Acta Biotheor (2008) 56:123–135
DOI 10.1007/s10441-008-9033-1

REGULAR ARTICLE

Imaging Oxygen Distribution in Marine Sediments. The Importance of Bioturbation and Sediment Heterogeneity

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Received: 19 December 2007 / Accepted: 19 December 2007 / Published online: 5 February 2008

Abstract The influence of sediment oxygen heterogeneity, due to bioturbation, on diffusive oxygen flux was investigated. Laboratory experiments were carried out with 3 macrobenthic species presenting different bioturbation behaviour patterns: the polychaetes *Nereis diversicolor* and *Nereis virens*, both constructing ventilated galleries in the sediment column, and the gastropod *Cyclope neritea*, a burrowing species which does not build any structure. Oxygen two-dimensional distribution in sediments was quantified by means of the optical planar optode technique. Diffusive oxygen fluxes (mean and integrated) and a variability index were calculated on the captured oxygen images. All species increased sediment oxygen heterogeneity compared to the controls without animals. This was particularly noticeable with the polychaetes because of the construction of more or less complex burrows. Integrated diffusive oxygen flux increased with oxygen heterogeneity due to the production of interface available for solute exchanges between overlying water and sediments. This work shows that sediment heterogeneity is an important feature of the control of oxygen exchanges at the sediment–water interface.

Keywords Bioturbation · Heterogeneity · Oxygen · Planar optode · Macrofauna

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1 Introduction

Physical and chemical habitat heterogeneity is critical to the functioning of ecosystems. Ecologists have only recently begun to explore how changes in physical and chemical habitat heterogeneity may influence ecosystem functioning, by affecting important processes such as primary production, decomposition or nutrient cycling (Aller 1994; Gustafson 1998; Poggiale et al. 2005). Moreover, there is more and more evidence that changes in ecosystem functioning can unequivocally be attributed to habitat variability, that is, spatial variation of physical and/or chemical properties (Cardinale et al. 2002).

In some environments, habitat is strongly influenced by biotic activities. This is the case for aquatic sediments where the bioturbation process (i.e. particle reworking and bio-irrigation) which results from the various faunal activities (e.g. feeding, gallery construction, ventilation) (e.g. Rhoads 1974; Snelgrove and Butman 1994; François et al. 1997; Pearson 2001) creates a complex mosaic of micro- and macro-environments (Aller 2001). The role of organisms in sedimentary particle redistribution depends on the organisms considered that can be classified in five different functional groups (for review see Gerino et al. 2003). Benthic organisms can construct more or less complex structures in the sediment column, presenting various shapes and sizes and being permanent or not (Dufour et al. 2005). Moreover, in order to renew oxygen and evacuate metabolites, these structures may be actively ventilated by their inhabitants in constant or intermittent ways (e.g. Foster-Smith 1978; Kristensen 1983; Aller and Aller 1998). Because of the bioturbation process, organic material and electron acceptors available for bacteria are redistributed in the sediment column (Aller 1982), strongly influencing the pathways, rates, and extent of organic matter mineralization during early diagenesis (e.g. Kristensen 1985; Aller 1994; Gilbert et al. 2003; Talin et al. 2003).

As highlighted by Cadenasso et al. (2006), ecologists often describe spatial heterogeneity as patches, which correspond to discrete homogeneous areas that differ in structure, composition or function. The complexity of this spatial heterogeneity may increase from simple cases where patch type and number of each type are described, to more complex cases where spatial configuration, and temporal changes in the mosaic are monitored (Li and Reynolds 1995). The quantification of environmental heterogeneity has long been an objective in ecology (e.g. Patil et al. 1971; Dutilleul 1993; Freestone and Inouye 2006). Attempts have thus been made to develop methods to quantify the spatial heterogeneity, in particular for landscape studies (e.g. O'Neill et al. 1988; Garrigues et al. 2006). Landscape ecology principles, however, have not been widely applied to marine systems, in part because of technical limitations. For instance, in the field of aquatic sediment biogeochemistry, it was difficult, until recently, to quantify oxygen spatial heterogeneity exhibited in the upper sediment column. The use of techniques such as micro-sensors, producing one-dimensional vertical oxygen profiles, was the only way to quantify oxygen distribution patterns within sediments (Revsbech et al. 1980). Only few destructive measurements can be performed, which makes this technique inappropriate in systems such as bioturbated sediments and ventilated worm burrows. Recently, a new tool (planar optodes) has been developed that

makes possible high resolution measurement of two-dimensional vertical distribution and spatial heterogeneity of solutes in the sedimentary column (Glud et al. 1996; Hulth et al. 2002; Zhu et al. 2006).

