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Influence of the mode of macrofauna-mediated bioturbation on the vertical distribution of living benthic foraminifera: First insight from axial tomodensitometry

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Abstract:

We investigated the influence of bioturbation by macrofauna on the vertical distribution of living (stained) benthic foraminifera in marine intertidal sediments. We investigated the links between macrofaunal bioturbation and foraminiferal distribution, by sampling from stations situated on a gradient of perturbation by oyster-farming, which has a major effect on benthic faunal assemblages. Sediment cores were collected on the French Atlantic coast, from three intertidal stations: an oyster farm, an area without oysters but affected by oyster biodeposits, and a control station. Axial tomodensitometry (CT-scan) was used for three-dimensional visualization and two-dimensional analysis of the cores. Biogenic structure volumes were quantified and compared between cores. We collected the macrofauna, living foraminifera, shells and gravel from the cores after scanning, to validate image analysis. We did not investigate differences in the biogenic structure volume between cores. However, biogenic structure volume is not necessarily proportional to the extent of bioturbation in a core, given that many biodiffusive activities cannot be detected on CT-scans. Biodiffusors and larger gallery-diffusors were abundant in macrofaunal assemblage at the control station. By contrast, macrofaunal assemblages consisted principally of downward-conveyors at the two stations affected by oyster farming. At the control station, the vertical distribution of biogenic structures mainly built by the biodiffusor Scorbicularia plana and the large gallery-diffusor Hediste diversicolor was significantly correlated with the vertical profiles of living foraminifera in the sediment, whereas vertical distributions of foraminifera and downward-conveyors were not correlated at the station affected by oyster farming. This relationship was probably responsible for the collection of foraminifera in deep sediment layers (> 6 cm below the sediment surface) at the control station. As previously suggested for other species, oxygen diffusion may occur via the burrows built by S. plana and H. diversicolor, potentially increasing oxygen penetration and providing a favorable microhabitat for foraminifera in terms of oxygen levels. By contrast, the absence of living foraminifera below 6 cm at the stations affected by oyster farming was probably associated with a lack of biodiffusor and large gallery-diffusor bioturbation. Our findings suggest that the effect of macrofaunal bioturbation on the vertical distribution of foraminiferal assemblages in sediments depends on the effects of the macrofauna on bioirrigation and sediment oxidation, as deduced by Eh values, rather than on the biogenic structure volume produced by macrofauna. The loss of bioturbator functional diversity due to oyster farming may thus indirectly affect infaunal communities by suppressing favorable microhabitats produced by bioturbation.

Keywords: Biogenic structures; Bioturbating modes; CT-scan; Interspecific interaction; Living foraminifera; Macrofauna

1. Introduction

Benthic foraminiferal assemblages are mostly studied in surface sediments. However, even if the highest numbers of living intertidal foraminifera are generally found in the surface 0-1 cm layer (review in Alve and Murray, 2001), they are not always restricted to the uppermost layer of the sedimentary column, and may be found at depths of up to 60 cm below the sediment surface (Goldstein et al., 1995; Saffert and Thomas, 1998; Hippensteel et al., 2000). Temperature, oxygen concentration and food availability are the main factors determining the vertical distribution of benthic foraminifera within sediment (Linke and Lutze, 1993; Jorissen et al., 1995; Gross, 2000). Using the TROX model, Jorissen et al. (1995) suggested that the vertical penetration of foraminifera into the sediment is limited to the redox boundary. The occurrence of benthic foraminifera deep in the sediment has been subject to considerable speculation concerning the possible presence of oxygen and organic-matter rich “oases” around macrofaunal burrows (Aller and Aller, 1986; Meyers et al., 1988; Bernhard, 1989; Thomsen and Altenbach, 1993; Goldstein et al., 1995; Koller et al., 2006; Diz and Francès, 2008), and/or passive transport by macrofaunal bioturbation activities (Lipps, 1983; Moodley, 1990). Benthic foraminifera may also display active dispersion through self-locomotion within the sediment (Gross, 2000). Denitrification capacity has also recently been found among foraminifera (Bernhard et al., 2006; Risgaard-Petersen et al., 2006). Foraminifera may therefore thrive in low-oxygen environments. Foraminifera have also been shown to be sulfide-tolerant (Bernhard et al., 2003; Duchemin et al., 2005) and therefore able to live in the harsh conditions occurring in sediments.

Experimental evidence is accumulating to suggest that positive interactions between benthic fauna species and favoring the success of certain species in marine soft-bottom communities are common and important ecological processes in intertidal and shallow subtidal habitats (Reise, 1985; Schaffner, 1990). The relationships between bioturbators and macro- and meiofaunal community structure have already been investigated (Widdicombe et al., 2000; Olafsson, 2003; Dashfield et al., in press). The relative importance of processes promoting the survival of particular species or of interactions between species remains unclear in most communities. The diversity of bioturbators (i.e. different bioturbation modes) is probably related to the diversity of the sediment infauna (Widdicombe et al., 2000). Previous work (Reise, 1985) suggests that promotion phenomena are probably common in situations in which the biogenic alteration of the sediment facilitates ‘accommodating’ relationships between species (e.g. commensalism, mutualism), stabilizes sediment (e.g. worm reefs, seagrass beds), or alters sediment biochemistry and near-bed hydrodynamics. However, more information about the effects of macrofaunal bioturbating activities on the distribution of benthic foraminifera within the sediment is required, to complete the foraminiferal distribution model and to provide more general information about infaunal microhabitats and macro-/meiofaunal interactions.

In sedimentary coastal habitats, ecosystem engineering may regulate community composition and ecological processes (Fonseca and Fisher, 1986; Contessa and Bird, 2004). For instance, the reworking of sediment by callianassid sand prawns from the tidal flats in Durban Bay (South Africa), inhibiting the microbial biofilm, has emerged as one of the principal mechanisms structuring macrofaunal communities (Pillay et al., 2007). The reworking activities of the macrofauna also generate many microhabitats (Reise, 1981; Bell, 1983), and burrow structures are typically seen as biogeochemical extensions of the sediment-water interface (Aller, 1988). By reworking the sediment, the benthic macrofauna increase solute and sediment fluxes at the sediment-water interface (Aller, 1982; Meysman et al., 2005). Bioturbation also has profound effects on both the physical and geochemical properties of the substratum (Rhoads, 1974; Aller, 1982), stimulating sediment oxygen uptake (Kristensen, 2000), nutrient fluxes (Michaud et al., 2006) and coupled nitrification-denitrification (Pelegri et al., 1994). The resulting microhabitats have specific chemical and biological properties that may favor the growth and development of micro-, meio- and macrobenthic communities (Meyers et al., 1988; Widdicombe and Austen, 1999; Papaspyrou

et al., 2006). The effects of the macrofauna on such biogeochemical processes are species-specific, but depend principally on the modes of feeding and bioturbation (Pelegri and Blackburn, 1995; Mermillod-Blondin et al., 2004; Michaud et al., 2005). Regardless of the mode of bioturbation, the size of the organism is also a key factor determining the effects of bioturbation on community and ecosystem function (Solan et al., 2004; Thrush et al., 2006; Gilbert et al., 2007). Burrow shape and burrow-wall architecture may also play an important role in controlling oxygen diffusion (Zorn et al., 2006). Five functional groups of bioturbators have been described: downward-conveyors, upward-conveyors, biodiffusors, gallery-diffusors and regenerators (François et al., 2002; Gérino et al., 2003). Downward- and upward-conveyors are responsible for the active, non-local transport of particles through their gut and the passive and advective transport of particles surrounding them. Biodiffusors move sediment particles in a random manner over short distances, resulting in diffusive sediment transport. Gallery-diffusors dig tube systems, resulting in the non-local transport of matter from the surface to deeper parts of the tubes. Regenerators are gallery-digging species causing both biodiffusive mixing, with large amounts of sediment released into the water column during digging, and the net movement of the surface sediment to the bottom of the burrow after the burrow has been deserted. These functional groups are defined based on sediment reworking, but the effects of their bio-irrigation activities on water-sediment fluxes differ (e.g. Michaud et al. 2006). Little is known about the roles of these different groups in macrofauna-meiofauna interactions, including foraminiferal assemblages, and quantitative approaches are required to assess these interactions.

Various techniques have been proposed for quantifying the volume of biogenic structures in the sedimentary column. Gerino and Stora (1991) used Araldite resin to produce casts of burrows. These casts were then digitized to estimate their volume. The general morphology of burrows has been investigated with X rays (e.g. Davey, 1994; Migeon et al., 1999), photography (Rosenberg and Ringdahl, 2005) and sediment profile imaging, as developed by Rhoads and Cande (1971) and subsequently improved (e.g. Solan and Kennedy, 2002; Rosenberg et al., 2003). Most of these techniques are destructive, as they alter the sedimentary column. Axial tomodensitometry can be used to determine the volume of biogenic structures, making it possible to visualize the three-dimensional structure of the sedimentary column without destructive effects. Geologists have used this technique to characterize sedimentary structures (e.g. Boespflug et al., 1994; Moreau et al., 2006), and this method has been used for about 20 years in ecological studies (e.g. Warner et al., 1989; Fu and Werner, 1994). New software developed over the last few years has considerably facilitated quantification of the volume of biogenic structures by CT-scan (review in Dufour et al., 2005). This technical development has resulted in greater use of CT-scans being made in both marine (e.g. Perez et al., 1999; Mermillod-Blondin et al., 2003; Rosenberg et al., 2007; Mazik et al., 2008; Rosenberg et al., 2008) and terrestrial studies (Daniel et al., 1997). Computed tomography is now recognized to be an efficient tool for the three-dimensional exploration of biogenic structures and accurate volume quantification in soil and sediments. Moreover, the great precision of this technique also makes it possible to link biogenic structure to bioturbation functional groups (e.g. to link a gallery of burrows with a gallery diffusor).

