PAR: 6.9 ± 3.7 µmol m^{-2} s^{-1}). Interestingly, the present study did not point out correlations between O_2 fluxes and hydrodynamic parameters. In the Bay of Brest, current velocity variations at the muddy station were weak between consecutive bursts retained after our quality EC data procedure. Nevertheless, a decrease in current velocity of only 2 cm s^{-1} led to a decrease in O_2 uptake by at least a factor of two (e.g. from 16:22 to 17:07, the velocity decreased from 4.2 to 2.4 cm s^{-1} while O_2 uptake decreased from -34.9 to -17.8 mmol m^{-2} d^{-1}; Fig. 4). Transient flow velocities and water hydrodynamic more generally, could then explain a significant part of the variability observed our EC fluxes during the tidal cycle as furthermore highlighted by Holtappels et al. (2013) through theoretical EC flux calculations and turbulence modeling applied to field data.

4.3. Benthic metabolism of the contrasted biotopes studied in the Bay of Brest

Primary production and respiration of coralline algae communities

Coralline algae-dominated communities, associated with abundant heterotrophic organisms living in the sub-layers of cohesive muddy sediments, form a complex habitat largely involved in nutrient and organic matter recycling (Barbera et al. 2003, Martin et al. 2007b). In temperate regions, slow-growing algae such as Maerl beds can significantly contribute to the benthic primary production (Roberts et al. 2002, Martin et al. 2005). We measured by EC and BC techniques net community production (NCP) (Table 1) that are consistent with previously published values and reveal a strong contribution of Maerl beds and associated autotrophic organisms to the benthic primary production. Attard et al. (2015) observed under similar environmental conditions, though lower PAR values were reported, a close net daytime production on average over Maerl beds in the temperate Loch Sween (Table 2). Martin et al. (2007b), in winter over a Maerl bed located in the southern basin of the Bay of Brest, measured by BC under very similar light conditions, a similar average NCP value (Table 2). These measurements highlight the potential low-light adaptation of Maerl communities in the terrestrial-influenced turbid water masses at this location in the Bay of Brest, close to the Elorn River. The study of Attard et al. (2015) resolved this low-light adaptation of temperate Maerl beds, when measuring the highest mean rate of daytime net O_2 release in winter. The low value of minimum saturating irradiance estimated by Ni Longphuirt et al. (2007) in winter in the Bay of Brest also suggested an adaptation of the microphytobenthic communities associated with Maerl beds to the reduced light levels reaching the sediment-water interface.

Despite their high productivity, coralline-dominated communities remain generally heterotrophic with community respiration (CR) values for temperate systems in the range of the benthic communities dominated by macroalgae, i.e. from -72 to -240 mmol m^{-2} d^{-1} (Middelburg et al. 2004). Indeed, these high-biodiversity communities host a number of heterotrophic organisms (microbial, microfauna, larger grazers) and sustain intense organic matter mineralization (Martin et al. 2005). In the southern part of the Bay of Brest, Martin et al. (2005, 2007b) concluded from their seasonal surveys that maerl communities were heterotrophic systems (Table 2). Despite substantial benthic primary production, Attard et al. (2015) also concluded after 300 hours of EC and BC measurements that Maerl beds in Loch Sween were net heterotrophic during each seasonal sampling campaign (Table 2). The present

EC measurements also suggested a near-balanced or heterotrophic status of Maerl beds in the Bay of Brest, although longer deployments should be required to confirm this metabolic status. Assuming 9.6 daylight hours (Meteo France data), daily O_2 fluxes estimated from hourly BC flux values revealed a net autotrophic status of Maerl beds with a positive NCP of 35.0 ± 5.8 mmol m^{-2} d^{-1}. Positive NCP values obtained by BC in the present study seemed to be due to lower CR values compared to those measured by Martin et al. (2005; 2007b) in the Bay using the same technique (Table 2).

Benthic metabolism of bare muddy sediments

Sediment O_2 uptakes through EC measurements (Table 1) were mainly noticed at the bare muddy station as observed elsewhere in other EC studies (Table 2). Our EC and BC measurements are in good agreement with CR values measured by Martin et al. (2007a) in winter in the Bay of Brest; dark BC were deployed over a muddy station covered by low densities of *Crepidula fornicata*. Ni Longphuirt et al. (2007) also found very similar CR values in winter, with the same BC technique, at a bare sediment site in the Brest Strait without any *C. fornicata* or coralline algae (Table 2). Assuming 9.7 daylight hours (Meteo France data) during the day of deployment, daily O_2 fluxes estimated from hourly BC flux values revealed a slightly net heterotrophic status of bare muddy sediments in the Bay of Brest with GPP and CR values of 3.9 ± 2.3 and -7.6 ± 4.0 mmol m^{-2} d^{-1}, respectively (Table 2). The few positive O_2 flux values measured at our station suggest a certain O_2 production by microphytobenthos communities, though limited by reduced light availability. The same result was found in BC data, when comparing net O_2 fluxes between light and dark incubations (Fig. 4). However, these microphytobenthic production values are far below those estimated by Ni Longphuirt et al. (2007) in winter over shallower bare sediments in the Bay of Brest from biomass-irradiance relationships obtained in one specific site (GPP: 15.3 ± 6.4 mmol m^{-2} d^{-1}).

Conclusion: perspectives and implications for the global functioning of the Bay

This study performed measurements of benthic O_2 exchange by aquatic EC and BC techniques over contrasting coastal biotopes: a non-cohesive Maerl substrate vs. cohesive bare muddy sediments in the Bay of Brest (France). Using both techniques, and based on our specific winter measurements, opposed ecological functioning were found since Maerl bed

communities and muddy sediments generally released and consumed O_2, respectively. The present study highlights that O_2 flux variations and their controlling factors can be captured by the EC technique on comparable spatial and temporal scales. It shows the real potential of the EC technique in benthic O_2 flux assessment under true *in situ* conditions over large spatial and temporal scales. However, our knowledge of flux dynamics is still limited due to the complexity of flux controlling factors and their interactions. Efforts involving multidisciplinary methodological approaches (with simultaneous EC and BC deployments) are clearly necessary to go further in our comprehension of factors controlling benthic O_2 exchange. Such approaches will allow understanding at a larger scale the ecological and biogeochemical functioning of coastal sedimentary areas, which are well known to be systems particularly complex with a high degree of heterogeneity (Stockdale et al. 2009).

Acknowledgements

The EDDYCO project (INSU EC2CO/DRIL program) provided financial support for this study. The Région Aquitaine (FEBBA project) and the IZOFLUX project from the French National Research Agency (white program) funded the EC system. The Région Aquitaine (FEBBA project) and the Vrije Universiteit Brussel supported the two-year postdoctoral fellowships awarded to P.P. The development of the new EC system, EC^2, was realized in collaboration with *Unisense A/S* and the NIOZ-Yerseke. We would like to express our thanks to the INSU team from L'Albert Lucas and Henry Bouillard and Christian Portier from EPOC. This work has been carried out within the framework of the Cluster of Excellence COTE. We thank the two reviewers and Editor-in-Chief Gunnar Lauenstein for their constructive comments that improved the clarity and overall quality of the manuscript.