Oxygen plays a key role in benthic ecology because it is the most important electron acceptor for organic matter decomposition (Revsbech et al. 1981; Thamdrup 2000). The aim of this study was to investigate the influence of sediment heterogeneity, induced by the bioturbation process, on diffusive oxygen flux. For that purpose, oxygen planar optodes were used during laboratory experiments carried out with 3 macrobenthic species which present different bioturbation behaviour patterns: *Nereis diversicolor* and *Nereis virens*, gallery-builder polychaetes which actively ventilate their burrows and the burrowing gastropod *Cyclope neritea* which does not construct any galleries in sediments.

2 Biologic Material and Sampling

The annelid polychaetes *Nereis diversicolor* (O.F. Müller, 1776) and *Nereis virens* (Sars) are common ragworms inhabiting intertidal mudflats of estuaries and shallow water bodies (Clay 1967; Kristensen 1988). They construct semi-permanent U- or Y- shaped mucus-lined burrows in the upper 10 cm of sediments (Fig. 1c, d and e) but burrows may develop into multibranched structures extending down to 30 cm depth (Gérino and Stora 1991; Davey 1994). Construction and maintenance of their burrows is known to generate significant particle mixing defined as a gallery-diffusion process (François et al. 2002). Moreover, they periodically renew oxygen in their burrows by actively ventilating water through their gallery system (Kristensen et al. 1991).

The small marine mollusc *Cyclope neritea* (C. Linnaeus 1758) is commonly found in soft sediments of shallow and sheltered shores (Tardy et al. 1985). During periods of low water, this snail emerges from the sediment and crawls over it in search of food (Trueman and Brown 1992). Gliding is facilitated by foot secretion

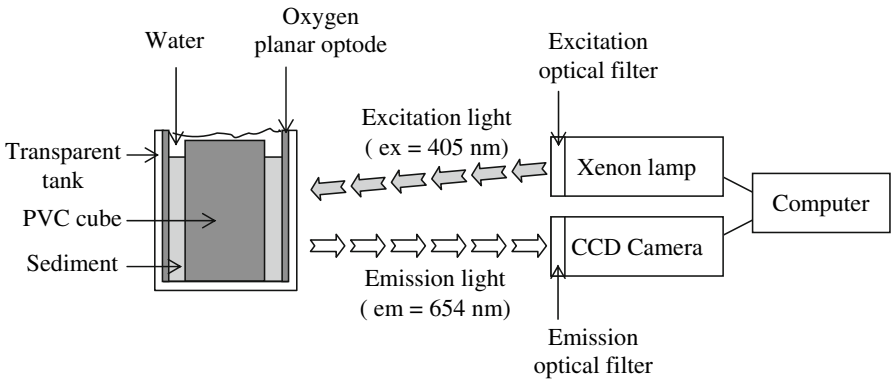

Fig. 1 Schematic representation of the experimental design (lateral view)

of a mucous bed. Burrowing is achieved by discontinuous movements of the shell and ceases as soon as the shell is covered. This results in a shallow burrow from which the siphon can maintain contact with the overlying water (Trueman and Brown 1992). Its reworking mode is still not defined but on the basis of its behaviour, *C. neritea* would appear to belong to the biodiffusor group.

In September 2006, in the Carteau cove (Gulf of Fos, Mediterranean Sea), *N. diversicolor* specimens (8.9 ± 2.1 cm long, $n = 19$) were collected by shovel sampling in the Saint-Antoine canal (between 0 and 0.5 m water depth), while on same day, at low tide on the Carteau beach, the gastropods *C. neritea* (1.2 ± 0.1 cm long, $n = 8$) were collected on the sediment surface. Sediments from both sites were also sampled. *N. virens* specimens (13.8 ± 2.6 cm long, $n = 13$) were collected in the Cotentin (Channel, France) by the company "Normandie-Appâts". Worms and molluscs were brought to the laboratory and allowed to acclimatize to experimental conditions for two weeks (24 ± 1°C, natural photoperiod) in tanks filled with muddy-sand sediment (mixture of Saint-Antoine canal and Carteau beach sediments) and aerated sea-water (38 ± 0.2 psu).