In this study, we aimed 1) to describe the vertical distribution of both living (stained) foraminifera and macrofauna, 2) to quantify biogenic structure volumes, by means of non destructive CT-scans for the main relevant bioturbating functional groups, represented by annelid, nemertean and bivalve species, and 3) to determine whether the occurrence of benthic foraminifera deep in the sediment was linked to the presence of specific macrofaunal biogenic structures. We investigated links between macrofaunal bioturbation and foraminiferal distribution, by sampling from stations inhabited by different benthic faunal assemblages. As oyster farming decreases benthic species diversity, by increasing sedimentation, and modifies the abundance and nature of macrofaunal communities (Nugues et al., 1996; Kaiser, 2001; Bouchet and Sauriau, 2008), we selected three stations affected to different extents by oyster farming. The impact of human activity on the environment, over local to global scales, not only causes a general decline in diversity, but

also causes predictable functional shifts, as sets of species with particular traits are replaced by others with different traits (Grime et al., 2000). As species composition, richness and evenness are affected by ecosystem properties (Hooper et al., 2005), we hypothesized that differences in the functional diversity of macrofaunal bioturbators between stations would influence the spatial distribution of foraminifera in sediments through specific macrofauna-foraminifera interactions.

2. Materials and methods

2.1. Sampling strategy

This study was carried out in the Pertuis Charentais region (Atlantic coast, SW France, Fig. 1), which has large intertidal areas consisting mostly of muddy sediments (Sauriau et al., 1989). These mudflats are widely used for cultivation of the Pacific oyster *Crassostrea gigas* (Thunberg), the Pertuis Charentais region being the largest area of Pacific oyster production in Europe (Goulletquer and Héral, 1997). In this region, oysters were traditionally cultivated directly on the sediment. However, in recent years, rack culture has become the commonest technique. This method involves placing the oysters in plastic mesh bags tied to metal trestles. The presence of trestles arranged in parallel rows in the intertidal area (Goulletquer and Héral, 1997) significantly reduces the strength of tidal currents (Nugues et al., 1996). Three intertidal stations, differing in their exposure to oyster farming, were sampled on 29 October 2004. The first station was an intertidal station located at Esnandes in Aiguillon Cove, far from the influence of oyster farms, used as control (Fig. 1). The two other stations were located on the north coast of Ile de Ré, in an area devoted to oyster cultivation, at Rivedoux (Fig. 1). The control sampling station (Stn C) and its benthic faunal assemblages were similar to those reported for mid-tidal level mudflats in Aiguillon Cove (Degré et al., 2006). One of the stations at Rivedoux was in an area hereafter referred to as the 'oyster zone' (Stn OZ) and was characterized by significant organic enrichment of the silt deposits due to the biodeposition of oyster feces and pseudofeces. The second sampling station at Rivedoux was in an area hereafter referred to as the 'oyster-free zone' (Stn OFZ). It was located about 100 m north-west of Stn OZ, in an intertidal mudflat on which oysters were not grown. However, due to the hydrodynamic features of the site (Faure, 1969), oyster biodeposits were naturally transported to Stn OFZ. This resulted in a moderate effect of oyster culture on local benthic faunal assemblages at Stn OFZ (Bouchet and Sauriau, 2008).

2.2. Sediment

Seawater salinity was determined *in situ* with a salinometer. At each sampling station, sediment temperature and redox levels (Eh) were determined *in situ* using a Cyberscan pH 300 series probe (EUTECH Instruments) 1 and 4 cm below the water-sediment interface of sediment cores sampled at low tide. Measurements were made immediately through holes that had previously been drilled into the core tube, 1 cm apart.
For sediment organic matter (SOM), chlorophyll *a* (chl *a*) and phaeopigment analyses, the top 1 cm of sediment cores (n = 3, diameter = 75 mm) was sliced off and homogenized. Sediment organic matter was analyzed for particulate organic carbon and nitrogen (POC and PON), using a C/N analyzer (Carlo Erba NA 1500). Chlorophyll a and phaeopigment concentrations were determined according to Lorenzen's method (Holm-Hansen et al., 1965). Samples were freeze-dried, extracted by incubation overnight in 90% acetone (4°C), centrifuged for 10 minutes at 2000 rpm, analyzed spectrophotometrically (Turner 10 AU), and

corrected for phaeopigments, which were determined after treatment with 1N HCl (Yentsch and Menzel, 1963).

2.3. Radioisotope analysis

For radioisotope analysis, sediment was sampled by removing cores (n = 1, diameter = 75 mm, 6 cm long) at each sampling station. Only one core was taken per sampling station, as in previous studies conducted in similar coastal environments and showing non significant variability between replicates (Schmidt et al., 2007). ^{234}Th, ^{7}Be and ^{210}Pb levels were determined in the uppermost sediment layers, using a low-background/high efficiency well-type germanium γ-detector (Schmidt et al., 2002). IAEA standards (RGU-1, RGTh-1, IAEA-375) were used to calibrate the γ detectors. These measurements had to be carried out within one month of sampling, due to the rapid decay of ^{234}Th. Sediment layers were investigated moving down the core, until ^{7}Be disappeared and constant levels of ^{234}Th activity were reached, these levels being considered to correspond to the level of activity supported. The excess of ^{234}Th and ^{210}Pb was calculated by subtracting the supported activity — ^{238}U and ^{226}Ra, respectively — from total activity in the sediment. Both $^{234}Th_{xs}$ and ^{7}Be activities were corrected for the radioactive decay occurring between sample collection and counting (Schmidt et al., 2007). The simplest way to obtain mixing rates (D_b) from radionuclide profiles assumes that bioturbation is a diffusive process occurring at a constant rate within a surface mixed layer at steady state (Lecroart et al., 2007):

$$A_z = A_0 exp(-z\sqrt{\frac{\lambda}{D_b}}) \qquad (1)$$

where A_z and A_0 are the activities (mBq g^{-1}) of ^{7}Be or excess ^{234}Th at depth z and at the water-sediment interface (Schmidt et al., 2007).

2.4. Fauna

Three cores (30 cm long, 9.5 cm in diameter), were collected at each station for studying the vertical distributions of macrofauna. Two cores were sliced immediately in the laboratory from the top, at intervals of 0.5 cm for a depth of 0 to 1 cm, 1 cm for a depth of 1 to 5 cm, 2.5 cm for a depth of 5 to 10 cm, and 5 cm for a depth of 10 to 30 cm, and the third was prepared for CT-scan analysis. The vertical distribution of benthic living (stained) foraminiferal species was also studied in scanned cores. As access to the medical CT-scanner for non-medical purposes is limited, we scanned only one core per sampling site in this study. This lack of replication would bias the study if the scanned core was not representative of the station. We tried to overcome this problem, by checking that the composition and vertical distribution of fauna in the scanned core were similar to those obtained for the two other cores collected at the same station. We assumed that a similar distribution of fauna in scanned and non scanned cores from the same station was indicative of the scanned core being representative of the conditions *in situ*.
Sediment slices were preserved in 1 g l^{-1} Rose Bengal in 70% ethanol to distinguish between stained (living) foraminifera and dead specimens (Murray and Bowser, 2000). The Rose Bengal staining method proposed by Walton (1952) is considered to be a rapid, efficient method for recognizing living foraminifera, as suggested by Murray and Bowser (2000), although Rose Bengal does also stain dead tissues and is not necessarily an accurate indicator of whether an organism is alive or dead. Langer and Lipps (2003) checked for live specimens by observing freshly collected specimens under seawater in the laboratory. If, after 12–24 h, the animals collected had extended pseudopodia or protoplasm, they were considered to be alive; if not, they were considered to be dead. This observation provides

genuine proof that the specimen is alive, but is highly time-consuming. Most researchers therefore prefer to use Rose Bengal staining. We also considered bright staining at the time of collection to be a reasonable indicator of the organism being alive, to ensure that the results obtained could be compared with those of previous studies.
Each slice was washed through 500 µm and 50 µm mesh sieves to retain the macrofauna and foraminifera, respectively. The sediment retained on the 50 µm mesh sieve was dried at 50 °C. Heavy liquid flotation with carbon tetrachloride (CCl_4) was then used to concentrate the foraminifera. We identified and counted all living macrofaunal and foraminiferal specimens from the retained sediment. Where possible, the macrofauna and foraminifera were identified to the species level. The abundance of stained foraminiferal specimens was standardized and expressed per 50 cm^3 of sediment (total number of specimens in 50 cm^3 of sediment), and abundances of macrofauna species were expressed as the total number of individuals per species per cm^2.

2.5. CT-scans

During collection, the tops of the cores to be scanned were sealed with a paraffin plug, according to standard protocols, to preserve the water-sediment interface and biogenic structures (de Montety et al., 2003; Michaud et al., 2003). They were stored in a cold room to limit faunal movement and scanned 12 hours later. The time between sampling and scanning was shorter than the three weeks reported in the study by Dufour *et al.* (2005).
Many studies since the original study by Warner *et al.* (1989) have described CT-scan procedures in detail (review in Dufour et al., 2005). The sediment cores were scanned using an axial tomodensitometer (Siemens SOMATOM® Sensation 16 scanner) at Hôtel-Dieu University Hospital, Nantes. The cores were scanned in the horizontal position, along their entire length, without interruption and from all spatial directions. We obtained 4.5 mm-thick CT transverse sections from the water-sediment interface down to a depth of 30 cm, giving 60 images per core. CT transverse section is the uniform distance between sequential slices. We obtained two-dimensional (2D) images composed of pixels (a single area of equal length and width) and three-dimensional (3D) images composed of voxels (units of volume). The pixel resolution was 0.45 mm x 0.45 mm, the pixel area was 0.203 mm^2 and the voxel volume was 0.911 mm^3. All image data for each sediment core were stored in Digital Imaging and Communications in Medicine (DICOM) format.
After scanning, cores were sliced according to their respective sedimentary facies, observed on 2D images, to determine the composition and vertical distribution of the benthic fauna.

2.6. Image analysis

OSIRIS software was used to analyze 2D images (Ligier et al., 1994). Pixels in an image obtained by CT scanning are displayed in terms of relative radiodensity. The pixel itself is displayed according to the mean attenuation of the tissue that it corresponds to on a scale from −1024 to +3071 on the Hounsfield scale. Water has an attenuation of 0 Hounsfield units (HU) while air is −1000 HU (Dufour et al., 2005). The 2D images were visualized and manipulated with OSIRIS software, to highlight biogenic structures. These structures were clearly visible as their intensity on the scan differed from that of the surrounding sediments. Biogenic structures were dark (with a Tomographic intensity (TI) similar to that of water TI = 0 HU) and bivalve shells were shown in white (with TIs similar to those classically measured for gravel – TI > 215 HU) (Fig. 2). All 2D images of each core were also initially treated to highlight the continuity of biogenic structures, in combination with 3D images. This prior treatment was essential for the differentiation of functional structures (connected to the

overlying water) from relict structures (not connected to the water-sediment interface), and for the assignment of each identified structure to bivalves (shells, cavity and siphons) or worms (burrows of annelids and nemerteans).