Bibliography

Aller, R. C. 2014. Sedimentary diagenesis, depositional environments and benthic fluxes. In: Holland H.D. and Turekian K.K. (eds.), Treatise on Geochemistry, Second Edition, **8**: 293-334. Oxford: Elsevier.

Aller, R. C., R. N. Glud, D. Mcginnis and S. Rysgaard. 2014. Seasonal rates of benthic primary production in a Greenland fjord measured by aquatic eddy correlation. Limnol. Oceanogr. **59**: 1555-1569. doi: 10.4319/lo.2014.59.5.1555.

Attard, K. M., H. Stahl, N. A. Kamenos, G. Turner, H. L. Burdett and R. N. Glud. 2015. Benthic oxygen exchange in a live coralline algal bed and an adjacent sandy habitat: an eddy covariance study. Limnol. Oceanogr. **535**: 99-115. doi: 10.3354/meps11413.

Attard, K. M., I. F. Rodil, R. N. Glud, P. Berg, J. Norkko, and A. Norkko. 2019. Seasonal ecosystem metabolism across shallow benthic habitats measured by aquatic Eddy Covariance. Limnol. Oceanogr. **4**: 79-86. https://doi.org/10.1002/lol2.10107

Aubinet, M., A. Grelle, A. Ibrom, U. Rannik, J. Moncrieff, T. Foken, A. S. Kowalski, P. H. Martin, P. Berbigier, C. H. Bernhofer, R. Clement, J. Elbers, A. Granier, T. Grunwald, K. Morgenstern, K. Pilegaard, C. Rebmann, W. Snijders, R. Valentini, and T. Vesala. 2000. Estimates of the annual net carbon and water exchange of European forests: the EUROFLUX methodology. Adv. Ecol. Res. **30**: 113-175.

Baldocchi, D. D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Glob. Change Biol. **9**: 479-492.

Barbera, C., C. Bordehore, J.A. Borg, M. Glémarec, J. Grall, J. M. Hall-Spencer, C. H. De La Huz, E. Lanfranco, M. Lastra, P.G. Moore, J. Mora, M.E. Pita, A.A. Ramos-Esplá, M. Rizzo, A. Sánchez-Mata, A. Seva, P.J. Schembri, and C. Valle. 2003. Conservation and management of northeast Atlantic and Mediterranean maerl beds. Aquatic Conserv. Mar. Freshw. Ecosyst. **13**: 65-76.

Berg, P., M. H. Long, M. Huettel, J. E. Rheuban, K. J. McGlathery, R. W. Howarth, K. H. Foreman, A. E. Giblin, and R. Marino. 2013. Eddy correlation measurements of oxygen fluxes in permeable sediments exposed to varying current flow and light. Limnol. Oceanogr. **58**: DOI: 10.4319/lo.2013.58.4.1329, 1329-1343.

Berg, P., R. N. Glud, A. Hume, H. Stahl, K. Oguri, V. Meyer, and H. Kitazato. 2009. Eddy correlation measurements of oxygen uptake in deep ocean sediments. Limnol. Oceanogr. Meth. **7**: 576-584.

Berg, P., and M. Huettel. 2008. Monitoring the Seafloor Using the Non-invasive Eddy Correlation Technique: Integrated Benthic Exchange Dynamics. Oceanogr. 21: 164-167.

Berg, P., H. Røy, and P. L. Wiberg. 2007. Eddy correlation flux measurements - the sediment surface area that contributes to the flux. Limnol. Oceanogr. **52**: 1672-1684.

Berg, P., H. Røy, F. Janssen, V. Meyer, B. B. Jørgensen, M. Huettel, and D. de Beer. 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. Mar. Ecol. Prog. Ser. **261**: 75-83.

Brand, A., D. F. McGinnis, B. Wehrli, and A. Wüest. 2008. Intermittent oxygen flux from the interior into the bottom boundary of lakes as observed by eddy correlation. Limnol. Oceanogr. **53**: 1997-2006.

Camillini, N., K. M. Attard, B. D. Eyre, and R. N. Glud. (in press). Resolving community metabolism of eelgrass *Zostera marina* meadows by benthic flume-chambers and eddy covariance in dynamic coastal environments. DOI: https://doi.org/10.3354/meps13616

Cathalot, C., D. Van Oevelen, T. J. S. Cox, T. Kutti, M. Lavaleye, G. Duineveld and F. J. R. Meysman. 2015. Cold-water coral reefs and adjacent sponge grounds: hotspots of benthic respiration and organic carbon cycling in the deep sea. Front. Mar. Sci. **2**: 37. doi: 10.3389/fmars.2015.00037

Chauvaud, L., F. Jean, O. Ragueneau, and G. Thouzeau. 2000. Long-term variation of the Bay of Brest ecosystem: benthic–pelagic coupling revisited. Mar. Ecol. Prog. Ser. 2**00**: 35-48.

Chauvaud, L., G. Thouzeau, and Y. M. Paulet. 1998. Effects of environmental factors on the daily growth rate of *Pecten maximus* juveniles in the Bay of Brest. J. Exp. Mar. Biol. Ecol. **227**: 83-111.

Chipman, L., M. Huettel, P. Berg, V. Meyer, I. Klimant, R. N. Glud, and F. Wenzhoefer. 2012. Oxygen optodes as fast sensors for eddy correlation measurements in aquatic systems. Limnol. Oceanogr. Meth. **10**: 304-316.

Crusius, J., P. Berg, D. J. Koopmans, and L. Erban. 2008. Eddy correlation measurements of submarine groundwater discharge. Mar. Chem. **109**: 77-85.

Donis, D., D. F. McGinnis, M. Holtappels, J. Felden and F. Wenzhoefer. 2016. Assessing benthic oxygen fluxes in oligotrophic deep sea sediments (HAUSGARTEN observatory), Deep Sea Res.Part I: Oceanogr. Res. Pap. **11**: 1-10.

Donis, D., M. Holtappels, C. Noss, C. Cathalot, K. Hancke, P. Polsenaere, F. Wenzhoefer, A. Lorke, F. Meysman, R. N. Glud and D. F. McGinnis. 2015. An Assessment of the Precision and Confidence of Aquatic Eddy Correlation Measurements. Jour. of Atm. and Ocea. Tec. **32**: 642-655. 10.1175/JTECH-D-14-00089.1.

Foken, T. and B. Wichura. 1996. Tools for quality assessment of surface-based flux measurements, Agr. Forest Meteorol. **78**: 83-105.

Garcia, H. E., and L. I. Gordon. 1992. Oxygen solubility in seawater: Better fitting equations. Limnol. Oceanogr. **37**: 1307-1312.