3 Image Acquisition

3.1 Oxygen 2D Quantification

The two-dimensional oxygen distribution in sediments and overlying water was measured using oxygen planar optodes (for a complete description of the technique, see Glud et al. 1996). This recent optical technique allows calculation of the oxygen concentration for each pixel of a digital image. Oxygen measurement is based on the quantification of the decrease of the fluorophore fluorescence by oxygen (i.e. oxygen quenching, Kautsky 1939). In this work, the oxygen-quenchable fluorophore used was the platinium (II) meso-tetra (pentafluorophenyl) porphyrin. Recording of fluorescence intensity ($\lambda_{excitation}$: 405 ± 10 nm; $\lambda_{emission}$: 654 ± 24 nm) during an acquisition time of 30 seconds, allowed the capture of grey scale images by a Peltier cooled 12 bit monochrome CDD camera. Pixel size varied between 300 × 300 µm and 800 × 800 µm. Calibration was performed for each optode by a 3-point calibration method before the introduction of organisms, and before and after each series of measurements. For the two intermediate calibration points (90%, air bubbling and 50%, N_2 bubbling) the oxygen concentration was first measured just behind the optode with an oxygen probe (LDO HQ10, Hach) and immediately followed by the capture of the oxygen image. The 0% saturation was taken in deepest no bioturbated zones.

During this experiment, we used a measurement of the oxygen concentration based on fluorescence intensity. Contrary to time-lapse and ratiometric measurements, this method can present some drawbacks (e.g. uneven illumination, dye distribution, changes in the excitation light source; Strömberg 2006) that were reduced as much as possible. No optical insulation from the ambient sediment (black silicone foil) allowing minimizing background fluorescence was employed as it would have prevented the capture of the sediment structure images (used for the

detection of the sediment–water interface) and the quantification of fluorescent particulate tracers (luminophores) within the sedimentary column (data not shown).

3.2 General Experimental Design

Experimental design is presented in Fig. 1. Transparent tanks, equipped with an oxygen optode on each face, were used for the experiment. Tank size (length × width × height) was 6 × 6 × 17 cm and 20 × 20 × 20 cm for the snails and the worms, respectively. In order to maintain the worm close to the tank side (optode), a PVC cube was inserted inside the tank that reduced the sediment thickness to 6 mm in front of the optodes. Tanks were then filled with about 10–12 cm depth of sieved sediments (mesh: 1 mm, porosity: 0.69), and 6–10 cm of aerated overlying water (24 ± 1°C, 38 ± 0.2 psu).

