



# Macrobenthic diversity and sediment-water exchanges of oxygen and ammonium: Example of two subtidal communities of the eastern English Channel



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## ARTICLE INFO

### Keywords:

Benthic communities  
Sediment-water fluxes  
Organic carbon mineralization  
Eastern English Channel  
Macrofauna diversity  
*Abra alba*  
*Ophiothrix fragilis*

## ABSTRACT

In organic-rich shallow habitats, benthic macrofauna is known to play a major role in the geochemical functioning of surficial sediments through its metabolism, as well as its bioirrigation and/or bioturbation activity. In this paper, the effects of benthic macrofauna on metabolic fluxes at the sediment-water interface were studied at four dates, from winter to late summer, on two major macrobenthic communities of the eastern English Channel (macrotidal system): the fine sand *Abra alba* community (2 stations) and the sandy gravel *Ophiothrix fragilis* community (1 station). Oxygen and ammonium fluxes showed temporal changes that could be attributed to the variation of sea water temperature. Once the effect of temperature removed (using  $Q_{10} = 2.5$ ), the average fauna mediated fluxes ( $F_{Fauna}$ ) represented respectively 77% and 76% of average total fluxes. Considering the whole dataset, species number and biomass showed a significant correlation with fauna mediated fluxes of  $O_2$  and  $NH_4^+$ , while the relationships with abundance were not significant. The species composition of the community might influence ecosystem functioning, but in the present study, functional groups have a very poor relationship with  $F_{Fauna}$  ( $O_2$ ) and  $F_{Fauna}$  ( $NH_4^+$ ). Despite the presence of engineer species, establishing general and simple rules to link macrofaunal parameters to functional attributes remains very difficult, suggesting that communities rather followed the idiosyncrasy and rivet hypothesis.

## 1. Introduction

In coastal ecosystems, surficial sediments play a major role in nutrient recycling and organic matter decomposition (Middelburg et al., 1996) and can behave either as sinks or sources of carbon and nutrients for the water column (Berner, 1989). Sediment organic matter can be buried or go through a cascade of reactions that lead to the oxidation of sedimentary carbon (Froelich et al., 1979); this succession, called diagenetic sequence, causes the release of dissolved inorganic compounds that accumulate in the pore water and create concentration gradients at the sediment-water interface (Boudreau, 1997).

The exchange of dissolved substances and mineralization processes are mainly related to microbial organisms (Blackburn, 1988), but the presence of benthic meio- and macro-organisms might largely modify the dynamics of benthic mineralization. Indeed, macrofaunal activities affect sediment properties (water content, porosity, mixing by bioturbation...), increase the surface area available for particles and

solutes exchanges at the sediment-water interface, and contribute to interfacial dissolved exchanges through their physiological activities (respiration, excretion...; Aller, 1994; Welsh, 2003; Meysman et al., 2005; Kristensen et al., 2012). Moreover, benthic macrofauna enables and promotes dissolved substances' transfer between neighboring and non-adjacent sediment layers (Marinelli and Boudreau, 1996).

In recent years, several experimental studies have been conducted in mesocosms to evaluate the relationship between mineralization processes and macrobenthic species diversity. These experiments have shown that the presence of macrofauna increases the intensity of mineralization processes, with higher sediment oxygen demand (e.g. Waldbusser et al., 2004; Michaud et al., 2005; Ieno et al., 2006) or enhanced ammonium release (Marinelli and Williams, 2003; Waldbusser et al., 2004). However, most of these experiments were performed in enclosures containing a single species (Michaud et al., 2010) or an artificial combination of few species (Michaud et al., 2006), whereas most of the authors advocate the need to consider the complex

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interactions between the different functional groups constituting benthic assemblages (Raffaelli et al., 2003; Mermillod-Blondin et al., 2005). Indeed, two species belonging to the same functional group may have contrasting effects on the mineralization processes [for example: two biodiffuser bivalves *Macoma balthica* (Linnaeus) and *Mya arenaria* (Linnaeus); Michaud et al., 2006]. Hence, all those specificities might have large consequences on the functioning of coastal benthic ecosystems, in the context of the general loss of diversity in marine populations (Snelgrove, 1998), and the accurate determination of the role of intact macrobenthic communities on geochemical processes appears to be crucial (Raffaelli et al., 2003; Rossi et al., 2008). Several studies have evaluated in various environments the relationship between natural macrobenthic communities and geochemical processes, and have shown that macrofaunal functional richness is a predictor of prime interest to understand the variability of benthic exchanges (Belley and Snelgrove, 2016, 2017) and its temporal variability (Link et al., 2013). Moreover, depending on the environmental forcings and conditions, engineer species or specific benthic groups (omnivores, detritivores, funnel feeders) have a wider impact on organic matter distribution and mineralization (Queirós et al., 2011; Belley and Snelgrove, 2016, 2017). A variety of hypotheses summarizes the possible relationship between species diversity and ecosystem function, among which (1) the “rivet” hypothesis, which suggests that each species has a unique effect on ecosystem function, and (2) the “redundant species” hypothesis, which suggests that only a minimum number of species is necessary for ecosystem function. The “idiosyncratic” hypothesis suggests non-significant effects of changes in species richness on ecosystem functioning (Covich et al., 2004).

Unfortunately, accurately dissociating the role of macrofaunal biodiversity among mineralization processes (mainly bacteria-mediated) remains a challenge, especially in coastal zones characterized by a high spatial heterogeneity or where abiotic forcing prevail (Strong et al., 2015). However, the difference between total fluxes and diffusive fluxes has already been proven to be a good proxy and has been used to evaluate fauna-mediated impact on sediment geochemistry (Kuwaie et al., 1998; Glud et al., 2003; Wenzhöfer and Glud, 2004; Dedieu et al., 2007).

In the present work, we examined the temporal variability of benthic mineralization processes in two undisturbed natural macrobenthic communities which represent the major subtidal communities encountered in the shallow soft-bottom sediments of the Eastern English Channel: the muddy fine sand *Abra alba* (Wood) community and the sandy gravels *Ophiothrix fragilis* (Abildgaard) community: (Davoult et al., 1988; Gentil and Cabioch, 1997; Dauvin et al., 2002, 2013). The *A. alba* community covers around 80% of the shallow (< 15 m) seabed of the Eastern English Channel and Southern North Sea (Desroy et al., 2002) and dense aggregations in the *O. fragilis* community were already proven to have a significant effect on organic matter exchanges at the sediment-water interface (Davoult et al., 1998). These two communities are characterized by the presence of few dominant species such as the polychaetes *Lagis koreni* (Malmgren), *Owenia fusiformis* (Delle Chiaje), *Lanice conchilega* (Pallas), the introduced bivalve *Ensis directus* [(Conrad); in the muddy fine sand *A. alba* community] and the ophiurid *O. fragilis* (in the sandy gravels community), likely to have a major influence on the exchange of dissolved substances at the sediment-water interface. Moreover, most of these dominant species are well known as engineer species, actively modifying sediment trapping, particulate settling and resuspension processes (Allen, 1998; Dannheim and Rumohr, 2011; Wrede et al., 2017).

In this habitat context, the objectives of this study were: 1) to determine the temporal and spatial variability in fluxes of dissolved substances at the sediment-water interface (oxygen and ammonium) so that budgets might be established in those subtidal coarse sediments where measurements are scarce, 2) to evaluate the role of benthic macrofauna on mineralization processes and to test whether general

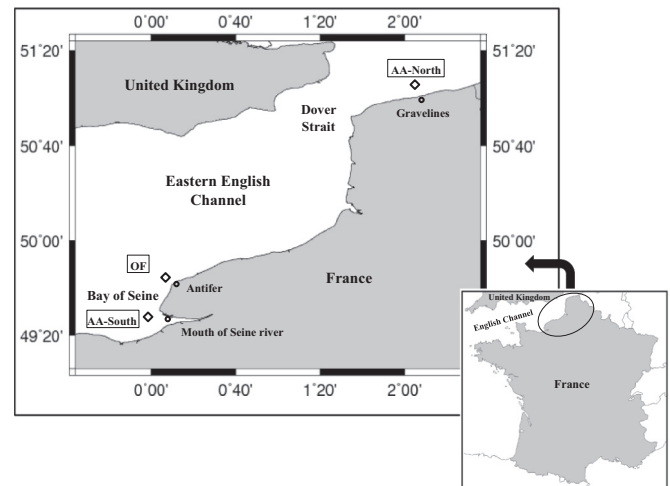


Fig. 1. Map and locations of the sampling sites (open diamonds) in the Eastern English Channel. Station AA-South: *A. alba* community of Bay of Seine (mouth); station OF: sandy gravels community with *O. fragilis* of Antifer and station AA-North: *A. alba* community of Gravelines, Dover Strait.

rules for such interactions can be established for the two selected habitats.