Glud, R. N., P. Berg, A. Hume, P. Batty, M. E. Blicher, K. Lennert, and S. Rysgaard. 2010. Benthic O_2 exchange across hard-bottom substrates quantified by eddy correlation in a sub-Arctic fjord. Mar. Ecol. Prog. Ser. **417**: 1-12.

Glud, R. N. J. Woelfel, U. Karsten, M. Kühl, and S. Rysgaard. 2009. Benthic microalgae production in the Arctic: applied methods and status of the current database. Bot. Mar. **52**: 559-571.

Glud, R. N. 2008. Oxygen dynamics of marine sediments. Mar. Biol. Res. **4**: 243-289.

Glud, R. N., J. K. Gundersen, H. Røy, and B. B. Jørgensen. 2003. Seasonal dynamics of benthic O_2 uptake in a semi enclosed bay: importance of diffusion and fauna activity. Limnol. Oceanogr. **48**: 1265-1276.

Grall, J., F. Le Loc'h, B. Guyonnet and P. Riera. 2006. Community structure and food web based on stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) analyses of a North Eastern Atlantic maerl bed. J. Exp. Mar. Biol. Ecol. **338**: 1-15.

Grall, J. 2002. Biodiversité spécifique et fonctionnelle du maerl : réponses à la variabilité de l'environnement côtier. PhD thesis, Université de Bretagne Occidentale, Brest.

Hall-Spencer, J. M., J. Grall, P. G. Moore, and R. J. A. Atkinson. 2003. Bivalve fishing and maerl-bed conservation in France and the UK - retrospect and prospect. Aquat. Conserv. Mar. Freshw. Ecosyst. **13**: 33-41.

Holtappels, M., R. N. Glud, D. Donis, B. Liu, A. Hume, F. Wenzhöfer, and M. M. M. Kuypers. 2013. Effects of transient bottom water currents and oxygen concentrations on benthic exchange rates as assessed by eddy correlation measurements. J. Geophys. Res. **118**: 1157-1169.

Huettel, M., P. Berg and J. E. Kostka. 2013. Benthic exchange and biogeochemical cycling in permeable sediments. Ann Rev Mar Sci, **6**: 23–51. 10.1146/annurev-marine-051413-012706.

Huettel, M., P. Cook, F. Janssen, G. Lavik, and J. J. Middelburg. 2007. Transport and degradation of a dinoflagellate bloom in permeable sublittoral sediment. Mar. Ecol. Prog. Ser. **340**: 139-153.

Huettel, M., and G. Gust. 1992. Impact of bioroughness on interfacial solute exchange in permeable sediments. Mar. Ecol. Progr. Ser. **89**: 253-267, doi:10.3354/meps089253

Hume, A. C., P. Berg, and K. J. McGlathery. 2011. Dissolved oxygen fluxes and ecosystem metabolism in an eelgrass (*Zostera marina*) meadow measured with the eddy correlation technique. Limnol. Oceanogr. **56**: 86-96.

Jahnke, R. A., J. R. Nelson, R. L. Marinelli, and J.E. Eckman. 2000. Benthic flux of biogenic elements on the Southeastern US continental shelf: influence of pore water advective transport and benthic microalgae. Cont. Shelf Res. **20**: 109-127.

Kamenos, N.A., P. G. Moore and J. M. Hall-Spencer. 2004a. Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? ICES J. Mar. Sc. **61**: 422-429.

Kamenos, N. A., P. G. Moore and J. M. Hall-Spencer. 2004b. Attachment of the juvenile queen scallop (*Aequipecten opercularis* (L.)) to maerl in mesocosm conditions; juvenile habitat selection. J. Exp. Mar. Biol. Ecol. **306**: 139-155.

Koopmans, D. J., and P. Berg. 2015. Stream oxygen flux and metabolism determined with the open water and aquatic eddy covariance techniques. Limnol. Oceanogr. **60**: 1344-1355. doi:10.1002/lno.10103

Kristensen, E., G. Penha-Lopes, M. Delefosse, T. Valdemarsen, C. Quintana and G. Banta. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Marine Ecology Progress Series, **446**: 285-302. Doi:10.3354/meps09506.

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.

Kuwae, T., K. Kamio, T. Inoue, E. Miyoshi and Y. Uchiyama. 2006. Oxygen exchange flux between sediment and water in an intertidal sandflat, measured *in situ* by the eddy-correlation method. Mar. Ecol. Prog. Ser. **307**: 59-68.

Khalil, K., M. Raimonet, A.M. Laverman, C. Yan, F. Andrieux-Loyer, E. Viollier, B. Deflandre, O. Ragueneau and C. Rabouille. 2013. Spatial and temporal variability of sediment organic matter recycling in two temperate eutrophicated estuaries. Aquatic Geochem. **19**: 517-542.

Long, M. H., P. Berg, D. de Beer and J. C. Zieman. 2013. *In situ* coral reef oxygen metabolism: an eddy correlation study. PLoS ONE. **8**(3): e58581. Doi:10.1371/journal.pone.0058581.

Lorrai, C., D. F. McGinnis, P. Berg, A. Brand, and A. Wüest. 2010. Application of oxygen Eddy Correlation in aquatic systems. J. Atmos. Ocean Tech. **27**: 1533-1546.

Maire, O., J. N. Merchant, M. Bulling, L. R. Teal, A. Grémare, J. C. Duchêne and M. Solan. 2010. Indirect effects of non-lethal predation on bivalve activity and sediment reworking. J. Exp. Mar. Bio. and Ecol. **395**: 30-36.

Martin, S., G. Thouzeau, M. Richard, L. Chauvaud, F. Jean and J. Clavier. 2007a. Benthic community respiration in areas impacted by the invasive mollusk, *Crepidula fornicata* L. Mar. Ecol. Prog. Ser. **347**: 51-60.

Martin, S., J. Clavier, L. Chauvaud, and G. Thouzeau. 2007b. Community metabolism in temperate maerl beds. I. Carbon and carbonate fluxes. Mar. Ecol. Prog. Ser. **335**: 19-29.

Martin, S., J. Clavier, J.-M. Guarini, L. Chauvaud, C. Hily, J. Grall, G. Thouzeau, F. Jean and J. Richard. 2005. Comparison of *Zostera marina* and maerl community metabolism. Aqua. Bot. **83**: 161-174.

McGinnis, D. F., S. Cherednichenko, S. Sommer, P. Berg, L. Rovelli, R. Schwarz, R. N. Glud, and P. Linke. 2011. Simple, robust eddy correlation amplifier for aquatic dissolved oxygen and hydrogen sulfide flux measurements. Limnol. Oceanogr. Meth. **9**: 340-347.