Each 2D image was then analyzed independently, to quantify the area occupied by each functional biogenic structure (relict structures were not quantified). OSIRIS can automatically delimit a region of interest (ROI) for a given range of tomographic intensities and measure its area in numbers of pixels. In this study, each ROI corresponded to a biogenic structure. The area occupied by each biogenic structure (ROI) was normalized with respect to a biogenic structure volume (bioturbated volume) in cm^3, for a single 4.5 mm-thick layer.
Sediment reworking intensity depends on the biovolume of the macrofauna (Gilbert et al., 2007). We therefore decided to determine the mean volume occupied per animal (worms and bivalves) for each scanned core. Due to pixel resolution, volumes of biogenic structures built by macrofaunal species less than 4.5 mm long — *Hydrobia ulvae* (Pennant) and *Cerastoderma edule* (Linnaeus) juveniles in particular — cannot be measured. Using the complete set of 2D images obtained for each core, we calculated the mean volume bioturbated by one worm (annelids and nemerteans, AN) or by one bivalve (B) within the whole sedimentary column.

$$V_{biot\ AN\ or\ B} = V_{tot\ AN\ or\ B} / N_{AN\ or\ B}$$

where $V_{tot\ AN\ or\ B}$ is the total volume occupied (bioturbated) by AN or B in the whole sedimentary column and $N_{AN\ or\ B}$ the number of specimens counted in the whole sedimentary column.
We used 2D images to reconstruct the three-dimensional structure of the sedimentary column and to produce 3D images. Using medical procedures for image processing, we developed techniques for distinguishing air structures (e.g. bivalve cavity, polychaete tube) and/or shell structures from sediment. For example, a procedure used to visualize bones was applied to shell structures in this study. When possible, 3D images were thus treated to highlight air structures and/or shell structures (Dufour et al., 2005).
The total length, height and thickness of the shell of the bivalve mollusc *Scrobicularia plana* and the total body length and diameter of annelids and nemerteans were measured with a digital caliper to the nearest 0.1 mm. Biovolumes of bivalves in cm^3, including their shells, were approximated with a formula defining an ellipsoid:

$$V = 4/3 \prod (L \times h \times t) /8$$

where L is total shell length, h is total shell height and t is total shell thickness.
Biovolumes of annelids and nemerteans in cm^3 were approximated with the formula defining a cylinder:

$$V = \prod (D/2)^2 \times L$$

where D is body diameter and L is total body length.
The mean individual biovolume was then calculated.

2.7. Data analysis

Differences in the composition of functional groups were then tested by a two-way ANOVA with replication (n = 3 cores per station) and both station and functional groups as fixed effects. The five following functional groups were considered in the analysis: downward-, upward- conveyor, regenerator, biodiffusor and gallery-diffusor. All data were tested for homoscedasticity with Bartlett's test (Zar, 1984) before ANOVA. When this statistical assumption

was not satisfied, data were log (X+1) transformed. In case of non-independent data due for instance to spatial continuity, non-parametric tests were used. The Friedman's Test was used to test for differences in faunal composition between cores (n = 3) for each station, with cores as treatment and species as blocks (see Table 3 for the number of species). The Friedman's test was also used to compare the vertical distributions of macrofaunal and foraminiferal abundances between the three cores for each sampling station; cores being the blocks and depths the treatments.The vertical distribution of biogenic structures and foraminifera were compared between stations, using the Kolmogorov-Smirnov test. Pearson's correlation tests were used to determine the links between vertical distributions of bioturbated volumes (total volumes and volumes assigned to each functional group) and foraminiferal abundances in sedimentary columns. All statistical analyses were performed with MINITAB package release 10 and Palaeontological Statistics (PAST) (Hammer et al., 2001).

3. Results

3.1 Sediment characteristics

Seawater salinity was lower at Stn C (27.5) than at Stns OFZ and OZ (31.6) (Table 1). Temperature, POC, PON, C/N were similar at all three stations. The lowest Eh was recorded at Stn OZ, with a value of -52 mV obtained at a depth of 1 cm depth and -112 mV obtained at a depth of 4 cm, whereas Eh was positive at Stn C and in surface sediment at Stn OFZ. Chlorophyll a concentrations were highest at Stn OZ (103 ± 6 mg m^{-2}), and phaeopigment concentrations were lowest at Stn OFZ (120 ± 17 mg m^{-2}) (Table 1).

3.2. Radioisotopes

The radioisotope profiles of the two stations influenced by oysters were different (Table 2). $^{210}Pb_{xs}$ activities remained fairly constant, from 0 to 6 cm at Stn OZ, whereas two layers, from 0 to 1 cm and from 1 to 6 cm, could be distinguished at Stn OFZ. The thickness of the apparently mixed layer ranged from 6 cm at Stn OZ to 1 cm at Stn OFZ. At Stn OFZ, the two layers were associated with a rapid decrease in $^{210}Pb_{xs}$ activity, consistent with discontinuous sedimentation, as previously observed in this area (Gouleau et al., 2000).
At Stn OZ, $^{234}Th_{xs}$ and ^{7}Be profiles in the sediment displayed a sharp, exponential decrease in activity, indicative of bioturbation activities (Table 2). Given their short half-lives (24.1 and 53 days, respectively) and sedimentation rates (Gouleau et al., 2000), in the absence of bioturbation, $^{234}Th_{xs}$ and ^{7}Be should be present only at the water-sediment interface. The profiles obtained for Stn OZ and Stn OFZ showed that both these short-lived radionuclides penetrated to various depths, indicating that efficient mixing of the upper sediments — usually referred to as bioturbation — occurred (Table 2). The bioturbation rates derived from data for the two radionuclides were similar, at about 7 to 9 $cm^2\ y^{-1}$, at Stn OZ. At Stn OFZ, $^{234}Th_{xs}$ and ^{7}Be were detected only in the uppermost 1 cm, giving much higher bioturbation rates of about 29 to 30 $cm^2\ y^{-1}$.

3.3. Macrofaunal assemblages

The abundance of each macrofaunal species did not differ significantly between the three cores sampled at each station (Friedman's test, p = 0.11 for the Stn C, p = 0.28 for the Stn OFZ and p = 0.23 for the Stn OZ), indicating that despite some variability may exist, macrofaunal assemblages are similar in three cores within a station. Vertical distributions of total macrofaunal abundances were similar for all three cores taken from the same site,

despite the scanned core being sliced 12 hours after the others (Friedman's test, p = 0.529 for Stn C, p = 0.387 for Stn OFZ and p = 0.717 for Stn OZ).
Biogenic structures built by benthic macrofauna were observed on 3D images (Fig. 3). Burrow type, gallery shape, and structure continuity were used to identify the species responsible for a given biogenic structure (Fig. 3). For instance, bivalves produce easy-to-recognize cavities and *Hediste diversicolor* (O.F. Müller) constructs straight or "Y"-shaped burrows.
Macrofaunal assemblages are reported in Table 3. The macrofaunal assemblage of Stn C was dominated by three species: a small biodiffusor gastropod *Hydrobia ulvae*, small tube builders such as *Streblospio shrubsolii* (Buchanan) and large cavity builders such as *Scrobicularia plana* (da Costa) (Table 3). The assemblage was composed of 60% biodiffusors, 38% downward-conveyors and 2 % gallery-diffusors (Fig. 4). Biodiffusors, such as *S. plana*, were observed in the uppermost 10 cm, extending up to 15 cm down into the sediment and generating characteristically large cavities (Fig. 3A). Downward-conveyors, such as *S. shrubsolii*, were mostly found in the surface layer (0-3 cm). Gallery-diffusors, such as *Nephtys hombergii* Savigny, were observed deeper in the sediment. The large tube builder *Hediste diversicolor* colonized the layer extending between depths of 10 and 15 cm, constructing large "Y"-shaped burrows (Fig. 3A). The head of a specimen of *N. hombergii* was also observed in the 1 to 2 cm slice, whereas its pygidium was observed in the 5 to 7.5 cm slice, demonstrating the continuity of the galleries constructed by this individual. *Nemertina* sp. was observed at depths of 7.5 to 10 cm.
Small, tolerant and opportunistic polychaetes — *Cossura pygodactylata* Jones, *Pseudopolydora antennata* (Claparède) and *Streblospio shrubsolii* – and opportunistic *Oligochaeta* spp. predominated at Stns OFZ and OZ (Table 3). These organisms build small tubes, mostly burrowing in the top 8 cm of sediment (Fig. 3 B and C). The OFZ and OZ assemblages consisted of 88 and 64% downward-conveyors, 11 and 34% upward-conveyors and 1 and 2% gallery-diffusors, respectively (Fig. 4). Significant differences were observed in the functional bioturbating group compositions of the macrofaunal assemblages of the three sampling stations (two-way ANOVA, $p < 0.05$), particularly between the control station and the stations affected by oysters. Significant interactions between station and functional group (two-way ANOVA, $p < 0.001$) also indicated that functional group profiles differed between the control and oyster-affected stations. At Stn OFZ and Stn OZ, downward-conveyors were present mostly in the surface layer (0-3 cm), producing a dense network of burrows (Fig. 3B) extending for up to 15 cm below the sediment surface. Upward-conveyors (*Oligochaeta* spp.) were concentrated in the 3-8 cm layer, but were found right down to depths of 30 cm. Gallery-diffusors, such as *Nephtys hombergii*, *N. cirrosa* Ehlers and *Tubulanus polymorphus* Renier, were poorly represented, despite burrowing from the surface down to deep sediment layers in the sedimentary column: up to 15 cm and 25 cm below the sediment surface for the Nephtydae and *T. polymorphus*, respectively (Fig. 3C). Discontinuities (an absence of connections) were also observed between tubes located in the intermediate layer and tubes located in deep layers at Stn OFZ and Stn OZ (Fig. 3B and C).