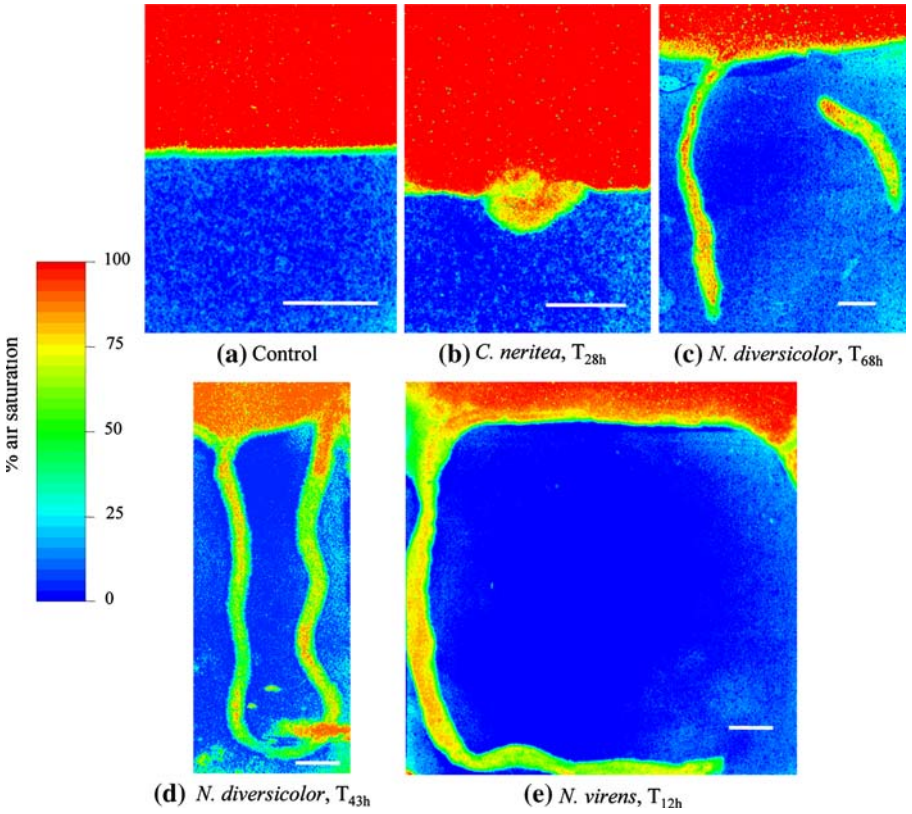

Fig. 2 Examples of oxygen distribution in sediments. The grey scales images were converted to false colour. (**a**) Control without organism (resolution: 570 × 570 µm); (**b**) *C. neritea* (resolution: 610 × 610 µm); (**c** and **d**) *N. diversicolor* (resolution: 500 × 500 µm and 790 × 790 µm); and (**e**) *N. virens* (resolution: 770 × 770 µm). Times after which the picture have been acquired are indicated

Before introduction of the organisms, a first set of oxygen measurements were performed on the 4 sides of each tank and constituted the controls. Nineteen *N. diversicolor*, five *N. virens* and eight *C. neritea* were then introduced into their respective tank. After three days, multiple time series of oxygen measurements and corresponding sediment structure images were carried out during five days.

3.3 Data Set

The data set presented is composed of fifteen oxygen images, with their corresponding sediment structure images, which were chosen within the overall data set in order to illustrate, for each species, different patterns of biogenic

Table 1 Variability index, sediment–water interface (SWI) length, mean flux (surface and structures) and integrated flux, for the different species

Species	Variability index (10^{-2})	Sediment–water interface		Structure		Integrated flux (mmol m^{-2} d^{-1})
		SWI length (cm)	Mean flux (mmol m^{-2} d^{-1})	SWI length (cm)	Mean flux (mmol m^{-2} d^{-1})	
Nereis diversicolor						
Control	3.7	4.8	16.1 ± 1.0	–	–	16.1 ± 1.0
T19 h	31.4	8.1	13.0 ± 3.4	11.6	12.6 ± 4.5	52.3 ± 1.7
Control	4.9	3.7	7.9 ± 1.7	–	–	7.9 ± 1.7
T43 h	21.9	4.1	7.0 ± 1.4	33.3	5.2 ± 0.8	55.1 ± 1.7
Control	2.9	6.8	6.5 ± 1.9	–	–	6.5 ± 1.9
T68 h	19.0	5.9	5.5 ± 0.7	22.3	5.6 ± 1.0	23.2 ± 1.4
Nereis virens						
Control[a]	–	9.6[a]	–	–	–	–
T12 h	32.8	10	6.5 ± 1.2	25.6	6.5 ± 0.9	25.7 ± 1.2
Control[a]	–	12.4[a]	–	–	–	–
T35 h	25.6	12.5	7.2 ± 1.4	50.4	7.1 ± 1.1	36.5 ± 1.3
Cyclope neritea						
Control	3.2	4	13.6 ± 3.5	–	–	13.6 ± 3.5
T22 h	9.4	4.4	7.9 ± 1.5	2.1	7.2 ± 1.1	12.6 ± 1.7
T28 h	3.9	2	14.8 ± 3.9	2.9	8.1 ± 1.8	14.2 ± 1.7
Control	2.0	3	17.2 ± 3.1	–	–	17.2 ± 3.1
T10 min	3.3	3.3	21.3 ± 5.1	[b]	[b]	27.3 ± 4.0
T8 h	3.8	2	18.8 ± 2.1	2.1	11.0 ± 2.4	19.9 ± 1.8
T9 h	5.3	2	15.7 ± 3.0	1.9	13.3 ± 3.5	21.5 ± 2.5

$n = 6$ for the controls

$n = 15$ for both *Nereis diversicolor* and *Nereis virens*

$n = 9$ for *Cyclope neritea*

[a] Values estimated assuming a flat initial sediment–water interface

[b] Neither organism nor biogenic structure detected

structures created by the organisms (some representative images are presented in Fig. 2a–e). Therefore, the interval between images was not necessarily equivalent for the three species. For *N. diversicolor*, the three selected images, with their respective controls, came from three different faces of the tank and were taken 19 h, 43 h and 68 h after the organism introduction (Table 1). The two oxygen images of *N. virens* biogenic structures were taken after 12 h and 35 h on two different tank faces (respective controls not available). For *C. neritea*, five oxygen images, with their respective controls came from two faces of the tank and were taken 10 min, 8 h, 9 h, 22 h and 28 h after the organism introduction.