McGinnis, D. F., P. Berg, A. Brand, C. Lorrai, T. J. Edmonds, and A. Wuest. 2008. Measurements of eddy correlation oxygen fluxes in shallow freshwaters: Towards routine applications and analysis. Geophys. Res. Lett. **35**, L04403, doi:10.1029/2007GL032747

McGinnis, D. F., I. C. Anderson and A. C. Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. Mar. Ecol. Prog. Ser. **216**: 1-15, doi:10.3354/meps216001

McGlathery, K. J., P. Berg and R. Marino. 2001. Using porewater profiles to assess nutrient availability in seagrass-vegetated carbonate sediments. Biogeochem. **56**: 239-263.

Middelburg, J. K., C. M. Duarte and J. P. Gattuso. 2004. Respiration in coastal benthic communities. In: del Giorgio PA, Williams PJB (eds). Respiration in aquatic ecosystems. Oxford University Press, Oxford, p 206-224.

Ni Longphuirt, S. N., J. Clavier, J. Grall, L. Chauvaud, F. Le Loc'h, I. Le Berre, J. Flye-Sainte-Marie, J. Richard and A. Leynaert. 2007. Primary production and spatial distribution of subtidal microphytobenthos in a temperate coastal system, the Bay of Brest, France. Estuarine, Coastal and Shelf Science. **74**: 367-380, ISSN 0272-7714, http://dx.doi.org/10.1016/j.ecss.2007.04.025.

Norling, K., R. Rosenberg, S. Hulth, A. Grémare, and E. Bonsdorff. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Mar. Ecol. Prog. Ser. **332**: 11-23.

Polsenaere, P., E. Lamaud, J.-M. Bonnefond, V. Lafon, P. Bretel, B. Delille, J. Deborde, D. Loustau and G. Abril. 2012. Spatial and temporal CO_2 exchanges measured by Eddy Covariance over a temperate intertidal flat and their relationships to net ecosystem production. Biogeosciences **9**: 249-268.

Rovelli, L., K. M. Attard, A. Binley, C.M. Heppell, H. Stahl, M. Trimmer and R.N. Glud. 2017. Reach-scale river metabolism across contrasting sub-catchment geologies: Effect of light and hydrology. Limnol. Oceanogr. **62**: S381-S399. doi:10.1002/lno.10619

Rovelli, L., K. M. Attard, L. D. Bryant, S. Flögel, H. Stahl, J. M. Roberts, P. Linke and R. N. Glud. 2015. Benthic O_2 uptake of two cold-water coral communities estimated with the non-invasive eddy correlation technique. Mar. Ecol. Prog. Ser. **525**: 97-104. doi: 10.3354/meps11211

Reimers, C. E., T. Özkan-Haller, P. Berg, A. Devol, K. Mccann-Grosvenor, and R. D. Sanders. 2012. Benthic oxygen consumption rates during hypoxic conditions on the Oregon continental shelf: Evaluation of the eddy correlation method. J. Geophys. Res. **117**: 1-18, C02021, doi:10.1029/2011JC007564

Reimers, C. E., R.A. Jahnke, and L. Thomsen. 2001. *In situ* sampling in the benthic boundary layer. In: Boudreau BP, Jørgensen BB (eds) The benthic boundary layer. Oxford University Press, New York, p 245-268.

Reynolds, O. 1895. On the dynamical theory of incompressible viscous fluids and the determination of the criterion. Phil. Trans. R. Soc. Lond. A Math. Phys. Sci. **186**: 123-164.

Rheuban, J. E., P. Berg, K. J. McGlathery 2014. Ecosystem metabolism along a colonization gradient of eelgrass (*Zostera marina*) measured by eddy correlation. Limnol. Oceanogr. **59**, doi: 10.4319/lo.2014.59.4.1376.

Rheuban, J. E., and P. Berg. 2013. The effects of spatial and temporal variability at the sediment surface on aquatic eddy correlation flux measurements. Limnol. Oceanogr. Methods **11**: 351-359.

Roberts, R. D., M. Kühl, R. N. Glud and S. Rysgaard. 2002. Primary production of crustose coralline red algae in a high arctic fjord. J. Phycol. **38**: 273-283.

Stockdale, A., W. Davison and H. Zhang. 2009. Micro-scale biogeochemical heterogeneity in sediments: A review of available technology and observed evidence. Earth-Science Reviews **92**: 81-97.

Stull R. B. 1988. Mean Boundary Layer Characteristics. In: Stull R.B. (eds) An Introduction to Boundary Layer Meteorology. Atmospheric Sciences Library, **13**: Springer, Dordrecht

Tengberg, A., H. Stahl, G. Gust, V. Muller, U. Arning, H. Andersson, and P. Hall. 2004. Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. Prog. Oceanogr. **60**: 1-28, doi:10.1016/j.pocean.2003.12.001

Thouzeau, G., J. Grall, J. Clavier, L. Chauvaud, F. Jean A. Leynaert S. Ni Longphuirt E. Amice D. Amouroux.2007. Spatial and temporal variability of benthic biogeochemical fluxes associated with macrophytic and macrofaunal distributions in the Thau lagoon (France). Est. Coast Shelf Sci. **72**: 432-447.

Thouzeau, G., 2003. Fonctionnement des écosystèmes marins côtiers : d'une approche populationnelle à une approche écosystémique. Mémoire d'Habilitation à Diriger des Recherches (HDR), spécialité Océanologie Biologique, Université de Bretagne Occidentale, Brest.

Thouzeau, G., 1991. Experimental collection of postlarvae of *Pecten maximus* (L.) and other benthic macrofaunal species in the Bay of Saint-Brieuc, France. II. Reproduction patterns and postlarval growth of five mollusc species. J. Exp. Mar. Biol. Ecol.**148**: 181-200.

Uchida, H., T. Kawano, I. Kaneko, and M. Fukasawa. 2008. *In Situ* Calibration of Optode-Based Oxygen Sensors. J. Atmos. Oceanic Technol. **25**: 2271-2281.

Viollier, E., C. Rabouille, S. E. Apitz, E. Breuer, G. Chaillou, K. Dedieu, Y. Furukawa, C. Grenz, P. Hall, F. Janssen, J. L. Morford, J. C. Poggiale, S. Roberts, T. Shimmield, M. Taillefert, A. Tengberg, F. Wenzhöfer, U. Witte. 2003. Benthic biogeochemistry: state of the art technologies and guidelines for the future of *in situ* survey. J. Exp. Mar. Biol. Ecol. **285-286**: 5-31, doi:10.1016/S0022-0981(02)00517-8

Yahel, G., R. Yahel, T. Katz, B. Lazar, B. Herut, and V. Tunnicliffe. 2008. Fish activity: a major mechanism for sediment resuspension and organic matter remineralization in coastal marine sediments. Mar. Ecol. Progr. Ser. **372:**195-209.

Zemmelink, H. J., H. A. Slagter, C. van Slooten, J. Snoek, B. Heusinkveld, J. Elbers, N. J. Bink, W. Klaassen, C. J. M. Philippart, and H. J. W. de Baar. 2009. Primary production and eddy correlation measurements of CO_2 exchange over an intertidal estuary. Geophys. Res. Lett. **36**, LI19606, doi:10.1029/2009GL039285

Fig. 1. Localization of the two study sites in the Bay of Brest (red square in the France map), Ma: Maerl beds (48°21.916'N 04°26.006'W), Mu: bare muddy station (48°17.358'N 04°28.267'W).