3.4. Biogenic structure volumes

The total volume occupied by biogenic structures within the whole sedimentary was very similar for all the stations, 33.5 cm^3 at Stn OZ, 27.3 cm^3 at Stn OFZ and 33.7 cm^3 at Stn C. The vertical distributions of biogenic structures deduced from 2D image analysis nevertheless differed between the three stations (Fig. 5), as the vertical profile obtained at Stn C differed significantly from those obtained at the other stations (Kolmogorov-Smirnov tests, $p < 0.005$ for comparison between Stn C and Stn OZ, $p < 0.05$ for comparison between Stn C and Stn OFZ; no significant difference between Stn OZ and Stn OFZ). This resulted mostly from differences in bioturbators in the 3-8 cm layer of sediment between stations, this sedimentary layer being dominated by bivalve siphons, shells and cavities at Stn C (Fig. 5C) and by annelids and nemerteans at Stn OZ and Stn OFZ (Fig. 5B).

The individual biovolume of the bivalve *Scrobicularia plana* (0.37 cm^3) is hardly greater than those of the annelids and nemerteans species, except for *Nepthys hombergii* (0.29 cm^3) and to a certain extent for *Hediste diversicolor* (0.15 cm^3) (Table 3). Calculation of the volume occupied by a single individual showed that a single bivalve disturbed a larger volume of sediment (1.60 cm^3) than a worm (annelid or nemertean) (0.20 cm^3) (Fig. 6). For the bivalve *S. plana*, we also calculated that the mean volume bioturbated by one specimen (1.60 cm^3) was four times the biovolume of its body including the shell (0.37 cm^3).

3.5. Foraminiferal assemblages

Stained (living) benthic foraminifera were represented by 11, 9 and 11 taxa at Stn C, Stn OFZ and Stn OZ, respectively (Table 4) Assemblages were dominated by four species — *Ammonia tepida* (Cushman), *Cribroelphidium excavatum* (Terquem), *Haynesina germanica* (Ehrenberg) and *Brizalina striatula* (Cushman) — which were present at all three stations (Table 4). The vertical distributions of abundances of stained (living) benthic foraminifera differed significantly between the three stations, foraminifera occurring deeper at Stn C than at Stn OZ and Stn OFZ (Kolmogorov-Smirnov test, $p < 0.001$ for comparison between Stn C and the other stations; no significant difference was found between Stn OZ and Stn OFZ; Fig. 7). Foraminiferal abundances decreased sharply with depth at Stn OZ and Stn OFZ. By contrast, mostly due to the greater abundance of *A. tepida*, abundance peaks were reported at three sediment depths (0-0.5 cm, 5-7.5 cm and 15-20 cm) at Stn C. *A. tepida, C. excavatum* and *B. striatula* colonized both surface and deep sediments at Stn C, whereas they were mainly concentrated in the surface layer at Stn OZ and Stn OFZ. By contrast, *H. germanica* was observed solely in the surface sediment of the three stations.

3.6. Correlation between foraminiferal abundance and volume per biogenic structure

At Stn C, the abundance of stained (living) benthic foraminifera were correlated with the total volume of biogenic structures (Pearson's correlation test, n = 9, $r = 0.80$, $p < 0.01$, respectively). Correlations between the abundance of stained (living) benthic foraminifera and the total volume of bivalve biogenic structures were significant (Pearson's correlation test, n = 9, $r = 0.76$, $p < 0.05$), whereas the abundance of stained (living) benthic foraminifera were not correlated with the total volume of annelid biogenic structures (Pearson's correlation test, n = 9, $r = 0.20$, $p = 0.61$). However, the peak of foraminifera observed in the 16-18 cm layer of Station C (Fig. 7) could not be linked to the bivalve biogenic structures (Fig. 6). The occurrence of a deep burrow of *H. diversicolor* in the scanned core of Station C most probably explained the deep distribution of foraminifera at this station. By contrast, at Stn OZ and Stn OFZ, there was no significant correlation between the vertical distributions of abundance of stained (living) benthic foraminifera and the total volume of biogenic structures due solely to annelids and nemerteans (Pearson's correlation test, n = 3, $r = -0.61$, $p = 0.58$ at Stn OZ and n = 4, $r = -0.08$, $p = 0.29$ at Stn OFZ).

4. Discussion

4.1. CT-scan to assess macrofaunal bioturbation

In accordance with previous studies (e.g., Rosenberg et al., 2007; Mazik et al., 2008), we found that computed tomography quantified biogenic structure volume and discriminated between the biogenic structures produced by bivalves and annelids / nermerteans. We could easily determine the structures produced by the biodiffusor functional group in the present

study. Nevertheless, it remained difficult to distinguish a structure built by a large annelid from one built by a smaller annelid, mainly due to the same shape of their burrows. It was thus not possible to assign annelid / nemerteans structures to the functional group it belongs. This distinction between functional group structures is of great interest for ecological studies, because the influence of an ecosystem engineer on sedimentary processes (water-sediment fluxes) is strongly linked to its bioturbation mode (sediment reworking and bio-irrigation activities) and its burrowing depth (e.g., Mermillod-Blondin et al. 2004; Michaud et al. 2006). Thus, by combining functional group information and biogenic structure quantification, it is possible to assess potential changes in the sedimentary habitat due to macrofauna. Even if CT-scan use needs improvements as specify below, this approach proved useful in this study, for linking the vertical distributions of biogenic structures and of foraminifera in sediments.
Due to the high cost of CT-scans and poor access to this technique for non medical studies, studies based on this technique have tended to involve the scanning of only one core per sampling site (de Montety et al., 2003; Mermillod-Blondin et al., 2003; Michaud et al., 2003; Mazik et al., 2008) or small numbers of replicates (Perez et al., 1999; Rosenberg et al., 2007). For these reasons, we were able to scan only one core per sampling station in this study. The use of core data without replication for each station is based on the assumption that the scanned core is representative of the environmental conditions at the station. We tested this hypothesis, by checking that the compositions of the macrofaunal and foraminiferal assemblages of the scanned core and the other two replicates sliced immediately after sampling were similar. The absence of a significant difference in the vertical pattern of macrofauna and foraminifera between the three cores indicated that the scanned core was indeed representative of the *in situ* fauna distribution. This comparison also showed that the delay of 12 h between sampling and scanning did not significantly modify the fauna distribution (potentially biasing the biogenic structures) in the sediment.

4.2. Control station

Total richness in foraminiferal species was similar for all three stations studied, but the abundances and vertical distribution of foraminifera differed between stations. Abundance peaks were observed several centimeters below the sediment surface at the control station, whereas foraminifera were restricted to the layer of sediment at the surface at stations affected by oyster farming. In this study, *Haynesina germanica* was epifaunal, and *Ammonia tepida, Cribroelphidium excavatum* and *Brizalina striatula* were both epifaunal and infaunal. These observations are consistent with the findings of Linke and Lutze (1993) and Thomsen and Altenbach (1993) for *C. excavatum* and Goldstein et al. (1995) for *A. tepida*.
At the control station, macrofaunal assemblages were composed of species belonging to the downward-conveyor, gallery-diffusor and biodiffusor functional groups. Infaunal depth distribution patterns showed that foraminiferal abundances, particularly for *Ammonia tepida*, increased in the 5-7.5 cm layer, an area in which bivalve cavities and gallery-diffusor activities are concentrated, and in the 16-18 cm layer in connection with the deep penetration of the gallery-diffusor *Hediste diversicolor*. The activities of these functional groups of organisms may greatly increase water exchange between the water column and the sediment (Riisgard and Banta, 1998; Mermillod-Blondin et al., 2004; Michaud et al., 2005). Usually, bivalve cavities are connected to the water-sediment interface through siphons, potentially facilitating the supply of oxygen and nutrients to deeper sedimentary layers, as suggested by Vaughn and Hakenkamp (2001) in freshwater ecosystems, thereby providing habitats for benthic fauna. *Hediste diversicolor* activity produces a continuous current of water carrying oxygen and food particles into the burrow (Mermillod-Blondin et al., 2004). As *H. diversicolor* burrows deeper into the sediment, it irrigates a great volume of sediment, having a great influence on pore water chemistry, ammonium release and bacterial communities (Mermillod-Blondin et al., 2004; Michaud et al., 2006). As diffusive properties are related to burrow microstructures and, presumably, the microbial communities living

within the burrow environment (Zorn et al., 2006), the oxygen-diffusing properties of structures built by the biodiffusor *S. plana* and the gallery-diffusor *H. diversicolor* may increase oxygen penetration. This hypothesis is supported by the positive redox values reported for the top 4 cm of sediment at the control station.

These two species were also the larger bioturbators observed in this study, suggesting that they should bioturbate a larger volume of sediment than smaller ones. Larger species are supposed to have stronger impact on bioturbation than smaller species (Solan et al., 2004; Gilbert et al., 2007). Thrush et al. (2006) also reported a much larger impact of large organisms than of small organisms to ecosystem function. Nonetheless, the effects of these organisms on ecosystem function depend on the attributes of individual species. The mean volume bioturbated by an individual bivalve at the control station was eight times higher than that bioturbated by a single annelid or nemertean at the other stations. In this study, CT scans showed that the volume bioturbated by an individual of *Scrobicularia plana* (1.60 cm^3) was four times its biovolume (0.37 cm^3). This difference may result from (1) vertical movements of the bivalve, creating a cavity in the sedimentary column with a volume greater than the body volume of the organism and (2) the feeding activities of bivalves, characterized by the extension of siphons up to the sediment water-interface. Even though it was not possible to discriminate between the structures produced by annelids / nemerteans for the calculation of biogenic structure volumes, it appeared on 3D images that *Hediste diversicolor* built larger burrows than the other annelids / nemerteans species. This finding is consistent with the hypothesis that large bivalve biodiffusors and large gallery-diffusors may have a greater influence on sedimentary habitats than small burrowers, such as upward- and downward-conveyors.