4 Sediment–Water Interface

The extension of the sediment–water interface, including the interface of biogenic structures, was measured for each oxygen image. Due to the organisms' reworking activity, sediment–water interface was enhanced by a factor ranging from 1.2 to 1.7, from 3.7 to 5.0 and from 4.1 to 10.0 for *C. neritea*, *N. virens* and *N. diversicolor*, respectively (Table 1).

5 Quantification of Diffusive Oxygen Flux

Vertical oxygen profiles extracted from images make it possible to determine diffusive oxygen flux ($J_{(z)}$) which was calculated from Fick's first law of diffusion (Berner 1980; Jorgensen and Revsbech 1985; Rasmussen and Jorgensen 1992): $J_{(z)} = -\Phi Ds(\partial C_{(z)}/\partial z)$, where Φ is the porosity, Ds is the oxygen diffusion coefficient in sediments ($cm^2\ d^{-1}$), C is the oxygen concentration ($\mu mol\ L^{-1}$), z is the depth (cm) and $\partial C(z)/\partial z$ is the oxygen gradient. This approach works on the assumption that molecular diffusion is the main oxygen transport mechanism. Sediment–water interface was localized on the sediment structure images and the gradient was taken from 0.09 to 0.23 mm above (3 pixels above the interface) and 0.63–2.89 mm below (down to 0% oxygen limit) the interface. Flux calculation was based on a mean oxygen profile which was calculated by averaging five neighbouring profiles randomly chosen on oxygen images, but presenting the same interface level. Calculations were performed using the PROFILE software (Berg et al. 1998) which assumes steady state conditions.

In this study, we used mean and integrated oxygen diffusive fluxes, which were quantified for all images, in burrowed and non-burrowed areas. Mean flux (i.e. local flux, M_f) correspond to the average of fluxes calculated in each area. Integrated flux (i.e. global flux, I_f) is a flux per surface unit and was obtained as follows:

$$I_f = [(M_{fs} \times W_s) + (M_{fb} \times W_b)]/W_i,$$

where M_{fs} and M_{fb} were the mean fluxes at the sediment surface, and in the biogenic structure respectively, *Ws*, *Wb* and *Wi* were the widths of the sediment surface, the biogenic structure and the image respectively.

Mean diffusive oxygen flux ranged from 6.5 ± 1.9 to 17.2 ± 3.1 mmol m^{-2} d^{-1} in the controls (Table 1). After the introduction of organisms, mean fluxes varied between 5.5 ± 0.7 and 13.0 ± 3.4 mmol m^{-2} d^{-1} at the surface, and between 5.2 ± 0.8 and 12.6 ± 4.5 mmol m^{-2} d^{-1} in the biogenic structure for *N. diversicolor*. *N. virens* presented values ranging from 6.5 ± 1.2 to 7.2 ± 1.4 mmol m^{-2} d^{-1} at the surface and from 6.5 ± 0.9 to 7.1 ± 1.1 mmol m^{-2} d^{-1} in the structure. With regard to *C. neritea*, mean flux was generally higher than for the polychaetes and varied between 7.9 ± 1.5 and 21.3 ± 5.1 mmol m^{-2} d^{-1} at the surface and between 7.2 ± 1.1 and 13.3 ± 3.5 mmol m^{-2} d^{-1} within the structure.

Integrated diffusive oxygen flux ranged from 6.5 ± 1.9 to 17.2 ± 3.1 mmol m^{-2} d^{-1} in the controls (Table 1) and was generally higher for the polychaetes than for the gastropod. After the introduction of organisms, integrated flux ranged from 23.2 ± 1.4 and 55.1 ± 1.7 mmol m^{-2} d^{-1}, between 25.7 ± 1.2 and 36.5 ± 1.3 mmol m^{-2} d^{-1} and between 12.6 ± 1.7 and 27.3 ± 4.0 mmol m^{-2} d^{-1} for *N. diversicolor*, *N. virens* and *C. neritea* respectively.

6 Quantification of Heterogeneity

Starting from an image of a sediment column, the variability along the vertical axis is distinguished from the variability along the horizontal axis. The former is due to the fact that, at the water-sediment interface, the oxygen is diffusing mainly from the water that is the upper layer, while the latter is mainly due to macrofaunal reworking activities.

This distinction is taken into account in our variability index. This index is a variation coefficient obtained as follows: $f(x, z)$ is the distribution of the oxygen concentration as a function of the horizontal position x and of depth z. For each fixed value of x, the function $z \mapsto f(x, z)$ is called the oxygen vertical profile at position x. The mean vertical profile of the image is defined by:

$$\bar{f}(z) = \frac{1}{L_H} \int_{x_m}^{x_M} f(x, z) dx$$

where L_H is the horizontal size of the image, x_m is the minimal abscissa and x_M is the maximum abscissa in the image. For instance we may choose $x_m = 0$ and $x_M = L_H$. The horizontal variability of the oxygen distribution can then be expressed by:

$$V_f(z) = \frac{1}{L_H} \int_{x_m}^{x_M} (f(x, z) - \bar{f}(z))^2 dx$$

The dimension of the last expression is the square of the dimension of the oxygen concentration. The ratio:

$$CV_f(z) = \frac{\sqrt{V_f(z)}}{f(z)}$$

is a variation coefficient. It corresponds to a normalized standard deviation of profile that is the standard deviation divided by the mean. If the previous function is null, then all the vertical profiles are the same and we can conclude that there is no

horizontal variability; whereas, if the function is not null, then some vertical profiles differ and we can conclude that there is a horizontal variability, which is as high as the function value is high. The horizontal variability is measured by the previous function. In order to get a number, which expresses this variability, the mean of the previous function along the depth is taken:

$$I = \frac{1}{L_V} \int_{z_m}^{z_M} CV_f(z)dz$$

where L_V is the vertical size of the image, z_m is the minimum depth and z_M is the maximum depth in the image. It is standard to consider the water-sediment interface at depth 0, thus typical images have negative z_m and positive z_M.

The variability index ranged from 2.0×10^{-2} to 4.9×10^{-2} for the controls (Table 1) and was higher for the worms than for the snail. After the introduction of the organisms, this index ranged from 3.3×10^{-2} to 9.4×10^{-2}, from 19.0×10^{-2} to 31.4×10^{-2} and from 25.6×10^{-2} to 32.8×10^{-2}, and for *C. Neritea, N. diversicolor* and *N. virens* respectively.

7 Sediment Heterogeneity and Oxygen Fluxes

The results showed that the burrowing organism, *C. neritea*, induced a weak spatial heterogeneity in the sediment oxygen distribution ($5.1 \times 10^{-2} \pm 2.5 \times 10^{-2}$, $n = 5$), which was close to that of the controls ($2.6 \times 10^{-2} \pm 0.9 \times 10^{-2}$, $n = 5$). The gallery-builder organisms, *N. diversicolor* ($24.0 \times 10^{-2} \pm 6.5 \times 10^{-2}$, $n = 3$) and *N. virens* ($29.2 \times 10^{-2} \pm 5.1 \times 10^{-2}$, $n = 2$) led, to a greater extent, to an oxygen distribution pattern which was more spatially heterogeneous compared to controls and *C. neritea*. Differences between the gastropod and the polychaetes may be explained by their bioturbation behaviour patterns (particle reworking and bioirrigation). *C. neritea*, when buried, did not affect more than the first centimetre. Each snail, by its behaviour, led to the production of a simple subsurface patch in the oxygen distribution. The polychaete worms constructed burrows in the sediment resulting in a more complex pattern of oxygen distribution. Moreover, the intermittent and active ventilation of their structure increased the degree of complexity of oxygen distribution in the sediment column.

These results are in accordance with those of Michaud et al. (2005) which showed that sediment oxygen uptake is more strongly stimulated in the case of a gallery-builder (*N. virens*) ventilating its structure than in the case of burrowers (*Macoma balthica* or *Mya arenaria*) that present steady activity patterns.

Concerning oxygen diffusive fluxes in presence of *N. diversicolor*, integrated fluxes were enhanced by 3–7 fold in comparison with their respective controls, in presence of incomplete and complete structures respectively (Fig. 2 and Table 1). In contrast, for *C. neritea*, there was only a weak increase of about 1.2-fold of the integrated fluxes compared to controls. Figure 3 shows the positive relationship between the integrated diffusive oxygen flux and the variability index (*t*-test, $p < 0.0005$, $n = 15$). It seems that integrated fluxes increased with spatial oxygen heterogeneity. Sediments inhabited by *C. neritea* presented low variability index

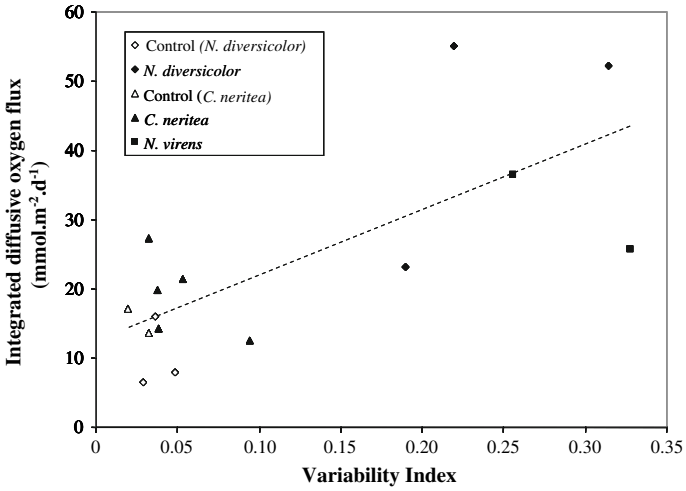

Fig. 3 Integrated diffusive oxygen flux *vs* variability index for the different species, and tendancy curve (*t*-test, $p < 0{,}0005$, $n = 15$)

and oxygen flux values that were close to those of controls whereas in the presence of the polychaetes, both values were higher. The integrated diffusive oxygen flux depended on the balance between local mean diffusive oxygen flux and the interface available for solute exchanges between overlying water and sediments, in both the sediment surface and within the biogenic structures. In this study, the integrated flux increase was mainly linked to the extension of the interfaces. Local fluxes were found to be lower in bioturbated sediments compared to controls, for all species (Table 1). The physical presence of the organisms in the biogenic structure and the deposition of mucus during the snail's displacement or the consolidation of the burrow walls by the worms may both have acted as a barrier to solute diffusion, thus reducing the oxygen flux (Hannides et al. 2004). However, this was compensated for and even reversed on the integrated scale by the extension of the exchange interface related to the organisms' activities. Only shallowly buried in subsurface sediments, the burrower *C. neritea* had the weakest effect (1.4-fold increase of the interface) while the two gallery-builders polychaetes, by building more or less complex burrows, produced more interface (from 2- to 9-fold increase).

8 Conclusion

Benthic dwelling organisms, by affecting the diffusive oxygen flux, may dramatically influence mineralization processes in sediments. The present work highlighted the influence of organisms, presenting distinct bioturbation behaviour patterns, on oxygen distribution heterogeneity in aquatic sediments. It has been shown that the gallery-builders produced greater spatial heterogeneity due to their complex ventilated structures compared to the burrower species. Moreover, this study has revealed the effect of oxygen distribution heterogeneity on diffusive oxygen flux,

both organisms enhancing oxygen exchanges between water and sediments. While the influence of benthic organisms on ecosystem functioning has already been demonstrated (e.g. Kristensen 2001; Mermillod-Blondin and Rosenberg 2004; Michaud et al. 2006), the present work showed that heterogeneity is important in the control of ecosystem functioning.

Acknowledgements This work is part of Laura Pischedda's PhD research. The work was supported by the EU commission (STREP COBO; contract number GOCE-CT-2003-505564), and the French program ANR DHYVA (project ANR-06-SEST-09). We thank Georges Stora for *Cyclope neritea* sampling and constructive discussions on the organisms, Prof. Robert C. Aller for his extensive advice on optodes, and reviewers whose comments have helped to significantly improve the manuscript. Thanks are also due to Georges Espeut of the company "Normandie Appâts" which kindly supplied the *Nereis virens* specimens. Nereis Park contribution number 27.

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