Fig. 2. Image of the aquatic EC system. (A) The EC system and associated sensors carried by the frame: (1) the EC system controller unit. (B) Main EC sensors; (2) acoustic doppler velocimeter ADV and (3) Oxygen (O_2) microelectrode (Clark type) with *in situ* eddy amplifier. The ADV transducer (the black ring represents the water current *x* direction). The other associated sensors are (4) O_2 optode directly connected to the EC system controller unit (front leg), (5) O_2 optode autonomously deployed, (6) STPS sensor for temperature, salinity and pressure measurements and (7, behind the left leg) SPAR sensor for photosynthetically active radiation PAR measurements.

Fig. 3. Aquatic Eddy Covariance O_2 fluxes and associated environmental parameters over the Maerl bed station (20/02/2013, from 11:30 to 17:30). Averaged EC Data from burst 1 (11:37:30) corresponds to EC raw data (at 64 Hz) averaged over 15 minutes between 11:30:00 and 11:45:00. (A) Photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}) and water height (H, meters), (B) Water temperature (T, °C) and salinity, (C) Mean water current velocity (cm s^{-1}), (D) O_2 concentration (µmol L^{-1}) measured by the microelectrode and *SDOT* optode and (E) Sediment/water O_2 fluxes measured by EC (EC FO_2, mmol m^{-2} d^{-1}). Averaged FO_2 measured by BC have been added (BC FO_2, mmol m^{-2} d^{-1}). Positive and negative FO_2 values represent O_2 production (from Maerl beds to water) and O_2 uptake (by Maerl beds), respectively.

Fig. 4. Aquatic Eddy Covariance O_2 fluxes and associated environmental parameters over the bare muddy station (21/02/2013, from 11:30 to 18:30). See Fig. 3 caption for variable details.

Fig. 5. Aquatic Eddy Covariance and Benthic Chamber O_2 fluxes comparison over Maerl bed (A) and bare muddy sediment (B) stations. EC fluxes (± standard deviations) were averaged over each corresponding BC incubation hour to allow comparisons; number of EC values used for calculations were 0, 4 and 4 at Maerl bed and 2, 3 and 3 at bare muddy sediment stations, respectively.

Fig. 6. Benthic O_2 fluxes measured by EC over the Maerl bed station plotted as a function of photosynthetically active radiation (PAR) and water height (H). A) $FO_2 = 0.6\pm0.1PAR - 13.2\pm6.5$ ($R^2 = 0.76^*$, $p < 0.0001$, $n = 17$). (B) $FO_2 = 54.1\pm8.1H - 291.4\pm47.4$ ($R^2 = 0.75^*$, $p < 0.0001$, $n = 17$).