## 2. Materials and methods

### 2.1. Study stations

Three stations were studied in the subtidal zone along the French coast of the eastern English Channel (Fig. 1). This epicontinental sea is characterized by strong tidal currents which favor a sedimentary cover dominated by 1) the gravely-sandy sediments and pebble bottoms offshore the Bay of Seine and in the Dover Strait, and 2) the muddy to fine sand bottoms in the eastern part of the Bay of Seine and along the Opal coast from the Bay of Somme to the Belgian frontiers (Larsonneur et al., 1982). Offshore-coastal gradients are well marked for hydrological parameters such as salinity, turbidity, temperature, nutrients and particulate organic matter concentrations (Salomon and Breton, 1991; Bodineau et al., 1999). Indeed, the influence of rivers (Seine, Somme, Canche and Authie) results in a freshening of the coastal water mass called in French “Fleuve Côtier” (Brylinski et al., 1991) affecting the littoral hydrological parameters mainly during spring tides. The sampling stations were chosen within the *A. alba* community and the sandy gravel *O. fragilis* community, on the basis of the maps drawn by Davoult et al. (1988), Gentil and Cabioch (1997) and Dauvin and Dewarumez (2002), describing sediment types and associated benthic communities in the eastern English Channel. The location of the stations studied, as well as the sampling dates and the expected macrofauna communities and sediment types are reported in Table 1. The *A. alba* community was studied both at the mouth of the Seine estuary and in the south of the North Sea at Gravelines (respectively stations AA-South and AA-North), whereas the sandy gravels community with *O. fragilis* was studied at Antifer station, offshore the Bay of Seine (OF station). The sampling stations were visited during seven campaigns between February 2010 and March 2011. For readability purposes, sampling dates were gathered according to a “seasonal” pattern: winter (Feb. and March samples), spring (April), early summer (June, July) late summer (September) (Table 1). Unfortunately, the station (AA-North) was not sampled in spring and late summer 2010 due to bad meteorological conditions.

### 2.2. Sediment-water exchanges

Due to the coarseness of *O. fragilis* bottoms and to the ambient

Table 1

Location, depth, sampling dates, sediment and bottom water characteristics (sediment fractions, porosity, organic matter content, oxygen concentration and saturation, ammonium concentration, temperature and Oxygen Penetration Depth in the sediment), as well as macrofauna communities parameters (taxonomic richness, abundance, biomass) and trophic information (bioturbation type, trophic group, abundance and biomass) for dominant species in the sites sampled in the eastern English Channel during the survey.

Stations name and location	AA-South			OF			AA-North			
	Winter	Spring	Early summer	Late summer	Winter	Spring	Early summer	Late summer	Winter	Early summer
Bay of Seine (mouth)					Bay of Seine (Antifer)				Dover strait (Gravelines)	
	(Latitude: 49°26'250 N, Longitude: 0°00'450 E)				(Latitude: 49°40'850 N, Longitude: 0°02'350 E)				(Latitude: 51°10'400 N, Longitude: 2°40'600 E)	
Water depth (m)	12				30				10	
Seasons and sampling dates	Winter	Spring	Early summer	Late summer	Winter	Spring	Early summer	Late summer	Winter	Early summer
	15/16-Feb-10	19/22-Apr-10	5/8-Jul-10	3/6-Sep-10	8/10-Mar-11	19/22-Apr-10	5/8-Jul-10	3/6-Sep-10	4-Feb-10	30-Jun-10
Sediment type	Muddy fine sand				Sandy gravel				Muddy fine sand	
Gravel percentage [ $> 5$ mm; 1.6 mm]	0.7	1.0	0.7	7.9	65.9	34.7	40.6	43.0	0.7	0.5
Sand percentage [1.6 mm; 0.05 mm]	91.3	98.6	93.0	81.6	33.1	63.3	55.4	54.7	86.6	90.3
Silt percentage [ $< 0.05$ mm]	8.0	0.5	6.4	10.7	1.0	2.0	4.0	2.3	12.6	9.2
Average Porosity (0–1 cm <sup>3</sup> /1.5–10 cm)	0.44/0.41	0.58/0.52	0.62/0.45	0.63/0.52	0.53/0.39	0.38/0.36	0.61/0.40	0.43/0.37	0.46/0.42	0.52/0.43
Average Organic Matter Content (0–3 cm) (% of dry weight, $\pm$ SD)	1.23 $\pm$ 0.14	3.45 $\pm$ 0.41	3.60 $\pm$ 0.72	3.69 $\pm$ 0.51	1.90 $\pm$ 0.75	1.84 $\pm$ 0.51	3.00 $\pm$ 2.09	1.83 $\pm$ 0.21	1.34 $\pm$ 0.36	1.79 $\pm$ 0.13
Average [O <sub>2</sub> ] bottom water ( $\mu$ M, $\pm$ SD)	311.0 $\pm$ 3.3	291.8 $\pm$ 8.2	220.6 $\pm$ 4.2	272.8 $\pm$ 3.9	315.6 $\pm$ 9.8	289.8 $\pm$ 7.5	238.2 $\pm$ 6.9	239.2 $\pm$ 8.3	328.6 $\pm$ 8.3	250.3 $\pm$ 15.4
Average [O <sub>2</sub> ] at saturation ( $\mu$ M, $\pm$ SD)	322.5	285.7	242.6	244.0	292.1	282.0	242.6	244.0	308.8	244.0
Average [NH <sub>4</sub> <sup>+</sup> ] bottom water ( $\mu$ M, $\pm$ SD)	12.4 $\pm$ 3.2	0.9 $\pm$ 0.4	12.8 $\pm$ 3.7	3.1 $\pm$ 1.1	0.4 $\pm$ 0.1	0.6 $\pm$ 0.3	3.5 $\pm$ 2.1	1.3 $\pm$ 0.3	1.5 $\pm$ 0.5	9.2 $\pm$ 2.6
Bottom water temperature (°C)	5.0	10.0	18.0	18.0	8.6	10.0	18.0	18.0	5.7	18.0
Average Oxygen Penetration Depth (OPD, mm, $\pm$ SD)	6.40 $\pm$ 1.19	2.13 $\pm$ 0.67	2.18 $\pm$ 0.80	3.70 $\pm$ 0.83	n.d.	3.58 $\pm$ 1.31	1.93 $\pm$ 0.37	4.15 $\pm$ 0.50	2.7 $\pm$ 0.96	1.28 $\pm$ 0.94
Macrofauna communities	<i>Abra alba</i> community				sandy gravel community with <i>Ophiotrix fragilis</i>				<i>Abra alba</i> community	
Average species richness (ind.0.016 m <sup>-2</sup> , $\pm$ SD)	10.0 $\pm$ 2.0	2.0 $\pm$ 1.0	13.0 $\pm$ 1.0	9.0 $\pm$ 1.0	4.0 $\pm$ 2.0	3.0 $\pm$ 1.0	3.0 $\pm$ 1.0	3.0 $\pm$ 1.0	17.0 $\pm$ 3.0	10.0 $\pm$ 2.0
Average abundances (ind.m <sup>-2</sup> , $\pm$ SD)	1719 $\pm$ 678	406 $\pm$ 363	9750 $\pm$ 9521	22,094 $\pm$ 8922	594 $\pm$ 237	188 $\pm$ 88	547 $\pm$ 107	359 $\pm$ 172	13,500 $\pm$ 2597	9422 $\pm$ 4208
Average Biomass (g of ash-free dry weight.m <sup>-2</sup> , $\pm$ SD)	18.5 $\pm$ 12.5	7.2 $\pm$ 11.9	165.5 $\pm$ 124.1	53.2 $\pm$ 21.8	16.6 $\pm$ 7.3	6.2 $\pm$ 4.2	16.0 $\pm$ 9.1	24.9 $\pm$ 19.9	160.6 $\pm$ 27.6	301.7 $\pm$ 108.2
Numerically dominant species, bioturbation type and trophic group (M: Mixed, SF: Suspension Feeder, SDF: Subsurface Deposit Feeder)	<i>Abra alba</i> , Biodiffusor, M				<i>Ophiotrix fragilis</i> , Biodiffusor, SF/SDF				<i>Abra alba</i> , Biodiffusor, M	
(Abundance in ind.m <sup>-2</sup> /Biomass in g of ash-free dry weight.m <sup>-2</sup> )	0/0.0	0/0.0	844/3.3	406/1.3	391/16.5	47/2.2	375/15.1	188/8.2	156/0.9	844/3.0
	828/3.1	281/0.8	5984/6.9	20,063/23.0					7891/122.0	1922/254.0
	47/0.2	0/0.0	1438/0.9	484/0.3					1031/2.6	4172/20.5