The living foraminifera found in anoxic sediment intervals may be associated with oxic halos surrounding macroinfaunal tubes (Meyers et al., 1988). For instance, Thomsen and Altenbach (1993), Koller et al. (2006) and Diz and Francès (2008) showed that benthic foraminifera were preferentially distributed around inhabited echiurid tubes, in burrows of the decapod *Callianassa* (= *Pestarella*) *tyrrhena* (Petagna) or in tubes of the polychete *Maldane glebifex* Grube. Foraminifera may respond to an increase in bacterial populations by multiplying or gathering around macrofaunal burrows, such that their densities in these areas are two or three times their mean density in sediment (Aller and Aller, 1986). Koller et al. (2006) also reported that *C. tyrrhena* activity resulted in the creation of a specific oxidized microenvironment within burrows inhabited by numbers of foraminifera twice those present in the surrounding non burrowed sediment. Just as biogenic structures have a positive effect on oxygen conditions in sediments, their walls are enriched in organic matter and bacteria (Koller et al., 2006; Papaspyrou et al., 2006). Bacteria within tubes and cavities may serve as a source of food for benthic foraminifera such as *Ammonia tepida* (Bernhard and Bowser, 1992; Langezaal et al., 2005; Nomaki et al., 2006). Thus, biogenic structures may act as preferred feeding zones for foraminifera in sediments. Non decomposed diatom masses, which are reported to be present in macrofaunal burrows (Aller and Aller, 1986), may also provide benthic foraminifera with a source of energy (Ward et al., 2003). The positive effects of biogenic structures on foraminiferal populations reported in previous studies are consistent with the strong correlation observed between the abundances of living foraminifera deep in the sediment and the presence of bivalve cavities and *Hediste diversicolor* burrows at the control station. Although we did not directly observe living foraminifera in the macrofaunal burrows and cavities, bioturbation is highly likely to have an effect, because the three sampling stations displayed different vertical distribution patterns.

In cases of efficient macrofaunal bioturbation, the vertical distribution of living benthic foraminifera may be not limited to the redox boundary, going against the predictions of the TROX and TROX-2 models (Jorissen et al., 1995; van der Zwaan et al., 1999). Patterns of species abundances and association suggest that biogenic alteration of the sedimentary environment, particularly through sediment amelioration (oxygen conditions and food), may modify microhabitat availability, thereby providing a positive mechanism for influencing foraminiferal abundances. Living benthic foraminifera may be transported passively through

the sediment by the movements of macrofauna (Lipps, 1983) or may move actively to these favorable microhabitats (Gross, 2000).

4.3. Oyster-affected stations

By contrast with what was observed for the control station, living (stained) benthic foraminifera were mostly concentrated in surface sediments at Stn OZ and Stn OFZ. Many studies have also demonstrated that living benthic foraminifera are typically found in the uppermost 0 to 1 cm layer (review in Alve and Murray, 2001). These observations are consistent with the TROX model proposed for the benthic foraminiferal fauna of open marine conditions (Jorissen et al., 1995). This model accounts for the existence of benthic foraminifera microhabitats in terms of trophic conditions and oxygen concentrations. Jorissen et al. (1995) concluded that living benthic foraminifera are mostly found in the surface layer and are limited by the redox boundary.

At Stn OZ, the abundance of foraminifera decreased exponentially with sediment depth. However, radioisotope analyses showed the sediment-mixing layer to be at least 6 cm thick at Stn OZ. We would therefore have expected a homogeneous vertical distribution of living benthic foraminifera from the surface to a depth of 6 cm (Berkeley et al., 2007). However, the hypoxic conditions reported for Stn OZ sediment may have generated an upward migration of most of the benthic foraminiferal species to escape unfavorable conditions. This hypothesis is consistent with the findings of several studies (Alve and Bernhard, 1995; Gross, 2000; Duijnstee et al., 2003; Ernst and van der Zwaan, 2004; Geslin et al., 2004) suggesting that hypoxic conditions may have a negative effect on foraminiferal abundances.

At Stn OFZ, the abundance of benthic foraminifera increased from the 0-1 cm to the 1-3 cm layer and decreased thereafter. Radioisotopes indicated that a new 1 cm deep layer of sediment had been deposited. The presence of this new sediment layer together with positive Eh values in surface sediment suggest that surface foraminiferal assemblages were covered very recently and that the relatively good oxygenation did not necessitate a rapid upward migration of the foraminiferal communities. This is consistent of the location of this area that is not protected by the presence of oyster trestles, sediment being exposed to a succession of erosion and deposition cycles mediated by the tidal cycle. This may have induced the observed distribution of benthic foraminifera.

At the two sampling stations affected by oyster farming, living foraminifera were mainly associated with downward-conveyors. The macrofaunal assemblage at Stn OZ differed from that at the control station in consisting mostly of small tube builders (e.g., *Cossura pygodactylata, Pseudopolydora antennata, Streblospio shrubsolii* and *Oligochaeta* spp.), typical of a disturbed system enriched in organic matter (Samuelson, 2001). Oyster farming is known to lead to the organic enrichment of sediment in intertidal areas and changes in the composition of macrofaunal assemblages (Nugues et al., 1996; Kaiser, 2001; Bouchet and Sauriau, 2008). The presence of similar macrofaunal assemblage compositions in Stn OFZ and Stn OZ suggests that organic matter (mainly pseudofeces and feces) was dispersed from the Rivedoux oyster parks to Stn OFZ by hydrodynamic mechanisms, enriching Stn OFZ sediments (Faure, 1969). This enrichment in organic matter favors small opportunistic polychaetes and oligochaetes (Bouchet and Sauriau, 2008).

Changes in species composition in disturbed areas are generally expected to reduce bioturbation, but the magnitude of this decrease depends on the effect on functional diversity (Solan et al., 2004). In our study, the total volume of biogenic structure did not differ between the three stations, but functional diversity did differ significantly between sites. In our study, the species found in the oyster-affected assemblages of Stn OZ and Stn OFZ had functional traits (modes of bioturbation) different from those found in control assemblages, with downward-conveyors dominating the bioturbator population. As the organisms of this functional group mostly act at the surface of the sediment whilst feeding, they do not produce a major flux of water between the overlying water and deep sediments, and may therefore have an effect on oxygen concentrations only in the superficial sediments. This hypothesis is

supported by the negative redox values reported at a depth of 4 cm in the sediment at Stn OZ and Stn OFZ. These findings suggest that although the total volume of biogenic structure was very similar at the different stations, it was not necessarily proportional to the extent of bioturbation in a core, given that many biodiffusive activities cannot be detected on CT-scans. Also, at Stn OZ, the deep-dwelling *Nepthys hombergii, N. cirrosa* and *Tubulanus polymorphus* appeared to be less accommodating facilitators of foraminiferal colonization than the biodiffusor *Scorbicularia plana* and the large gallery-diffusor *Hediste diversicolor* at Stn C. The limited abundances of larger species at Stn OFZ and Stn OZ and discontinuities in burrows from the intermediate and deep layers suggested that most of the burrows observed on CT-scans at depths greater than 15 cm were relict tubes. They probably had no functional role within the sedimentary column.

In the absence of efficient bioirrigation activities at the oyster-affected stations, living foraminiferal assemblages were restricted to the surface layers of sediment. The contrasting relationships between macrofauna and foraminifera distributions observed at the three stations suggest that the quality of bioturbation determined the ability of macrofauna to promote the survival of benthic foraminifera deeper in the sedimentary column. Although foraminifera may develop anaerobic respiration (Bernhard et al., 2006; Risgaard-Petersen et al., 2006), they do not seem to be able to colonize anoxic sediments at stations affected by oyster farming. The lack of foraminifera at depth and the relatively limited number of biodiffusor and large gallery-diffusor taxa at the oyster-affected stations suggest that oyster farming has a negative impact on overall ecosystem function. This suggests that oyster farming, by limiting the biodiversity of bioturbators, alters the biotic interactions in benthic communities (such as the interaction between foraminifera and bioturbating fauna). This result is consistent with the findings of Cardinale et al. (2006), who suggested that a decrease in the mean number of species present induces changes in the functioning of the ecosystem. Conversely, the preservation of biodiversity is essential to maintain the functioning of a wide variety of organisms and ecosystems.

5. Conclusion

At the control station, the cumulative activities of biodiffusors and gallery-diffusors led to living foraminifera occurring in deep sediment layers (> 6 cm below the sediment surface). By contrast, the lack of large bioturbator taxa at the sampling stations affected by oyster farming was associated with the concentration of living foraminifera in the 4 cm immediately below the sediment surface. Our preliminary study based on CT-scan observations supports the view that the effect of bioturbation on the vertical distribution of foraminiferal assemblages in sediments depends on the mode of bioturbation induced by macrofaunal species, this bioturbation mode determining the type of microhabitats produced by infaunal species in sediments. Our findings suggest that the bioirrigation and sediment oxidation capacity of macrofauna (as indicated by Eh values) has a greater effect than the total macrofaunal biogenic structure volume, which influenced foraminiferal distribution. How powerful and promising it is, CT-scan tool nevertheless still needs improvements to allow accurate discrimination between the biogenic structure volumes produced by different bioturbators. Based on our preliminary observations on the vertical distribution of living foraminifera, it is possible to investigate the relationship between the mode of bioturbation (related to its impact on oxygen concentration in sediments) and the vertical distribution of meiofaunal communities within sediment.

Experimental studies would be needed to determine how foraminifera migrate to deep habitat (passively transported by macrofauna or migrating actively), but it already appears that the structuration of foraminiferal assemblages by macrofaunal bioturbation activities is consistent with what has been reported for other meiofaunal communities, such as nematodes and plathyhelminthes (Reise, 1985). This suggest that, even if it must be further tested, it is possible to propose the use of benthic foraminifera as reliable indicators of the efficacy with

which macrofaunal bioturbation generates deep oxygen-rich microhabitats in coastal sediments.

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Tables

Table 1: Water salinity and sediment parameters measured at the three sampling stations (mean value ± standard deviation).