Fig. 1

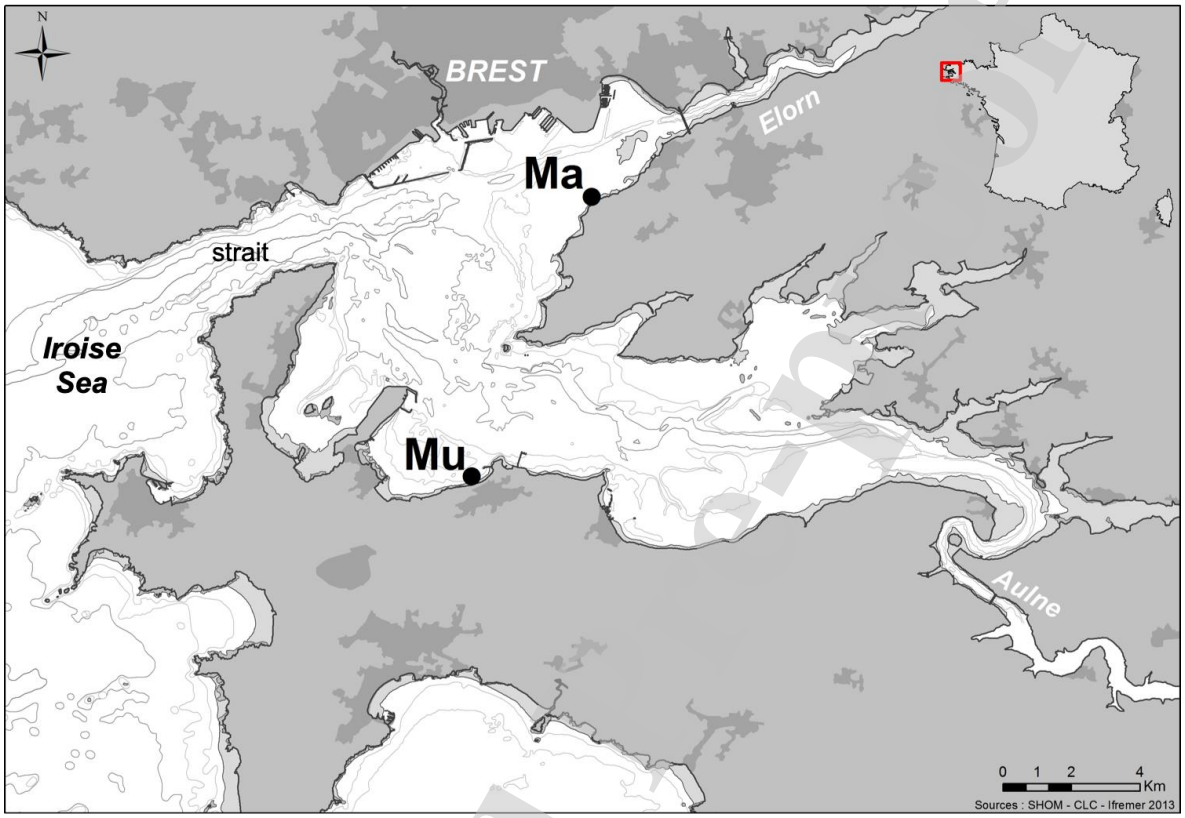

Fig. 2

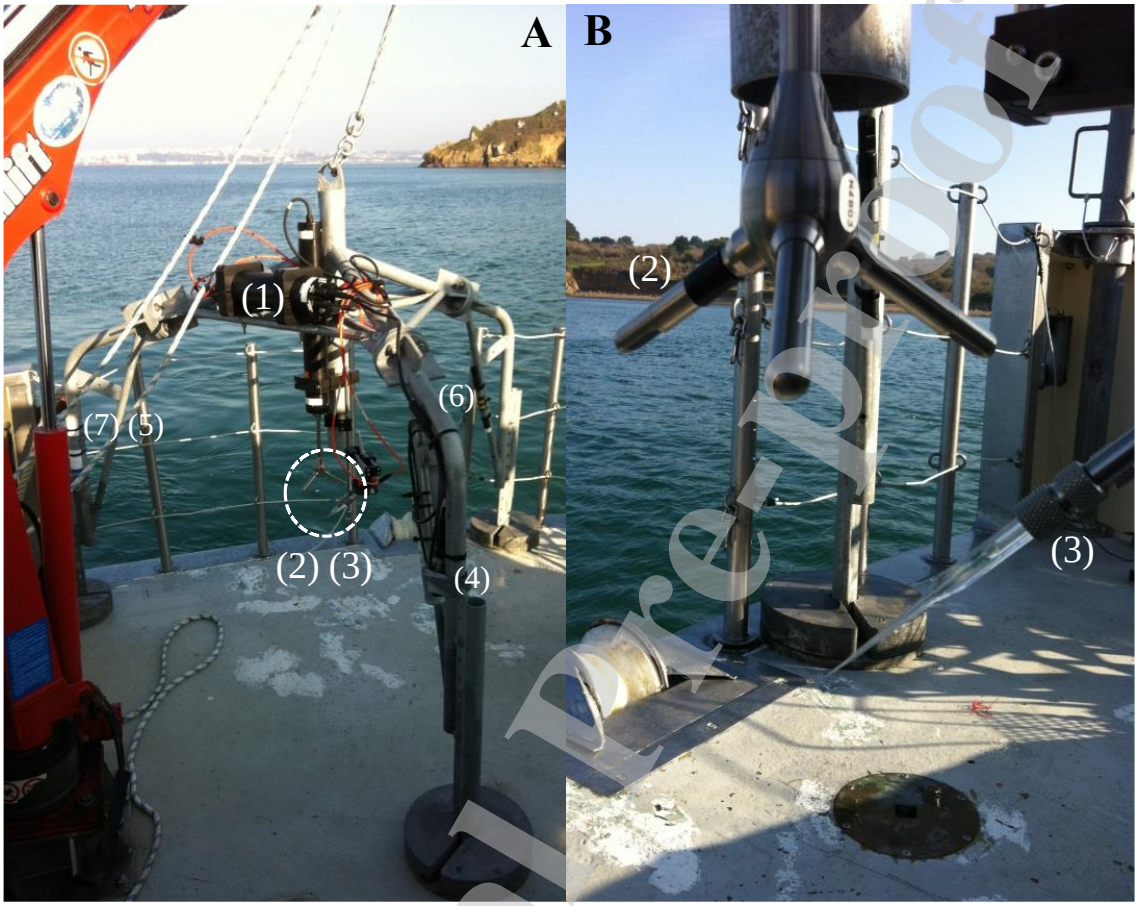

Fig. 3

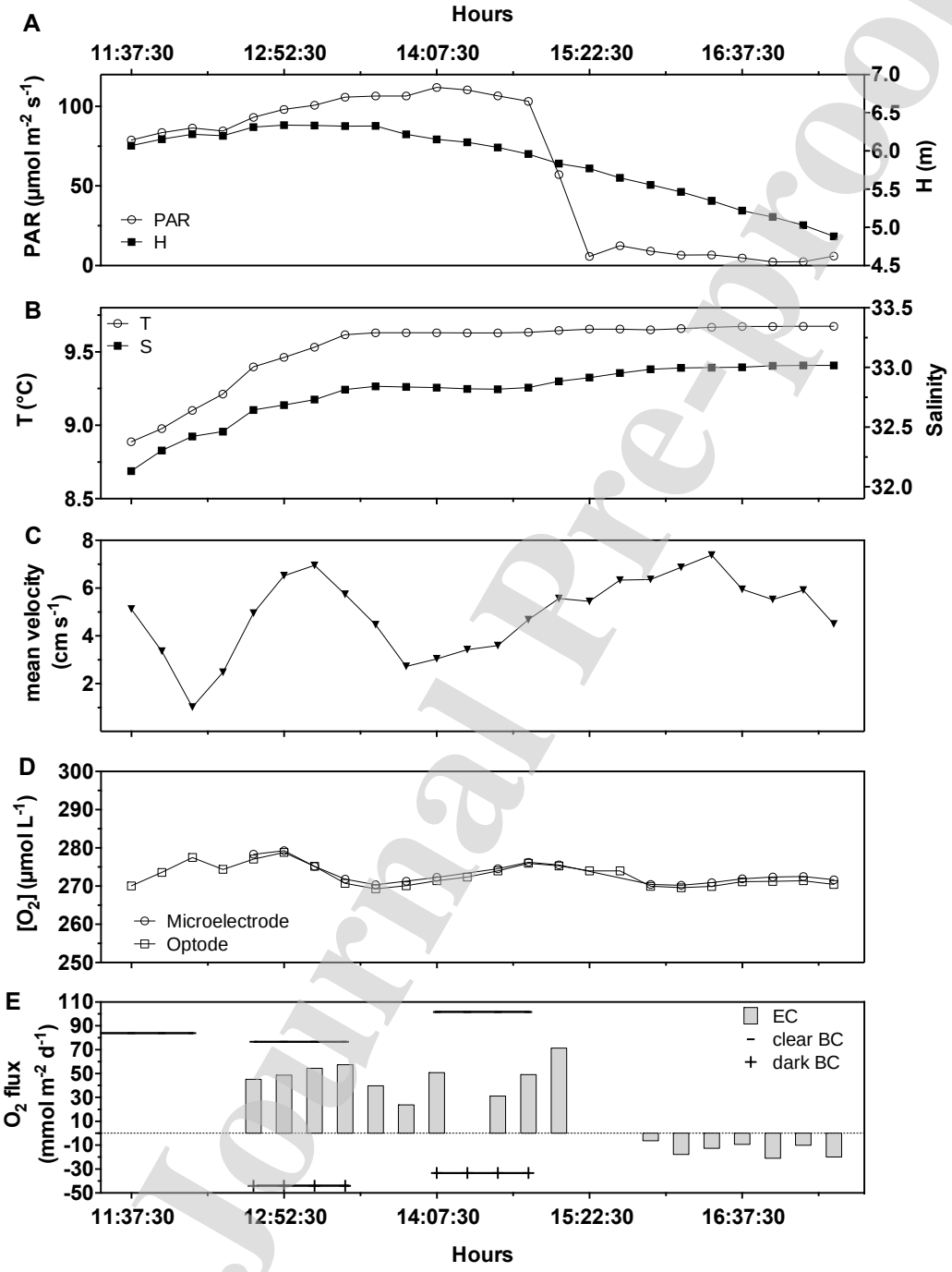

Fig. 4

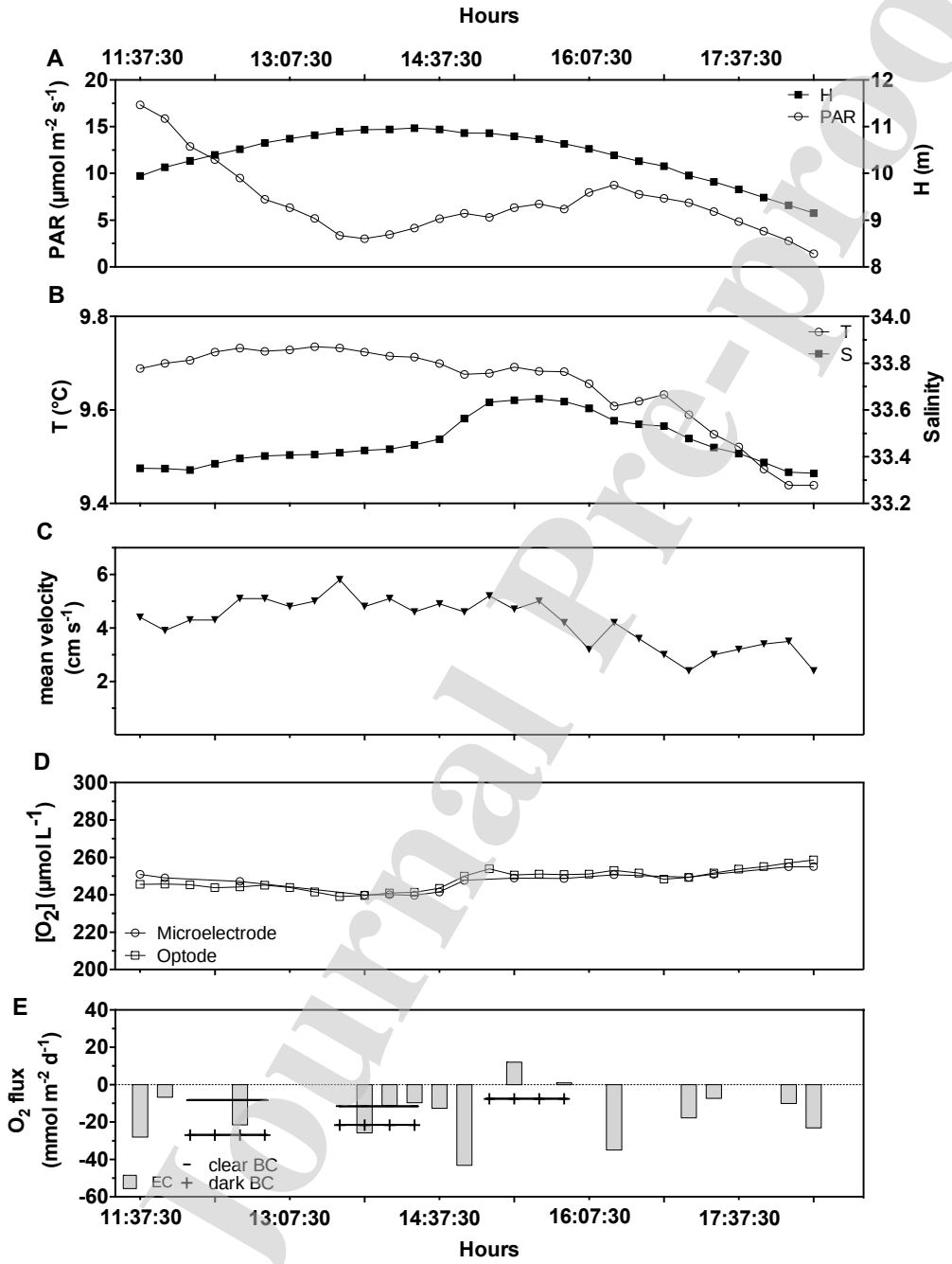

Fig. 5

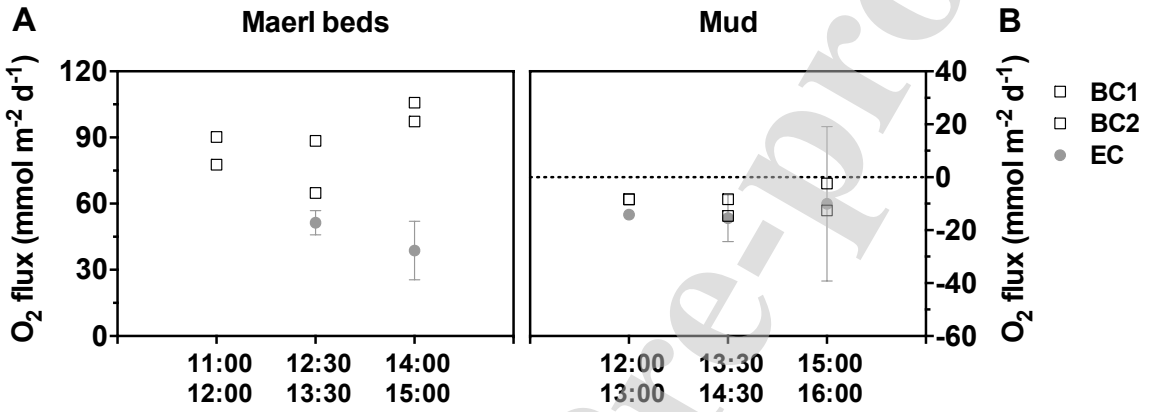

Fig. 6

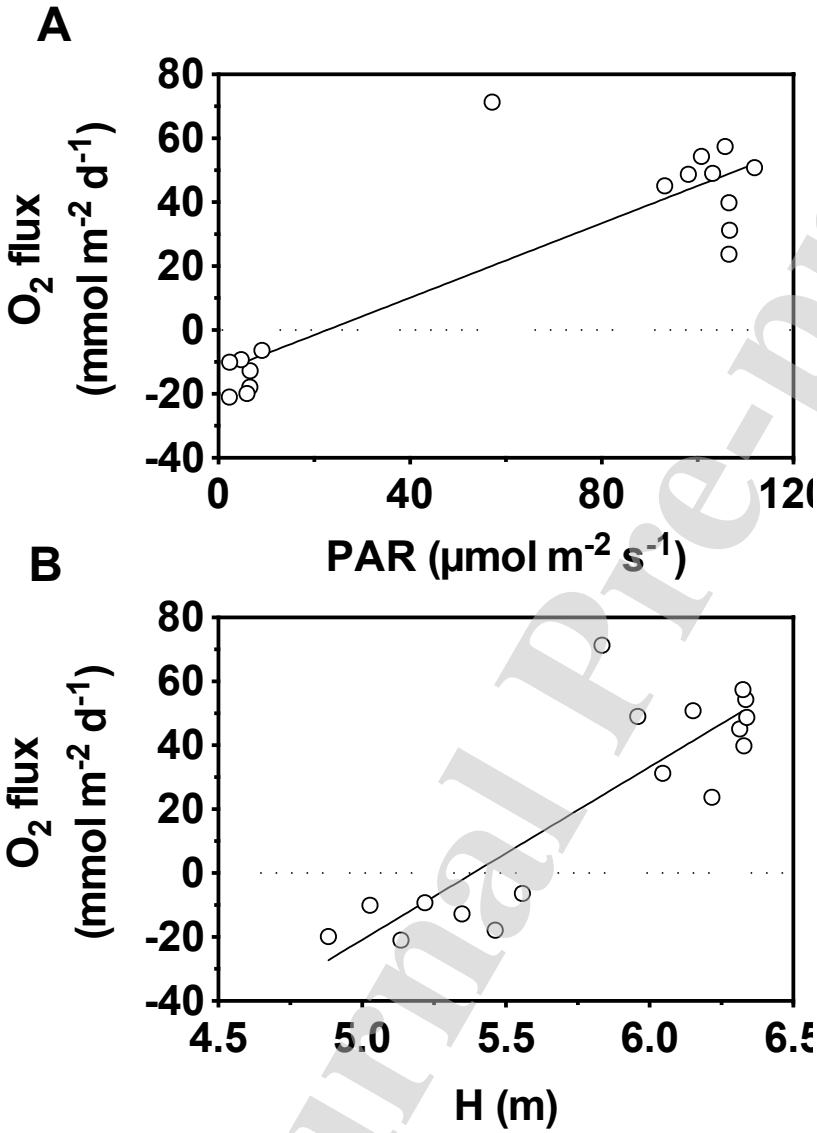

Table 1. Environmental parameters and benthic O_2 fluxes measured over Maerl beds (Ma) and bare muddy sediments (Mu) in the Bay of Brest (20-21/02/2013). Averages and ranges are presented in bold (± standard deviation) and in italic between brackets, respectively. PAR, photosynthetically active radiation. H, water height. T_w, water temperature. $[O_2]_\mu$ and $[O_2]_{sdot}$ oxygen concentrations measured by the EC microelectrode and the SDOT optode, respectively. EC FO_2, benthic O_2 fluxes measured by EC during the whole deployments. BC FO_2, O_2 fluxes measured by clear and dark benthic chambers during daytime. EC raw data have been sampled at 64 Hz and environmental parameters have been measured every two minutes. All values were averaged over 15 min. bursts.

	Maerl bed (M_a)	**Mud (M_u)**
PAR	**62.1** ± 44.0	**6.9** ± 3.7
(µmol m^{-2} s^{-1})	*(2.3 − 111.9)*	*(1.4 − 17.3)*
	N=24	N=28
H	**5.9** ± 0.4	**10.4** ± 0.5
(m)	*(4.9 − 6.3)*	*(9.1 − 11.0)*
	N=24	N=28
T_w	**9.5** ± 0.2	**9.6** ± 0.1
(°C)	*(8.9 − 9.7)*	*(9.4 − 9.7)*
	N=24	N=28
Salinity	**32.7** ± 0.3	**33.5** ± 0.1
	(32.1 − 33.0)	*(33.3 − 33.7)*
	N=24	N=28
Mean velocity	**4.9** ± 1.6	**4.2** ± 0.9