hydrodynamism, the sediments retrieved for flux measurements were always sampled using a Reineck boxcorer (1/36 m<sup>2</sup>) equipped with flapper vent, as the use of a sediment multicorer (better adapted for lower disturbance during retrieval) demonstrated poor sampling efficiency. After retrieval, each undisturbed core was immediately sub-sampled by hand with a Perspex tube (inner diameter (i.d.): 15 cm, length: 35 cm), with final heights of around 15 cm of sediments and 20 cm of overlying water. Four cores were collected at each station for total flux measurements. Furthermore, 20 l of bottom water (1–2 m above the sediment) were sampled with Niskin bottles and immediately transferred into an inflatable reserve tank, while excluding air bubbles. After retrieval, the cores and the reserve tank were maintained in the dark, at *in situ* temperature. Back to the laboratory, the four cores were carefully sealed with Perspex top plates equipped with peripheral sealing gaskets. Rotating magnets fixed below the upper plate of each sealed core prevented any gradient formation (Cowan et al., 1996). A hole in the plate allowed inserting a rubber stopper with two connections: one for the removal of overlying water for analysis and the other for the replacement of bottom water from the inflatable reserve tank. Cores were incubated for a period of 24 to 36 h in a dark refrigerated cabinet at *in situ* temperature  $\pm 1^\circ\text{C}$  [see Denis et al., 2001 for a detailed description of the incubation method]. During the incubations, the overlying water of each core and the reserve tank was sampled every 3 h using a 60 ml plastic syringe, carefully avoiding or excluding air bubbles. Only the incubations of the cores from Station AA-North in July were stopped after 9 h, due to a rapid decrease of oxygen concentrations in the water overlying each core. The overlying water removed from each core was immediately replaced by an equivalent volume of bottom water from the reserve tank. The water sampled in each core and in the reserve tank was transferred into pre-rinsed 20 ml glass flasks where oxygen was immediately analysed by Winkler microtitration (adapted from Aminot and Chaussepied, 1983; see Denis et al., 2001 for details). The remaining water sample was filtered through GF/F Whatman glass fibre filters (0.7  $\mu\text{m}$ ) and transferred into 20 ml polypropylene flasks where ammonium was determined following the indophenol-blue method of Solorzano (1969).

At the end of each incubation period, the four cores were intended to be used for various analyses:

- The first core was used for dissolved oxygen profiles examination. For each site, six or seven oxygen microprofiles were performed in the dark using miniaturized Clark-type O<sub>2</sub> microsensors (100  $\mu\text{m}$  tip diameter, OX100, Unisense, Denmark). Diffusive flux calculation procedure from microprofiles is explained in Section 2.5. A two-point linear calibration was achieved for each microsensor between the zero oxygen in the anoxic sediments (0% O<sub>2</sub>) and oxygen-saturated water (100% O<sub>2</sub> in bubbled water).
- Two cores were sub-sampled with seven small diameter cores (i.d.: 2.7 cm) for porosity measurement, organic matter content estimation and pore-water extraction (dissolved ammonium concentration). For interstitial water analysis, six of these subcores were cut with a vertical resolution of 0.5 cm down to 5 cm and every cm down to a 10 cm depth. Slices from the same depth of three subcores were pooled together, so that two similar vertical series were constituted and interstitial water was immediately extracted by refrigerated centrifugation (3000 rpm, 15 min), filtered (Whatman GF/F, 0.7  $\mu\text{m}$ ) and further analysed following the same analytical procedure as for overlying water. The two remaining subcores were used for porosity and organic matter measurements. They were sliced every 0.5 cm down to 3 cm depth and then every centimetre to a 10 cm depth. Then, each slice was dried in an oven (50  $^\circ\text{C}$ ) for 72 h and afterwards, 2 g of dry sediment were used for the analysis of organic matter content by the method of loss of weight on ignition (500  $^\circ\text{C}$ , 6 h), according to Luczak et al. (1997).
- The last core was dedicated to macrofauna analysis, as well as the

sediment remaining of the two cores sub-sampled and the core used for oxygen microprofiling.

### 2.3. Sediment characteristics

At each station, one additional sediment sample was collected by using a Van Veen grab. This sample was used to analyse grain-size characteristics of surficial sediment by sieving (18 sieves, 0.050–5 mm, AFNOR sizes) after drying in an oven (48 h; 110  $^\circ\text{C}$ ). Each size class of particles was weighted ( $\pm 0.01$  g) and results were expressed as a percentage of the total weight of dry sediment.

### 2.4. Macrofauna

For the macrofauna analysis, the sediment was sieved on 1 mm circular mesh, and fixed in a 10% formaldehyde solution. In the laboratory, macrofauna was identified to the lowest possible taxonomic level, counted and the biomass of each taxon was determined as g of AFDW-m<sup>-2</sup> (Ash-Free Dry Weight) by loss on ignition, without excluding shells. Macrofaunal data were analysed on the basis of the usual parameters (abundance, biomass and species richness) but also functionally, according to their bioturbation groups (*i.e.*, biodiffusers, gallery diffusers, upward conveyors, downward conveyors and regenerators; François et al., 1997) and their trophic groups (suspension feeders, surface deposit feeders, subsurface deposit feeders, carnivores and mixed; Pearson, 1971; Garcia et al., 2011; Jumars et al., 2015).

### 2.5. Flux calculations

Generally, in order to quantify the macrofaunal influence on the oxygen and ammonium exchanges at the sediment-water interface, the fauna-mediated fluxes ( $F_{\text{Fauna}}$ ) of marine sediments have been calculated from estimates of respiration or excretion of organisms without sediments or in low-reactive sediments (Wenzhöfer and Glud, 2004). Such estimates do not include irrigation related activity, where the enhanced transport of oxygenated water into the sediment leads to increasing sediment O<sub>2</sub> uptake rates and modifications in the mineralization pathways of nitrogen (Forster and Graf, 1995; Michaud et al., 2006; Braeckman et al., 2010). An alternative procedure consists in assuming that fauna-mediated fluxes are the difference between total uptake and diffusive uptake, hence allowing its calculation simply by subtracting diffusive flux ( $F_{\text{Diff}}$ ) from total flux ( $F_{\text{Total}}$ ) (Archer and Devol, 1992; Glud et al., 2003; Wenzhöfer and Glud, 2004).

Total fluxes were determined by regressing the change of oxygen and ammonium concentrations in the overlying water against time. The difference between concentration changes in the overlying water of each core and in the bottom water allowed the calculation of total oxygen and ammonium fluxes ( $F_{\text{Total}}$ ) at the sediment-water interface. This calculation was corrected for the dilution with bottom water at each sampling point, and for changes in oxygen and ammonium concentrations in the reserve tank, when significant. The variation in ammonium and oxygen concentrations over time were always statistically tested using a linear regression (Student *t*-test against a slope = 0,  $p < 0.05$ ).

From the microelectrode profiles, oxygen diffusive fluxes [ $F_{\text{Diff}}(\text{O}_2)$ ] were calculated according to Berg et al. (1998) by means of the PROFILE model, which uses a curve fitting approach (F-Statistics) by adjusting the calculated oxygen profile to the observed one. Ammonium diffusive fluxes [ $F_{\text{Diff}}(\text{NH}_4^+)$ ] were calculated from the interstitial profiles using Fick's first law of diffusion (Berner, 1980; see Denis et al., 2001 for details).

Fauna-mediated fluxes (considered as the influence of benthic fauna on the exchanges, through their bioirrigation, bioadvection and physiological activities) were calculated by subtracting the diffusive flux ( $F_{\text{Diff}}$ ) (which comprises microbial consumption plus re-oxidation of

reduced compounds) from total fluxes at the seafloor. Even if this indirect calculation only results in a “proxy” of faunal activity and influences on sediment-water exchanges, we considered that this method of calculation was the best way to consider *in situ* processes (avoiding effects of stress on organisms when placed in or handled out of the sediment).

The  $Q_{10}$  factor, which aims to quantify the direct temperature dependence of the process rate across a temperature range of 10 °C (using Arrhenius relation) (see Lloyd and Taylor (1994) for detailed calculation procedures) was used to recalculate fluxes for a “standard reference” temperature, so that the influence of temperature was removed. Based on previous works on aerobic respiration of Thamdrup et al. (1998) in coastal temperate sediments (Aarhus Bay, Denmark) and the approach developed by Dedieu et al. (2007) for the Mediterranean Sea,  $Q_{10}$  was set to 2.5.

## 2.6. Statistics

Because of the small number of samplings carried out on AA-North station, results from AA-North and AA-south were compared to determine the variability within one sedimentary habitat. Then, only results from AA-South and OF were compared to test the differences among the two contrasted habitats.

Temporal and spatial changes for each sediment characteristic (porosity and organic matter content) and fluxes of dissolved substances were tested using two-way crossed analyses of variance (ANOVA; considering dates and stations as orthogonal fixed factors; Scherrer, 1984). Homogeneity of variances was tested using Bartlett's Chi-squared test and data were log-transformed whenever necessary ( $O_2$  fluxes).