Sampling stations		OZ	OFZ	C
Salinity		31.6	31.6	27.5
T (°C)	1 cm	14.7	13	12.7
	4 cm	14.7	15.3	12.9
Eh (mV)	1 cm	-52	16	23
	4 cm	-112	-15	19
Chl *a* (mg m^{-2})		103 ± 6	68 ± 14	73 ± 7
Phaeopigments (mg m^{-2})		162 ± 17	120 ± 17	170 ± 19
POC (µg mg^{-1} dry sediment)		15.57 ± 3.68	15.74 ± 0.33	13.90 ± 2.23
PON (µg mg^{-1} dry sediment)		2.51 ± 0.60	2.51 ± 0.05	2.13 ± 0.10
C/N ratio		6.2 ± 0.1	6.3 ± 0.1	6.5 ± 0.1

Table 2: Vertical profiles of ^{210}Pb, ^{234}Th and ^{7}Be for sediment cores obtained at the sampling stations (Stns OZ and OFZ, no data for Stn C). Considering ^{210}Pb profile discontinuity, mixing rates (D_b) were deduced from profiles in ^{234}Th and ^{7}Be and calculated for the 0-2 and 0-1 cm layers for OZ and OFZ, respectively. (n.d.: non detectable).

Site	Depth (cm)	$^{210}Pb_{xs}$ (mBq g^{-1})	$^{234}Th_{xs}$ (mBq g^{-1})	^{7}Be (mBq g^{-1})
OZ	0-0.5	104 ± 8	114 ± 9	92 ± 10
	0.5-1	86 ± 11	51 ± 11	84 ± 14
	1-1.5	101 ± 12	34 ± 11	33 ± 11
	1.5-2	86 ± 7	16 ± 7	37 ± 7
	2-2.5	93 ± 7	n.d.	23 ± 7
	5-6	97 ± 4	n.d.	n.d.
		D_b (cm^2 y^{-1})	*7*	*9*
OFZ	0-0.5	103 ± 12	78 ± 12	104 ± 15
	0.5-1	100 ± 6	57 ± 8	85 ± 7
	1-1.5	54 ± 7	n.d.	n.d.
	1.5-2	67 ± 6	n.d.	n.d.
	5-6	58 ± 6	n.d.	n.d.
		D_b (cm^2 y^{-1})	*29*	*30*

Table 3: Counted specimens of macrofaunal species in scanned cores for the three sampling stations. Each species was assigned to a functional bioturbation group based on published findings (Gérino et al., 2003; Michaud et al., 2005; Mermillod-Blondin and Rosenberg, 2006; Gérino et al., 2007; Gilbert et al., 2007) and its total biovolume per core (in cm^3, n.d.: no data) was calculated.

Species	Phylum	Functional bioturbation group	Biovolume (cm^3)	C	OFZ	OZ
Streblospio shrubsolii	Annelida	Downward-conveyor	1.10^{-3}	48	23	31
Hydrobia ulvae	Mollusca	Biodiffusor	ND	44	0	0
Scrobicularia plana	Mollusca	Biodiffusor	0.37	14	0	0
Abra tenuis	Mollusca	Biodiffusor	ND	13	0	0
Nephtys hombergii	Annelida	Gallery-diffusor	0.29	2	0	1
Macoma balthica	Mollusca	Biodiffusor	ND	1	0	0
Hediste diversicolor	Annelida	Gallery-diffusor	0.15	1	0	0
Cossura pygodactylata	Annelida	Downward-conveyor	2.10^{-4}	0	81	62
Pseudopolydora antennata	Annelida	Downward-conveyor	4.10^{-3}	0	25	10
Oligochaeta spp.	Annelida	Upward-conveyor	1.10^{-4}	0	17	35
Polydora cornuta	Annelida	Downward-conveyor	1.10^{-3}	0	8	0
Aphelochaeta marioni	Annelida	Downward-conveyor	5.10^{-3}	0	4	4
Ampelisca brevicornis	Arthropoda	Regenerator	ND	0	1	0
Capitella capitata	Annelida	Downward-conveyor	1.10^{-3}	0	1	0
Tharyx multibranchiis	Annelida	Downward-conveyor	1.10^{-3}	0	1	0
Spionidae sp.	Annelida	Downward-conveyor	2.10^{-4}	0	1	0
Cerastoderma edule	Mollusca	Biodiffusor	ND	0	1	1
Nephtys cirrosa	Annelida	Gallery-diffusor	2.10^{-4}	0	1	1
Tubificoides benedii	Annelida	Downward-conveyor	1.10^{-4}	0	0	8
Capitella minima	Annelida	Downward-conveyor	1.10^{-3}	0	0	2
Tubulanus polymorphus	Nemertina	Gallery-diffusor	3.10^{-3}	0	0	1
			Species richness	7	12	11

Table 4: Counted specimens of foraminiferal species in scanned cores for the three sampling stations.

Species	C	OFZ	OZ
Ammonia tepida	441	110	19
Haynesina germanica	113	14	1
Cribroelphidium excavatum	69	100	6
Brizalina striatula	9	22	11
Cribroelphidium gunteri	7	18	0
Stainforthia fusiformis	1	0	0
Gavelinopsis praegeri	1	0	0
Cassidulina crassa	1	0	0
Bolivina pseudoplicata	1	0	0
Brizalina spp.	1	0	4
Cribrononion gerthi	1	0	1
Buliminella elegantissima	0	7	1
Fissurina lucida	0	2	4
Hopkinsina pacifica	0	1	2
Trochammina inflata	0	1	0
Quinqueloculina seminula	0	0	1
Eggerelloides scabrus	0	0	1
Species richness	11	9	11

Figures

Figure 1

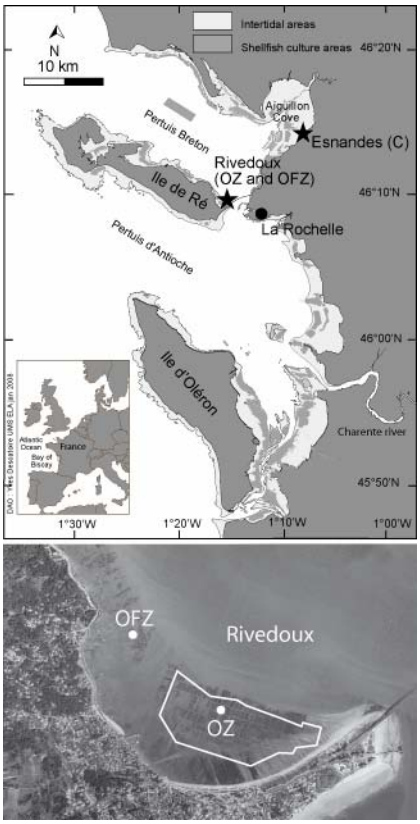


Figure 1: Map of the Pertuis Charentais and location of the three sampling stations (Stn C: control, Stn OZ: oyster zone and Stn OFZ: oyster-free zone), with details on the location of the two stations situated at Rivedoux (oyster parks delimited with a white line).

Figure 2

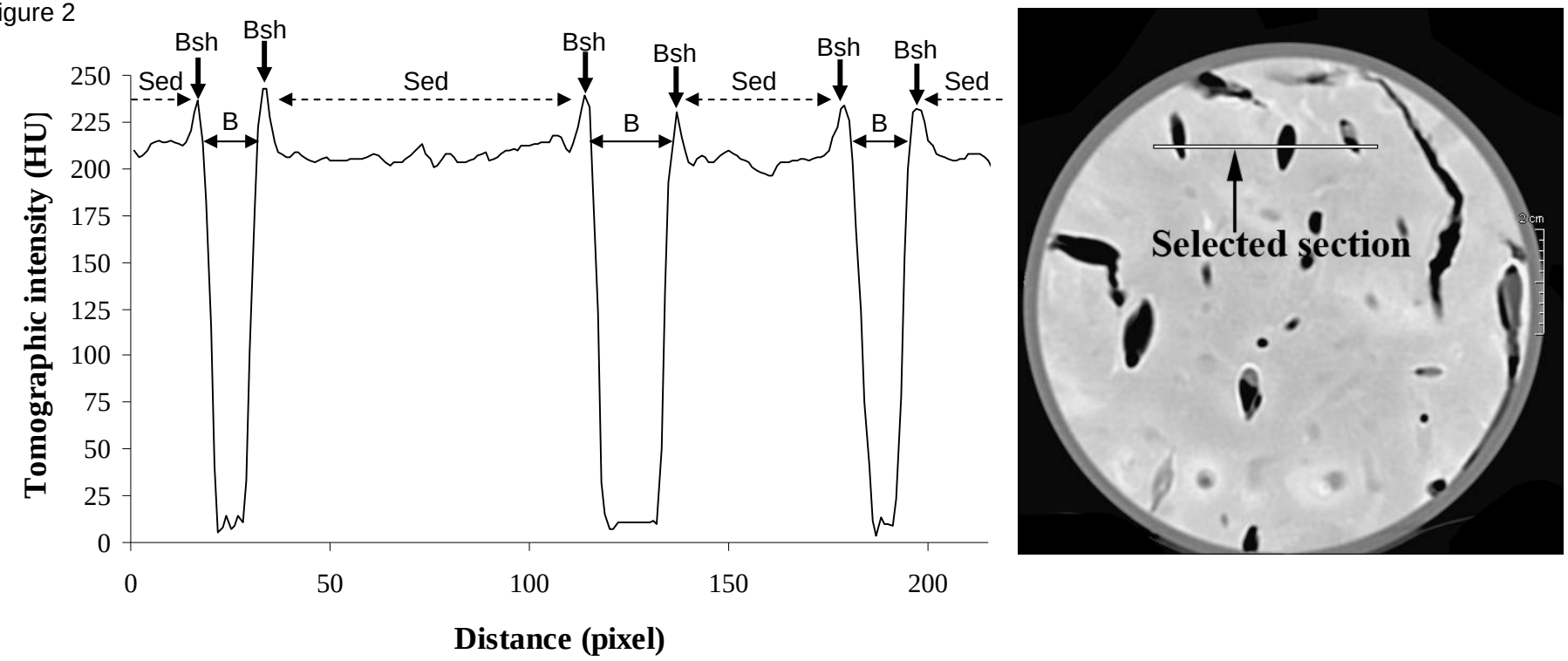
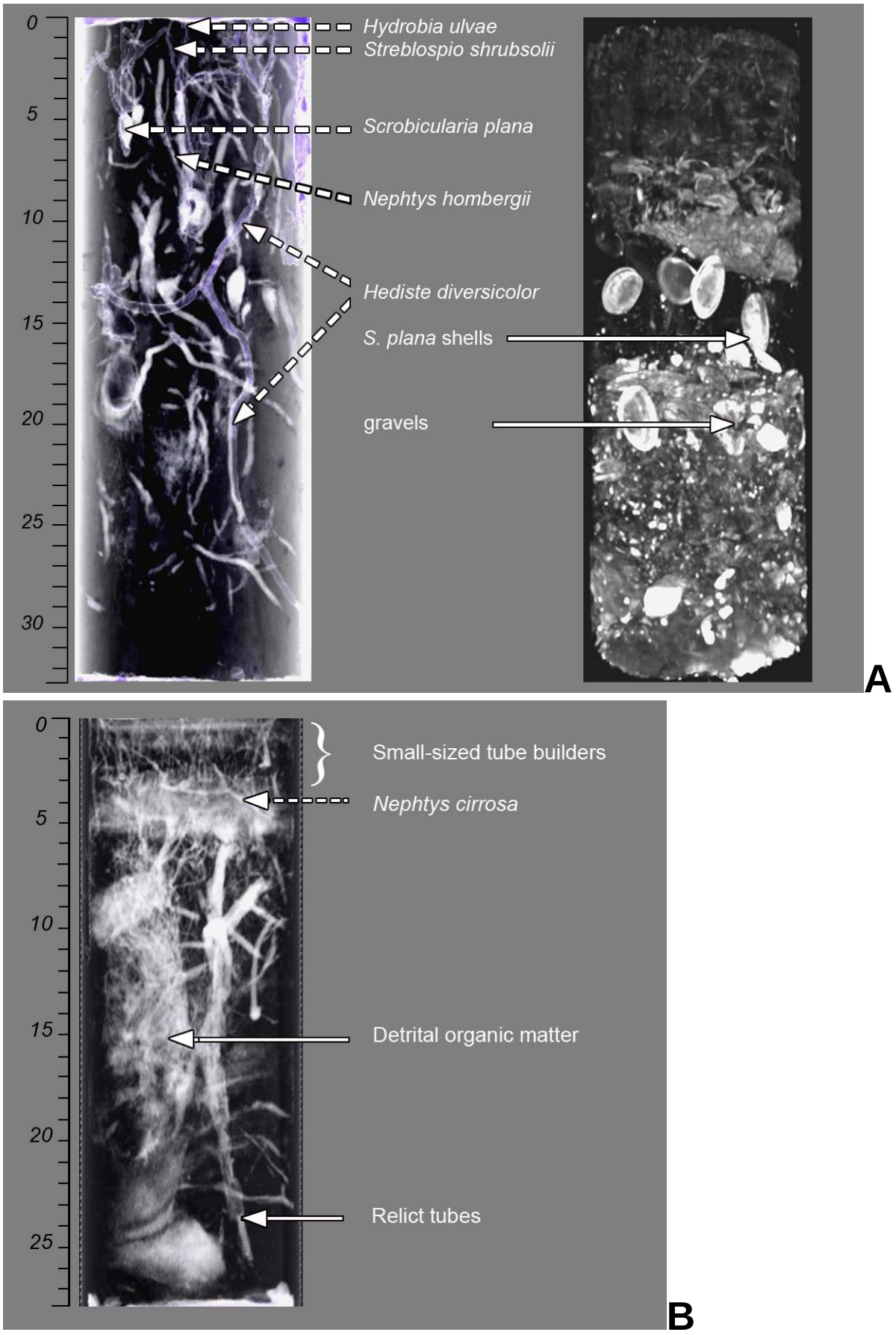


Figure 2: Tomographic intensities (in Hounsfield units) associated with biogenic structures (B), sediment (Sed) and bivalve shells (Bsh) from the Stn C core. For the selected section in the transverse image, OSIRIS software was used to determine the tomographic intensity (TI) of each pixel. Biogenic structures (dark) are bivalves (B) with a TI of about 0 HU, sediment appears in gray (TI ≈ 200 HU) and thin bivalve shells, in white (TI > 215 HU).

Figure 3


0
5
10
15
20
25
30
Hydrobia ulvae
Streblospio shrubsolii
Scrobicularia plana
Nephtys hombergii
Hediste diversicolor
S. plana shells
gravels
A
0
5
10
15
20
25
Small-sized tube builders
Nephtys cirrosa
Detrital organic matter
Relict tubes
B

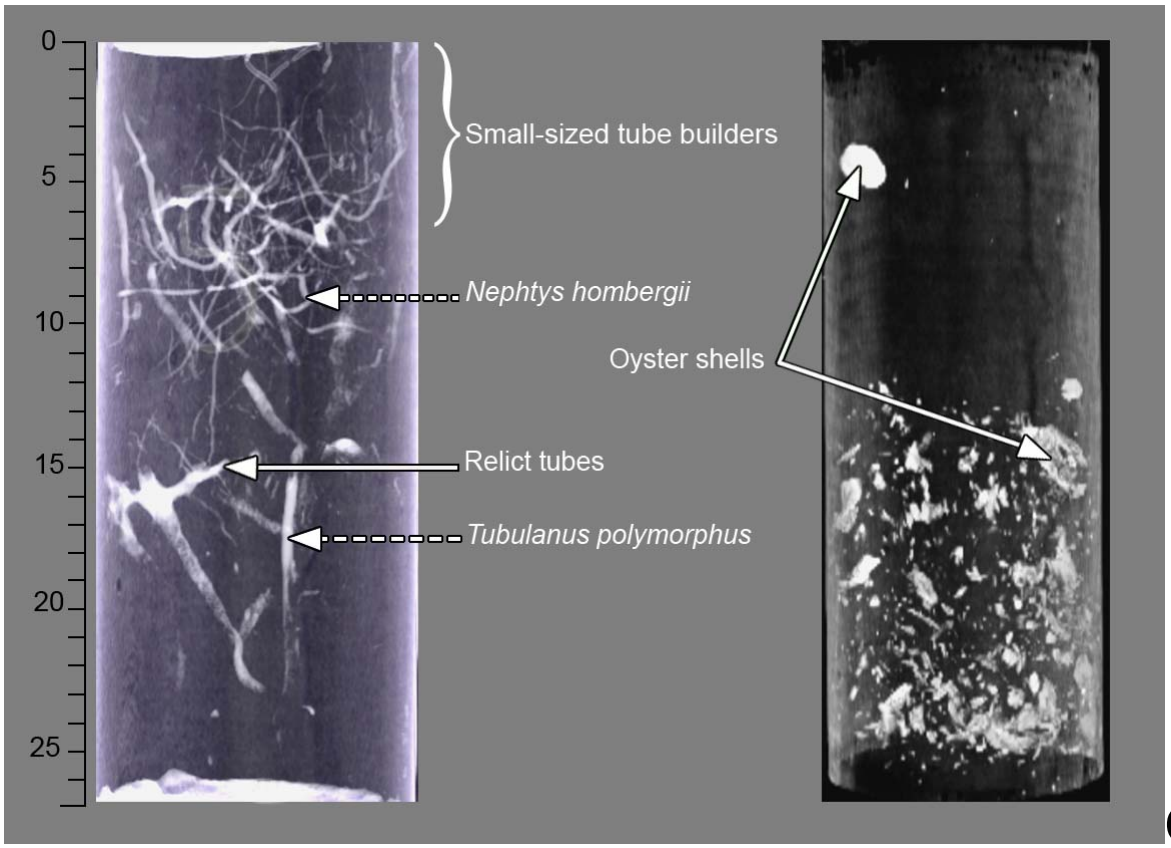


Figure 3: 3D images obtained by axial tomography and corresponding vertical distribution of macrofaunal species at the three sampling stations (A: Stn C, B: Stn OFZ and C: Stn OZ). Where possible, 3D images were treated to highlight air structures (left) and shell structures (right) from the same core.

Figure 4

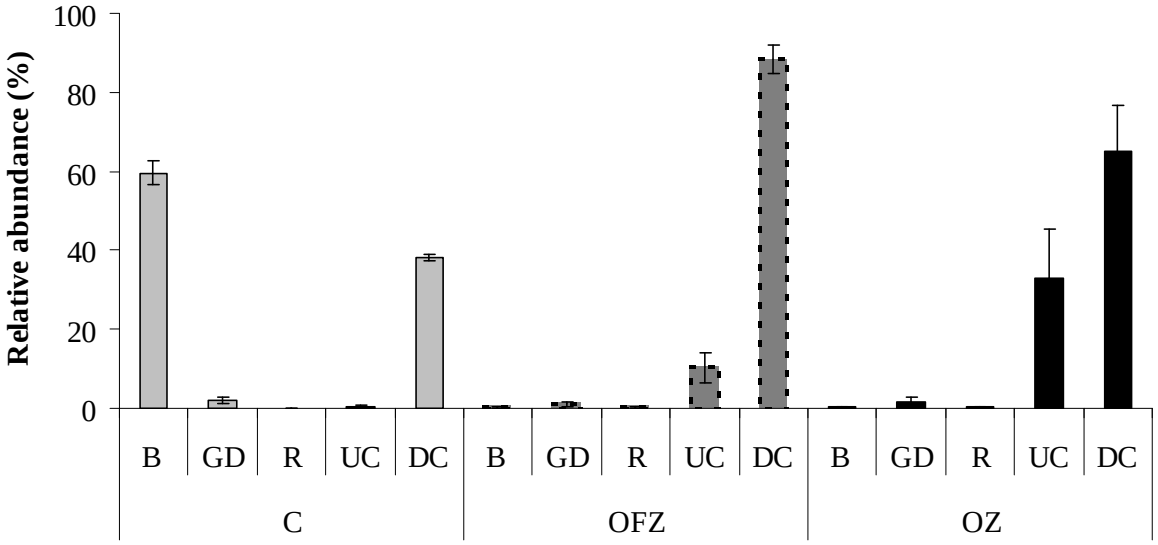


Figure 4: Relative abundances (%) of macrofaunal bioturbation modes (B: biodiffusors, GD: gallery-diffusors, R: regenerators, UC: upward-conveyors and DC: downward-conveyors) at each sampling station (gray: Stn C, dashed black: Stn OFZ, black: Stn OZ, bars: standard deviation).

Figure 5

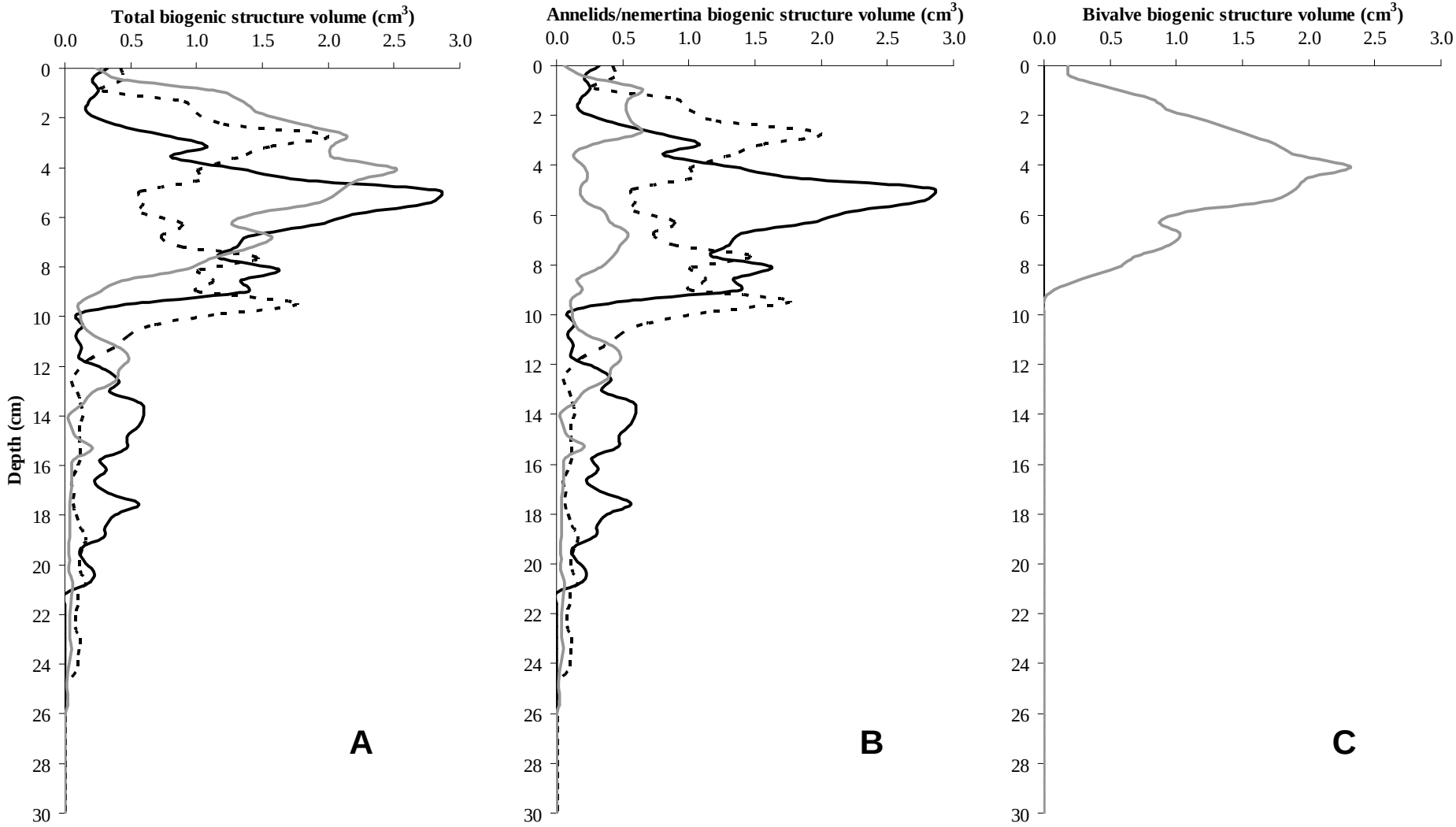


Figure 5: Total volumes (in cm^3) of biogenic structures (A) and specific volumes of biogenic structures associated with annelids and nemerteans (B) and bivalves (C) at the three sampling stations (gray line: Stn C, black dashed line: Stn OFZ, black line: Stn OZ)

Figure 6

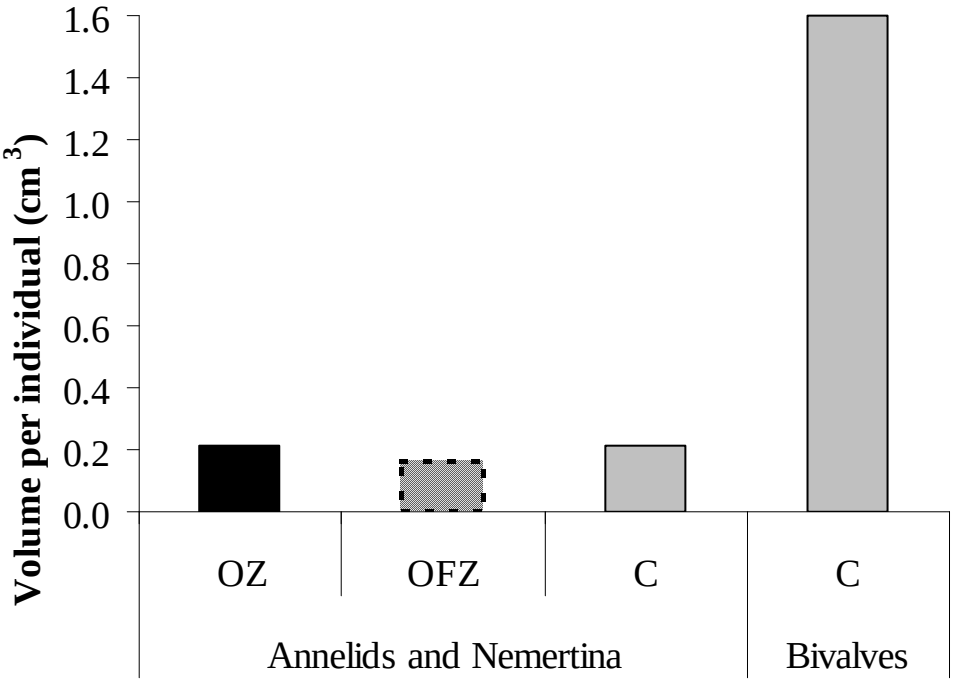


Figure 6: Volume (in cm^3) bioturbated per individual (annelids/nemerteans, and bivalves) for the three sampling stations (gray: Stn C, dashed black: Stn OFZ, black: Stn OZ, bars: standard deviation).

Figure 7

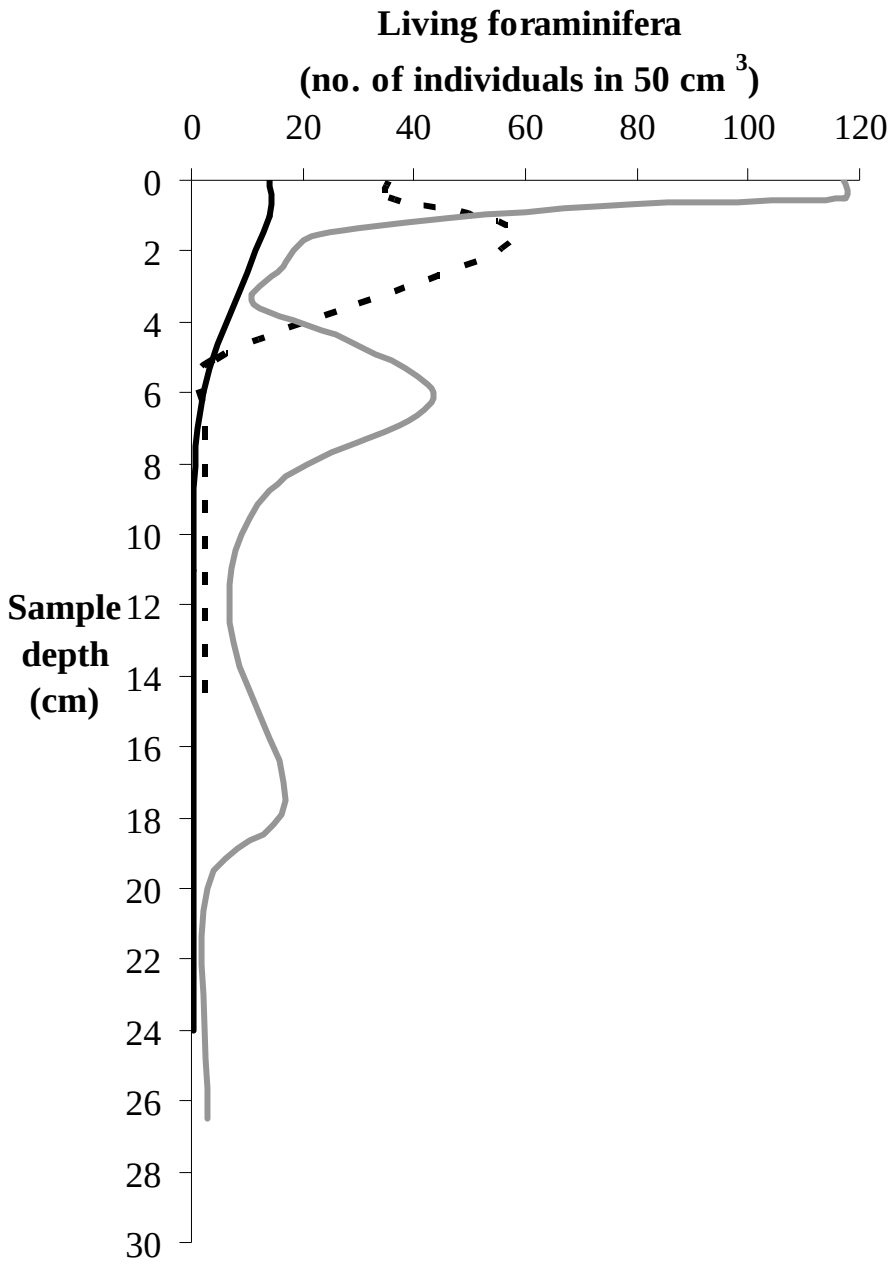


Figure 7: Vertical distribution of abundance of living (stained) foraminifera (no. of individuals in 50 cm^3 of sediment) in scanned cores at the three sampling stations (gray line: Stn C, black dashed line: Stn OFZ, black line: Stn OZ).