(cm s^{-1})	*(1.0 − 7.4)*	*(2.4 − 5.8)*
	N=24	N=28
$[O_2]_\mu$	**273** ± 3	**248** ± 5
(µmol L^{-1})	*(270 − 279)*	*(240 − 255)*
	N=17	N=15
$[O_2]_{sdot}$	**273** ± 3	**249** ± 6
(µmol L^{-1})	*(269 − 279)*	*(239 − 265)*
	N=24	N=26
EC O_2 flux	**22.0** ± 32.7	**-15.9** ± 14.0
(mmol m^{-2} d^{-1})	*(-21.0 − 71.3)*	*(-43.1 − 12.1)*
	N=17	N=15
Clear BC O_2 flux	**87.4** ± 14.5	**-9.1** ± 4.2
(mmol m^{-2} d^{-1})	*(64.8 − 105.7)*	*(-14.6 − -2.4)*
	N=6	N=6
Dark BC O_2 flux	**-38.6** ± 7.6	**-18.7** ± 10.0
(mmol m^{-2} d^{-1})	*(-44.0 − -33.3)*	*(-27.0 − -7.6)*
	N=2	N=3
Footprint length	**171** ± 64	**115** ± 35
(m)	*(63 − 257)*	*(57 − 195)*
	N=12	N=26
Footprint upstream	**7** ± 3	**5** ± 2
distance (m)	*(2 − 10)*	*(2 − 10)*
	n=12	n=26
Footprint width (m)	**2.6**	**2.6**

Table 2. Benthic O_2 flux regional comparisons across sites and methodologies (BC and EC techniques). Fluxes are in mmol m^{-2} d^{-1}. EC fluxes measured in this study and presented in Table 2 correspond to daily rates estimated from daylight hours.

Benthic O_2 fluxes (Maerl station)	**Benthic O_2 fluxes (Mud station)**	**Site characteristics**	**Methodology**	**References**
35.0 ± 5.8 (NCP)	**-3.7 ± 1.7** (CR)	Temperate (Bay of Brest)	Aquatic EC (Winter)	This study
87.4 ± 14.5 (NCP)	**-9.1 ± 4.2** (NCP)		Clear BC (Winter)	
-38.6 ± 7.6 (CR)	**-18.7 ± 10.0** (CR)		Dark BC (Winter)	
13.9 ± 7.2 (NCP)		Temperate (Loch Sween, Scotland)	Aquatic EC (Winter)	Attard et al. (2015)
-25.2 ± 9.1 (CR)			Dark BC (Winter)	