To identify the external factors responsible for oxygen and ammonium total fluxes, we graphically inspected all the univariate relationships with abiotic/biotic variables, checking for heteroscedasticity using the Shapiro-Wilk test, and log-transformation of data was applied when necessary ( $F_{Total}(O_2)$ ). The relationships between benthic fauna parameters and sediment fluxes were evaluated by means of linear Pearson's correlations. In addition, we analysed the contributions of independent external factors (temperature, organic matter, macrofauna parameters: biomass, species richness and abundance) to oxygen and ammonium total fluxes at the three stations using multiple linear regression based on the Akaike Information Criterion (AIC). Application conditions were checked, especially for homoscedasticity of variances, and the residual normality of the model was tested. All statistical analyses were implemented within the software products Statistica and R, with the probability  $\alpha$  set at 0.05.

## 3. Results

### 3.1. Sedimentary characteristics

The granulometry of the three stations studied covered a broad spectrum of grain sizes (Table 1), ranging from coarse gravel (station OF) to fine sand (stations AA-North and AA-South) with a low quantity of silt (between 0.5% in OF up to 1.3% in AA-North). The two stations of the *A. alba* community showed very similar granulometric distributions, with a unique modal class (up to 71.5% of total weight) centred on fine sands, while the silt fraction ranged up to 12.6%. On the contrary, the sandy gravels community (station OF) was characterized by a coarser sediments, with always > 20% of coarse gravel (up to 52% in winter), a main class generally constituted with medium sand, and a low fraction of silts (1 to 4%).

Porosity and organic matter content (Table 1) did not significantly differ neither within the *A. alba* community (between AA-North and AA-South; two-way ANOVA,  $p > 0.05$ ) nor between different communities (OF and AA-South; two-way ANOVA,  $p > 0.05$ ). Moreover,

no significant difference was observed between sampling dates (winter and early summer; two-way ANOVA,  $p = 0.284$ ).

### 3.2. Hydrological parameters of bottom waters

Neither temperature, nor bottom water oxygen were significantly different between the studied stations. The temperature of bottom water followed a typical temporal pattern, from an average of 6.8 °C in winter to 18 °C in late summer with a mean overall temperature of 13 °C (two-way ANOVA,  $p < 0.001$ ). In contrast to ammonium, oxygen concentrations in the bottom water showed a significant decrease from winter to late summer (two-way ANOVA,  $p < 0.01$ ), the lowest values of oxygen concentration in bottom waters being measured during the warmest months (early summer and late summer; Table 1). All calculations of oxygen saturation in bottom waters revealed that those values were close to 100% saturation, except for the *A. alba* community of Bay of Seine (AA-South, 90% in early summer).

### 3.3. Sediment-water total fluxes ( $F_{Total}$ )

For all stations and dates, sediment-water fluxes of oxygen measured by incubation were always significant and directed towards the sediment (Student *t*-test against a slope = 0,  $p < 0.05$ ). We used the term  $F_{Total}(O_2)$  and these oxygen exchanges were reported positively to facilitate graphing. In general,  $F_{Total}(O_2)$  increased from spring to early summer at all stations. Average  $F_{Total}(O_2)$  values ranged from 354 to 1314  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  for AA-South (Fig. 2a) and from 228 to 1359  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  for OF (Fig. 2b) while values recorded at AA-North were up to one order of magnitude higher, ranging from 2268 to 5799  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  (Fig. 2c). Consequently, within the *A. alba* community (AA-North and AA-South),  $F_{Total}(O_2)$  was significantly different between stations, and between sampling dates (Table 2). For AA-South and OF, we observed a significant interaction between sampling dates and stations.

Ammonium fluxes derived from incubated cores,  $F_{Total}(NH_4^+)$ , demonstrated significant interaction between stations and sampling dates within the *A. alba* community (Table 2,  $p < 0.05$ ; Fig. 2d, e, f) but also demonstrated a significant difference between dates when considering the two contrasted communities (OF and AA-south). Ammonium fluxes were mainly directed towards the water column, except in spring when fluxes became negative (sediment uptake instead of release) at stations AA-South and OF, showing a change in the balance of nitrogen metabolism. Again, sediment-water exchanges were clearly higher at AA-North station, where average  $F_{Total}(NH_4^+)$  values ranged from 158 to 3079  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ , whereas they only ranged from -2 to 403  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  on OF and from -83 to 356  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  on AA-South.

### 3.4. Pore water profiles and diffusive fluxes ( $F_{Diff}$ )

All oxygen profiles showed a similar pattern, with concentrations close to oxygen saturation in the water column and a sharp decrease with depth in the sediment (Fig. 3a–c). Oxygen Penetration Depth (OPD) showed spatial and temporal differences within the *A. alba* community, being generally twice higher on AA-South than on AA-North for the same sampling period, and highest values were generally obtained in winter (Table 1). When comparing different communities (OF and AA-South stations), both temporal and spatial changes were significant (Table 2). Diffusive oxygen uptake  $F_{Diff}(O_2)$  varied from 61 to 491  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ , and were always lower than corresponding total fluxes (Fig. 2a–c). AA-South and OF presented  $F_{Diff}(O_2)$  values two to three times lower than the *A. alba* community of AA-North (except in early summer).

For ammonium observed concentrations generally increased with depth in the sediment (Fig. 3d–f), resulting in average diffusive fluxes

$F_{Diff} (NH_4^+)$  ranging from 1 (OF) to  $147 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  (AA-North); however, no significant temporal or spatial change could be evidenced (Fig. 2d–f).

### 3.5. Fauna mediated fluxes ( $F_{Fauna}$ )

Due to the pronounced influence of temperature in the temporal variability of fluxes (see Discussion Section 4.2 for details), fauna mediated fluxes were standardized for the reference average annual water temperature ( $12^\circ\text{C}$ ) using a Q10 factor of 2.5. When considering all stations and dates, average  $F_{Fauna} (O_2)$  represented  $74\% \pm 17\%$  of  $F_{Total} (O_2)$  and  $F_{Fauna} (NH_4^+)$  represented  $83\% \pm 5\%$  of  $F_{Total} (NH_4^+)$ . Fauna-mediated fluxes ( $F_{Fauna}$ ) were about four times lower at AA-South station than in the same community of AA-North (Fig. 4). The lowest averaged  $F_{Fauna} (O_2)$  and  $F_{Fauna} (NH_4^+)$  were recorded in spring on AA-South (respectively  $163 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  and  $-95 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ) while the highest occurred in early summer on AA-North (respectively  $5305 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  and  $2932 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ).

### 3.6. Macrofauna characteristics

A total of 66 taxa were identified during this study with a mean taxonomic richness varying from  $3 \pm 1$  (OF station) to  $17 \pm 3$  (AA-North station). The macrozoobenthos was mainly composed of molluscs, polychaetes, crustaceans, and echinoderms in various proportions depending on the site and date.

Considering all sampling dates, the numerical dominant species at

AA-South were the polychaetes *Owenia fusiformis*, *Lagis koreni*, and the bivalve *A. alba*, while the biomass was dominated by the bivalve *E. directus* and *O. fusiformis* (Table 1). Minimal macrofaunal abundance and biomass values were recorded in spring, while maximal values were observed in early and late summer (concomitant with a massive recruitment of *O. fusiformis*). Other species such as *Liocarcinus marmoreus*, *Tritia reticulata*, *Euspira nitida*, *Nephtys* sp.(all Carnivorous) or *Phaxas pellucidus* (Suspension feeder) were also usually encountered.

On AA-North, high abundances of *E. directus* and *A. alba* were observed, as well as the polychaete *Lanice conchilega*, and the assemblage was also characterized by the presence of *T. reticulata* (Carnivorous), *Notomastus latericeus* (Surface Deposit Feeder), or *Ophiura albida* (Suspension Feeder). The total biomass was dominated by two species: *E. directus* and *L. conchilega*. Species richness and abundance decreased from winter to early summer, but not the biomass, which increased meanwhile, due to the presence of large individuals of *E. directus*. More generally, in the *A. alba* community (AA-North and AA-South), mixed and suspension feeders dominated, whereas biodiffusors (*E. directus*, *A. alba*) and downward conveyors (*L. conchilega* and *O. fusiformis*) were the most abundant bioturbation groups, even if upward conveyors (*L. koreni*) were present in low quantities at both stations.

In OF, the community was paucispecific and largely dominated by the echinoderm *Ophiotrix fragilis* (96% of total abundance and 81% of total biomass; Table 1), characterized by an adaptive feeding strategy between suspension feeding and surface sediment deposit feeding. A few individuals of *Liocarcinus holtsatus* (Carnivorous), *Upogebia deltaura* (Suspension Feeder) or *Psammechinus miliaris* (Mixed) were also

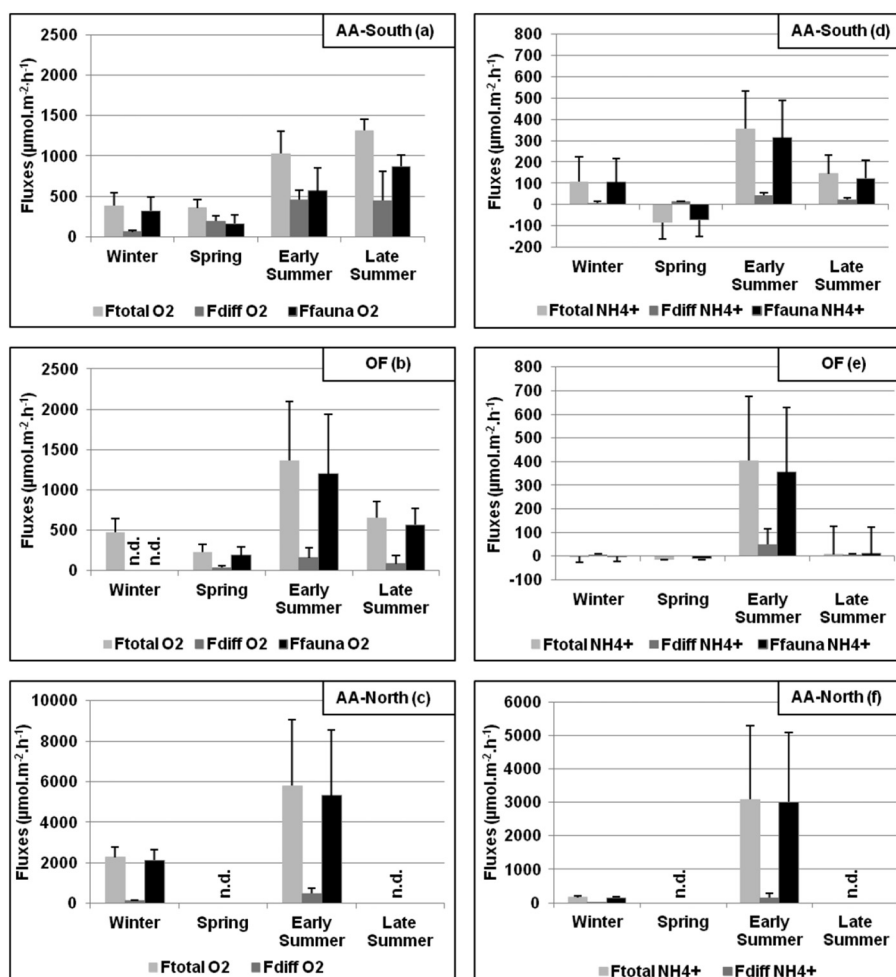


Fig. 2. Average ( $\pm$  S.D) total, diffusive and fauna mediated fluxes of oxygen and ammonium recorded *in situ* on the three sites. Oxygen uptake by sediment is represented positively to facilitate graphing. Scale of fluxes of AA-North is multiplied by 4 for fluxes ( $O_2$ ) and by 7.5 for fluxes ( $NH_4^+$ ). n.d.: no data.

**Table 2**

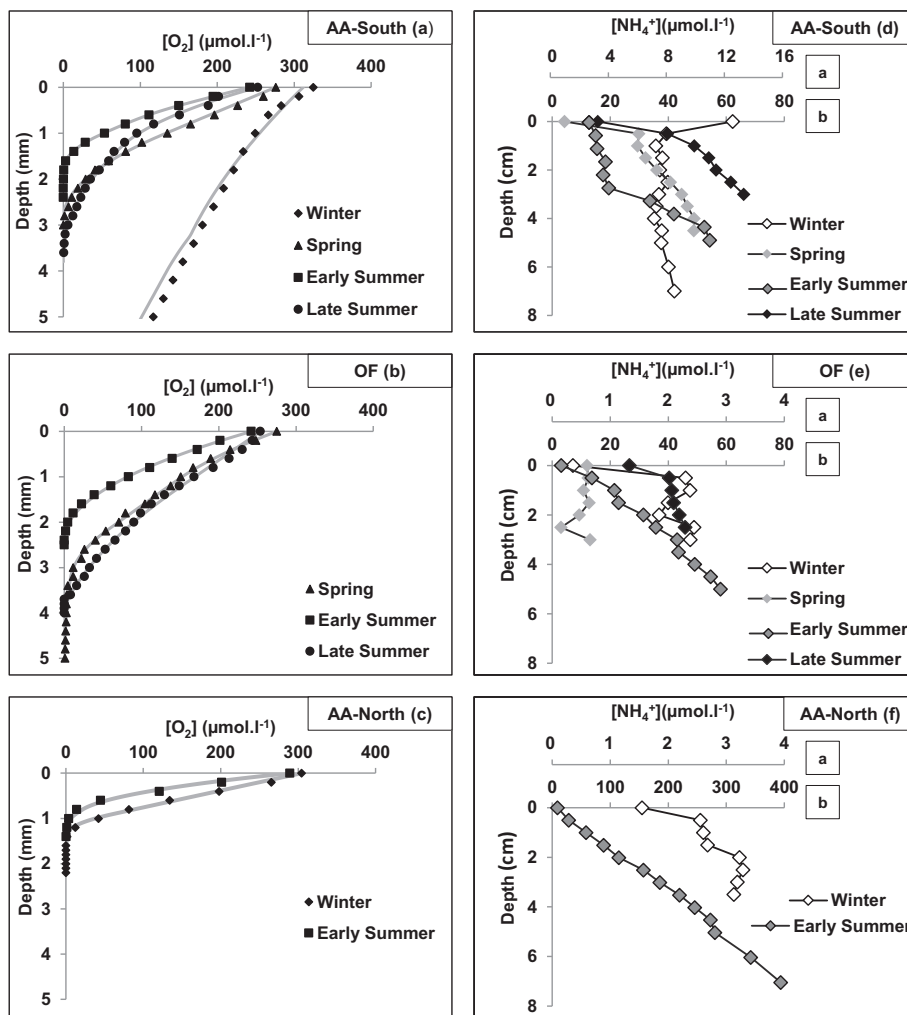
Two-way crossed analysis of variance for the effects of Stations (respectively between communities AA-south vs OF and within the *Abra alba* community AA-south vs AA-north) and Dates on total and diffusive fluxes of ammonium and oxygen. df: degree of freedom, MS: Mean Squares, F: value of F statistic, and p: significance level. Oxygen fluxes were log-transformed before analysis.

Variable	Factors	Between AA South and OF				Between AA South et AA North			
		df	MS	F	p	df	MS	F	p
Total oxygen fluxes (n = 4)	Stations	1	67,645.24	0.71	ns	1	44,269,897.12	16.16	***
	Dates	3	1,495,480.23	15.77	***	1	17,419,681.95	6.36	*
	Dates × Stations	3	358,417.12	3.78	*	1	8,310,799.62	3.03	ns
	Error	24	94,811.28			12	2,739,764.12		
Total ammonium fluxes (n = 4)	Stations	1	8172.6	0.44	ns	1	7,697,739.15	6.24	*
	Dates	3	272,296.47	14.82	***	1	10,046,071.12	8.14	*
	Dates × Stations	3	22,447.18	1.22	ns	1	7,135,770.11	5.78	*
	Error	24	18,368.8			12	1,234,277.78		
Oxygen diffusive fluxes (n = 6)	Stations	1	660,877.3	22.02	***	1	15,610.59	0.69	ns
	Dates	2	124,606.42	4.15	*	1	860,743.46	38.14	***
	Dates × Stations	2	33,900.93	1.13	ns	1	1928.8	0.09	ns
	Error	30	30,008.27			20	22,566.82		
Ammonium diffusive fluxes (n = 2)	Stations	1	141.15	0.18	ns	1	5154.35	1.11	ns
	Dates	2	1747.81	2.24	ns	1	15,858.42	3.42	ns
	Dates × Stations	2	119.82	0.15	ns	1	5564.31	1.2	ns
	Error	6	780.65			4	4641.39		

ns: not significant.

\* p < 0.05.

\*\*\* p < 0.001.



**Fig. 3.** Average profile oxygen and ammonium concentration ( $\mu\text{mol.l}^{-1}$ ) depending on the depth (mm for  $\text{O}_2$ , cm for  $\text{NH}_4^+$ ) measured at different times of sampling on the three sites. For ammonium, the x-axis (a) corresponds to winter, spring and late summer dates and the x-axis (b) corresponds early summer.

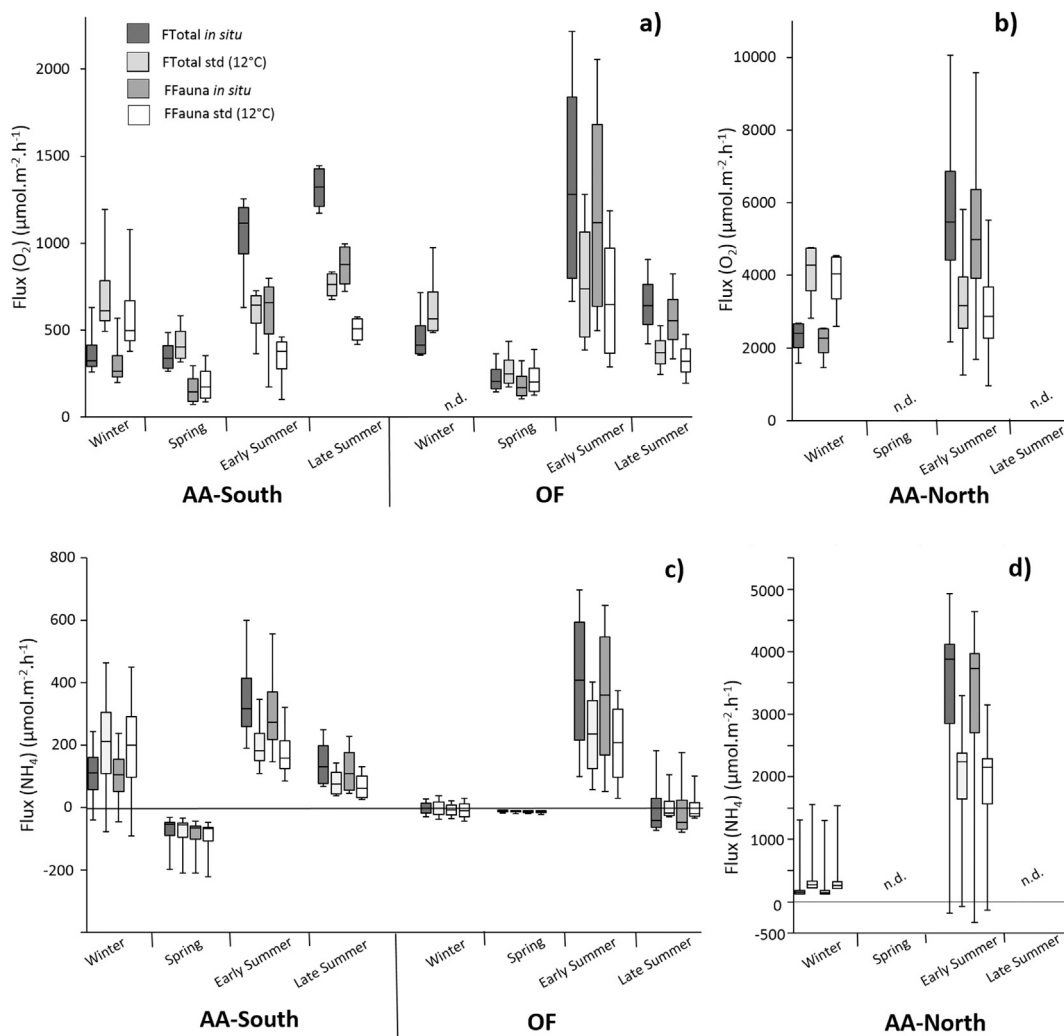


Fig. 4. Seasonal average values of total and fauna fluxes of oxygen (a, b) and ammonium (c, d) calculated at *in situ* temperature ( $F_{Total\ in\ situ}$  and  $F_{Fauna\ in\ situ}$ ) and standardized at the mean annual temperature ( $12^{\circ}C$ ) during the four cruises ( $F_{Total\ std.}$  and  $F_{Fauna\ std.}$ ). n.d.: no data.

collected. Biodiffusers were the most represented, due to the prevalence of *O. fragilis* at this station. Nevertheless, abundance and biomass values remained low all over the survey, ranging from minimal values in spring, to maximal ones in winter. When pooling all stations, species richness, abundance and biomass values shown in Table 1 were characterized by high spatial and temporal variability (two-way ANOVA,  $p < 0.05$ ) but abundance and biomass values also demonstrated high intra-station variability at each sampling date (large standard deviations).

Generally, the bioturbation and trophic structures did not present any temporal variability, except at the AA-North where the dominant trophic and bioturbation groups were different between winter and early summer (Table 1), due to the prevalence of *L. conchilega* for this last date.

### 3.7. Relationship between fluxes and other variables

Multiple regression analysis performed on the whole dataset allowed identifying the independent variables that significantly contributed to oxygen and ammonium fluxes. Biomass, temperature and fine particle content affected oxygen fluxes ( $R^2 = 70.8\%$ ,  $p < 0.05$ ). The other parameters (organic matter content, species richness and abundance of macrofauna) had no significant effect on total oxygen fluxes (respectively  $p = 0.912$ ;  $p = 0.754$ ;  $p = 0.375$ ).

For total ammonium fluxes, the effects of biomass, temperature and

organic matter content were significant ( $p < 0.05$ ), but only explained 44.3% of the flux variance. The other parameters did not significantly affect the temporal and spatial variability of total observed ammonium fluxes.

## 4. Discussion

### 4.1. Spatial variability

The stations studied during this survey belong to the main benthic communities of the subtidal Eastern English Channel (muddy fine sand *A. alba* community and sandy gravels *O. fragilis*). As previously reported by several authors (Davout et al., 1988; Desroy et al., 2002; Dauvin et al., 2013), the granulometry of the sandy gravels community is more heterogeneous than the one observed in the *A. alba* community (Table 1), where homogeneous fine sand dominated, with limited differences between stations (AA-North and AA-South). The average macrofaunal biomasses measured in the *A. alba* community ( $61.14 \pm 72.33$  AFDW  $m^{-2}$  for AA-South and  $231.16 \pm 99.78$  AFDW  $m^{-2}$  for AA-North) are in the same order of magnitude than the highest biomasses reported by Thiébaud et al. (1997) for the winter benthic assemblages of the Eastern Bay of Seine. The *O. fragilis* community was characterized by a low macrofauna biomass ( $14.96 \pm 7.88$  AFDW  $m^{-2}$ ) which is comparable to the data collected by Dauvin and Ruellet (2008) on a similar station in the offshore part of the Bay of Seine.



In the AA-North station of the *A. alba* community, average  $F_{Total}$  ( $O_2$ ) were always higher than values recorded in the other station of same community (AA-South) or the other community studied (OF: sandy gravels community with *O. fragilis*). AA-North displayed mineralization levels of greater intensity than the other two sites (Fig. 2). This was probably due to the massive presence of large *E. directus* individuals (up to 254 g of AFDW·m<sup>-2</sup> in early summer) and, to a lower extent, of *L. conchilega* (Table 1).

All stations presented several characteristics of permeable sediments for OF [low percentage of silts (< 13%) and low porosity (< 0.65)] and semi-permeable sediments for AA-South and AA-North. Indeed, the granulometry and low porosity (< 0.4 between 1.5 and 10 cm depth) of the sandy gravels community is typical of permeable sediments, whereas semi-permeable sediments are characterized by slightly higher porosity (0.4 to 0.5 between 1.5 and 10 cm) and silt percentage (6–13%). When measuring sediment-water fluxes of dissolved compounds, problems encountered include the accurate measurement of fluxes in coarse sediments. Indeed, in those permeable sediments, advective pore water transport can increase sediment uptake rates by a factor 1.4–3.0 (Ehrenhauss and Huettel, 2004; Janssen et al., 2005), and oxygen penetration depths as measured in the laboratory during our experiments probably largely underestimate those that would be observed *in situ*. The recent autonomous benthic chamber system *Sandy* allowed to quantify the impact of average hydrodynamic forcing on water-sediment exchanges (Janssen et al., 2005). However, the extreme variability in space and time characterizing pressure gradients in coastal areas remains hardly taken into account. Nevertheless, considering the high hydrodynamic forcing encountered in the English Channel and the nature of the sediments studied, we are aware that the fluxes reported in that study might have been underestimated, as the advective pore water transport was absent or minimal in our cores during measurements (Franco et al., 2010). Then, the fluxes reported for the sandy gravel OF station should be considered as minimal and are therefore difficult to compare with the other calculated values at AA-South and AA-North stations, where lower advection processes are expected.

In this context, measured fluxes were similar to those reported by Denis and Desroy (2008) in the *A. alba* community of the eastern English Channel (97 to 692  $\mu\text{mol } O_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ), Andersen and Helder (1987) on the island of Texel, NW Netherlands (395 to 2315  $\mu\text{mol } O_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ) and by Janssen et al. (2005) in the German Bight (1033 to 1200  $\mu\text{mol } O_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ). For ammonium,  $F_{Total}$  ( $\text{NH}_4^+$ ) fluxes were in the same range as the data obtained *in situ* on *A. alba* community in the Bay of Seine (–4 to 336  $\mu\text{mol } \text{NH}_4^+ \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ; Janson et al., 2012) or the eastern English Channel (–6 to 223  $\mu\text{mol } \text{NH}_4^+ \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ; Denis and Desroy, 2008). Ammonium fluxes followed a pattern similar to the one observed for  $F_{Total}$  ( $O_2$ ) (except in spring) because the mineralization pathways are tightly linked, and higher  $F_{Total}$  ( $O_2$ ) were coupled with a more intensive ammonium release, as previously investigated in the eastern English Channel by Rauch and Denis (2008).

#### 4.2. Temporal variability: temperature effect on bottom water oxygenation and fluxes

In the literature, it is recognized that temperature and organic matter inputs generally control a large part of benthic microbial activity in marine sediments (Hartwig, 1978; Grant, 1986; Kristensen, 1993; Magalhaes et al., 2002) and may affect the oxygen and ammonium fluxes (Hammond et al., 1985; Forja et al., 2004; Denis and Desroy, 2008; Alonso-Pérez and Castro, 2014; Belley et al., 2016). During this study, an increase in total ammonium and oxygen fluxes was observed during the early summer period. An elevation from 5 to 18 °C between winter and late summer led to an increase of sediment-water fluxes on the three stations, irrespective of their sedimentary composition, hence demonstrating that the temporal variability was largely due to the ambient temperature. With the aim to investigate the influence of

macrofauna on sediment-water exchanges (independently from any other factor), we tried to identify and quantify the influence of temperature, so that its effects might be subtracted from the observed variation.

First of all, temperature affects, *via* the solubility control, the concentration of dissolved  $O_2$  in bottom water. The  $O_2$  under-saturation recorded in early summer at AA-South and OF stations resulted from water column stratification and enhanced the consequences of bottom metabolism consecutive to higher temperatures. However, due to the ambient hydrodynamism, these under-saturations remained moderate, total and diffusive fluxes showed limited sensitivity to this variation of  $O_2$  concentration in bottom waters.

Temperature variation induce qualitative changes in benthic communities (micro- and macrofauna) but also modify the organic matter turnover rates through enhanced metabolic efficiency. Consequently, for each sampling date and each station, total and diffusive fluxes were standardized to the overall annual temperature (12 °C) (Fig. 4). The resulting average annual  $F_{Total}$  ( $O_2$ ) and  $F_{Diff}$  ( $O_2$ ) for each station (re-calculated at the average annual temperature of 12 °C) have been multiplied by a factor ranging from 1.05 to 1.56 in comparison with *in situ* values (Fig. 4a), while standardized average annual  $F_{Total}$  ( $\text{NH}_4^+$ ) and  $F_{Diff}$  ( $\text{NH}_4^+$ ) were multiplied by a factor ranging from 1.30 to 1.80 (Fig. 4b). After those calculations, the temporal variability has largely decreased at all stations, demonstrating that temperature was one of the major factors responsible for the temporal variability.

#### 4.3. Environmental and macrofaunal influence

As explained above, the elevation of temperature partly explained the temporal variation of fluxes recorded on the three stations. However, values of  $F_{Fauna}$  ( $O_2$ ) and  $F_{Fauna}$  ( $\text{NH}_4^+$ ) recalculated for a standard temperature (Fig. 4) may also help evaluating macrofauna contribution on dissolved exchanges at the sediment water-interface.

In this study, multiple regression analysis clearly evidence the role of both environmental (temperature, organic matter content, fine particle content) and macrofaunal variables (biomass) to explain sediment-water exchanges of oxygen and ammonium (up to 70% explained for oxygen, and 44% for ammonium). This is in great accordance with Belley and Snelgrove (2016) who demonstrated that macrofaunal benthic richness was a better predictor of fluxes than specific richness (up to 20% of benthic flux variation explained), but also evidenced that together with environmental variables, functional diversity indices explained > 62% of benthic flux variation. Working with an engineer species (*Ruditapes philippinarum*, Adams and Reeve), Queirós et al. (2011) demonstrated the tight link between bioturbation impact on sediment-water exchanges and the quality of the sediment. As the sediment is coarse (fine particle content always lower than 13%) in all the sites studied, the granulometry might mask the contribution made by biodiversity on sediments water exchanges, as previously stated by Hiddink et al. (2009) or Strong et al. (2015).

When considering the three sampling stations and all dates, average  $F_{Fauna}$  ( $O_2$ ) represented 77%  $\pm$  17% of average recalculated  $F_{Total}$  ( $O_2$ ). Other recent studies have emphasized the active role of macrofauna in exchange of dissolved oxygen at the sediment-water interface:  $F_{Fauna}$  ( $O_2$ ) contributes up to 40% of  $F_{Total}$  ( $O_2$ ) in Aarhus Bay (semi-enclosed Bay with muddy sediments; Glud et al., 2003), 66% in the Thau lagoon (Mediterranean lagoon with muddy sediment; Dedieu et al., 2007), 93% in shallow water subtidal station (muddy sediment) in Helsingør Denmark (Wenzhöfer and Glud, 2004). For ammonium, when considering all stations and dates, average  $F_{Fauna}$  ( $\text{NH}_4^+$ ) represented 76%  $\pm$  20% of average  $F_{Total}$  ( $\text{NH}_4^+$ ). These results are in accordance with the works published by Kuwae et al. (1998), who have also emphasized the active role of macrofauna in the exchange of ammonium at the sediment-water interface:  $F_{Fauna}$  ( $\text{NH}_4^+$ ) contributed up to 86%  $\pm$  5% of  $F_{Total}$  ( $\text{NH}_4^+$ ) in Banzu, Japan.

In the present study, a significant correlation was found between  $F_{Fauna}$  ( $O_2$ ),  $F_{Fauna}$  ( $\text{NH}_4^+$ ) and species richness (Fig. 5). Hence, this

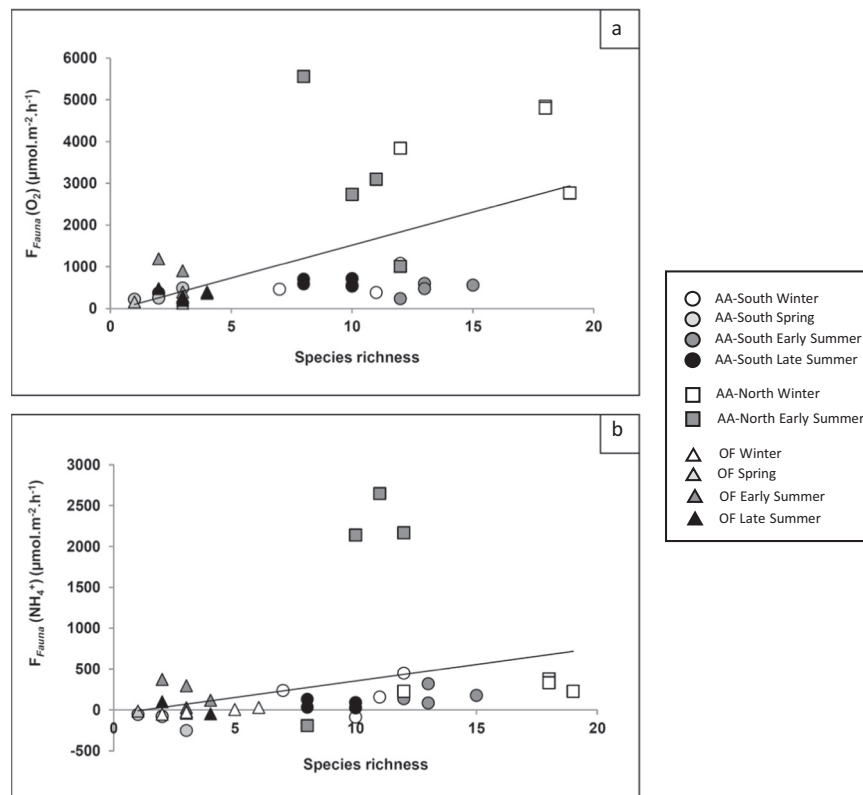


Fig. 5. Relationships between species richness (SR) and fauna-mediated fluxes (a)  $F_{Fauna} (O_2)$  and (b)  $F_{Fauna} (NH_4^+)$  re-calculated at the mean annual temperature ( $F_{Fauna} (O_2) = 157.7 \times SR - 61.5$ ,  $r^2 = 0.318$ ,  $n = 36$ ,  $p < 0.001$  and  $F_{Fauna} (NH_4^+) = 40.31 \times SR - 48.25$ ,  $r^2 = 0.114$ ,  $n = 40$ ,  $p < 0.05$ ).

correlation suggests that each species contributes to ecosystem functioning. However, high values obtained at AA-North station in early summer (leading to rapid suffocation of species within 9 h) largely contributed to this relationship (Fig. 5b). These values were representative of situations that may occur in natural communities and thus should not be considered as outliers. However, such an equilibrium can be brutally altered from a certain threshold of species extinction, as stated by the rivet hypothesis (Chapin et al., 1992). Our results therefore indicate that species richness is beneficial to ecosystem performance (Tilman et al., 1996). Nevertheless, ecosystem functioning cannot be explained only by species number (Giller et al., 2004; Hooper et al., 2005), and each species functional characteristics (e.g. feeding behaviour and bioturbation activities) might largely influence ecosystem functioning (Hooper et al., 2002; Thrush et al., 2006; Braeckman et al., 2014).

For species abundance and biomass, a positive correlation was only observed between  $F_{Fauna} (O_2)$ ,  $F_{Fauna} (NH_4^+)$  and biomass (respectively  $r = 0.594$ ,  $p < 0.001$  and  $r = 0.609$ ,  $p < 0.001$ ). The absence of significant relationship between fauna mediated fluxes and species abundance is consistent with the results of Marinelli (1994) and Marinelli and Williams (2003). These authors found nonlinear relationships between organisms' density and fluxes (irrigational oxygen fluxes and ammonium fluxes); they nevertheless indicated that intermediate infaunal abundance has a greater impact on ammonium fluxes as high infaunal abundance. They emphasized the importance of abundance, but also underlined that the diversity of infaunal functional activity can be an important parameter that modulates or promotes fluxes at the sediment-water interface. For biomass, our results were in agreement with the conclusions of Rossi et al. (2008) who demonstrated in field experiments that introducing bivalve *Cerastoderma edule* induced significant changes in the biomass of other species and consequently influenced respiration rates. In previous studies, the faunal respiration has been considered as a determining factor in sediment oxygen

demand (Nizzoli and Welsh, 1999; Welsh, 2003), but recent research demonstrated that macrofaunal activities of bioirrigation seem to have greater impact in sediment oxygen demand and release of ammonium (Glud et al., 2003; Michaud et al., 2006; Braeckman et al., 2010). Thus, functional characteristics (e.g. feeding behavior and bioturbation activities) of each species might largely influence ecosystem functioning (Hooper et al., 2002; Thrush et al., 2006) and needs to be taken into account.

In the present study, a significant correlation was observed between  $F_{Fauna} (O_2)$  and each of the parameters of two bioturbation groups (bioturbators and gallery-diffusers) and one trophic guild (surface deposit feeders; Table 3). Only bioturbators had a linear positive influence on  $F_{Fauna} (NH_4^+)$ . However, our results did not indicate that fluxes induced by fauna were related to one specific functional group. Indeed, the non-significant relationship between  $F_{Fauna} (O_2)$ ,  $F_{Fauna} (NH_4^+)$ , the species richness of two trophic guilds (subsurface deposit feeders and carnivorous) and few bioturbation groups (upward conveyors, re-generator) supports the idiosyncratic hypothesis (Lawton, 1994), suggesting that diversity influences ecosystem functioning, but for several environments, in an unpredictable way. Hence, the direction and magnitude of a possible change may remain unpredictable especially in permeable sediments, where advective porewater transport might override the effect of bioturbating infauna (Braeckman et al., 2014; Hiddink et al., 2009).

It has been recognized that the interactions that may exist between species, their environment, and the composition of these species can influence ecosystem functioning (Waldbusser and Marinelli, 2006; Rossi et al., 2008). Waldbusser et al. (2004) have shown that changes in species composition, as well as changes in functional diversity will thus significantly alter ecosystem parameters. But the key-point of our study was to work on the whole communities in place in the ecosystem (without addition/removal of macrofauna). In this framework, the presence, the activity of individuals and different functional

**Table 3**  
Pearson's correlations between fauna mediated fluxes [ $F_{Fauna}(O_2)$  and  $F_{Fauna}(NH_4^+)$ ] re-calculated at the mean annual temperature and the species number, abundance and biomass of each trophic guild and bioturbation group.

Trophic guild	$O_2$						$NH_4^+$						
	Species number		Abundance		Biomass		Species number		Abundance		Biomass		
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	
Trophic guild	Suspension feeders	0.256	p < 0.001***	0.798	p < 0.001***	0.554	p = 0.169 ns	0.222	p = 0.168 ns	0.222	p < 0.001***	0.558	p < 0.001***
	Surface deposit feeders	0.369	p < 0.05*	0.669	p < 0.001***	0.616	p = 0.840 ns	0.033	p = 0.914 ns	0.018	p = 0.944 ns	-0.011	p = 0.736 ns
	Subsurface deposit feeders	0.157	p = 0.134 ns	0.137	p = 0.427 ns	-0.017	p = 0.104 ns	0.261	p = 0.648 ns	0.074	p = 0.651 ns	0.074	p = 0.736 ns
	Mixed	0.589	p < 0.001***	-0.063	p = 0.716 ns	0.301	p < 0.01**	0.420	p = 0.651 ns	0.074	p < 0.001***	0.546	p < 0.001***
Bioturbation group	Camivorous	0.310	p = 0.066 ns	0.372	p < 0.05*	0.235	p = 0.062 ns	0.298	p < 0.001***	0.651	p = 0.992 ns	0.002	p = 0.992 ns
	Biodiffusers	0.466	p < 0.01**	0.782	p < 0.001***	0.592	p < 0.01**	0.413	p < 0.05*	0.329	p < 0.001***	0.550	p < 0.001***
	Gallery diffusers	0.433	p < 0.01**	0.500	p < 0.01**	0.412	p = 0.686 ns	0.066	p < 0.01**	0.500	p = 0.678 ns	0.068	p = 0.678 ns
	Upward conveyors	0.219	p = 0.199 ns	-0.174	p = 0.309 ns	0.018	p = 0.477 ns	-0.116	p = 0.635 ns	-0.078	p = 0.773 ns	-0.047	p = 0.773 ns
	Downward conveyors	0.686	p < 0.001***	-0.125	p = 0.844 ns	0.169	p < 0.05*	0.387	p = 0.782 ns	0.045	p < 0.001***	0.565	p < 0.001***
	Regenerators	-0.125	p = 0.469 ns	-0.125	p = 0.469 ns	-0.125	p = 0.753 ns	-0.051	p = 0.753 ns	-0.051	p = 0.753 ns	-0.051	p = 0.753 ns

ns: not significant.  
\* p < 0.05.  
\*\* p < 0.01.  
\*\*\* p < 0.001.

characteristics (bioturbation groups and trophic guilds) of species in the communities studied probably led to the observed idiosyncratic functioning. We are aware that only two functional traits of macrofauna were considered in this work, while several other functions (e.g. size, mobility), or a combination of functions might have a large influence on sediment-water exchanges, and more generally benthic ecosystem functioning, as already demonstrated by Belley and Snelgrove (2016). As the ecosystem complexity remains very high, even in communities where engineer species are present or dominant, integrating the intra-specific variability (e.g. population structure, life traits) might constitute a necessary step forward for the understanding of relationships between diversity and ecosystem functioning.

### 5. Conclusions

In agreement with Garcia et al. (2011), the results of this study helped to demonstrate that the substrate type (fine sediment or gravel) prevails over the station's location and environmental conditions in terms of functioning. The OF station, located in an area with strong current, was characterized by the exclusive dominance of suspension feeders compared to AA-North and AA-South stations which were defined by a higher diversity of functional groups.

The present paper also confirms the dominant role of benthic biodiversity on mineralization processes of surficial sediments (permeable and semi permeable). Benthic habitats constitute a mosaic of functional diversity; thus, it is very difficult to establish general and simple rules. Functional approaches describing the role of each species in the whole community are essential and allow the authors to take into account interactions that may exist between these different functional organisms. However, on the basis of the field experimental results (incubated cores), these different interactions cannot be clearly and precisely interpreted due to the complexity of the relationship between the exchanges of dissolved substances and macrofaunal parameters. Indeed, our study suggested that communities followed the idiosyncratic and rivet hypothesis. Therefore, it is difficult to predict the functional consequences of biodiversity changes (addition or loss of species) on the benthic ecosystems functioning.

### Acknowledgements

This study was supported by the European Union through its European Regional Development Fund (Interreg Channel 4a) as part of the CHARM III project (4037) coordinated by A. Carpentier and S. Vaz, Ifremer, Boulogne sur-mer. It is also a part of the COLMATAGE project coordinated by the GIP Seine-Aval- Normandie region. The authors would like to thank the captains and crews of the R/V "Côtes de la Manche" and "Sepia II". Thanks should be addressed to S. Marmin, S. Lozach, M. Gothland and A. Weppe for their help during sampling and laboratory work and Lisa Spencer for the English polishing.

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