79.2 ± 42.5 (NCP)		Temperate (Bay of Brest)	Clear BC (Winter)	Martin et al. (2007a, b)
-67.2 ± 12 (CR)	**21.3 ± 5.3** (CR)		Dark BC (Winter)	
-108.6 ± 29.8 (NCP)		Temperate (Bay of Brest)	Clear BC (Spring)	Martin et al. (2005)
	-19.2 ± 2.4 (CR)	Temperate (Bay of Brest)	Dark BC (Winter)	Ni Longphuirt et al. (2007)
	-39 ± 3; -46 ± 8 (CR)	Temperate (Aarhus Bay and Limfjorden Sound, Denmark)	Aquatic EC	Berg et al. (2003)

Highlights

- Benthic O_2 exchange was monitored in a temperate bay in winter
- The aquatic Eddy Covariance and benthic chambers were deployed over two stations
- Maerl beds and muddy sediments generally released and consumed O_2
- Techniques showed similar patterns of temporal O_2 flux changes at both sites
- Benthic chambers may have underestimated Maerl community respiration

Pierre Polsenaere: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing

Bruno Deflandre: Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Funding acquisition

Gérard Thouzeau: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - Review & Editing, Funding acquisition

Sylvain Rigaud: Methodology, Writing - Review & Editing

Tom Cox: Software, Validation, Formal analysis

Erwan Amice: Methodology, Resources

Thierry Le Bec: Methodology, Resources

Isabelle Bihannic: Methodology, Resources

Olivier Maire: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition

Declaration of interests

✚The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: