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STABLE OXYGEN AND CARBON ISOTOPES OF LIVE (STAINED) BENTHIC FORAMINIFERA FROM CAP-FERRET CANYON (BAY OF BISCAY)

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ABSTRACT

A 2800-m-deep station (Station I) from the lower part of Cap-Ferret Canyon (Bay of Biscay) was sampled with a multitube corer in January 1999, June 1999 and April 2000. Four cores (with two replicate cores in April 2000) were investigated to study the stable carbon and oxygen isotopes of live (rose-Bengal-stained) foraminiferal taxa. Eight taxa were analyzed: *Hoeglundina elegans*, *Cibicides wuellerstorfi*, *Uvigerina peregrina*, *Bulimina inflata*, *Melonis barleeanus*, *Pullenia quinqueloba*, *Chilostomella oolina* and *Globobulimina affinis*. By using the apparent oxygen utilization of the lower Northeastern Atlantic Deep Water (NEADW) in our study area, we calculated the bottom-water $\delta^{13}C_{DIC}$, which we compared with foraminiferal carbon isotope values. Next, we investigated the relationship between the foraminiferal $\delta^{13}C$ and the microhabitat of investigated species. By using the value of $\delta^{18}O$ (SMOW) for the lower NEADW, we calculated the equilibrium calcite $\delta^{18}O$ of the bottom water, which we compared with the foraminiferal $\delta^{18}O$. The occurrence of a living holothurian in its deep infaunal burrow from one of two replicate cores collected in April 2000 (core B) allowed us to investigate the impact of macrofaunal activity on foraminiferal isotopes. Our results are finally compared with data from shallower open-slope stations close to our study area.

The $\delta^{13}C$ signatures of most foraminiferal taxa are not correlated to the bottom-water $\delta^{13}C_{DIC}$ but seem to be controlled by a microhabitat effect. Only the $\delta^{13}C$ of *Cibicides wuellerstorfi* is close to the bottom water $\delta^{13}C_{DIC}$. When investigating oxygen isotopes, there is no obvious relationship between the foraminiferal microhabitat and the offset between the foraminiferal $\delta^{18}O$ and the equilibrium calcite $\delta^{18}O$. The presence of a living holothurian had no obvious effect on the $\delta^{18}O$ and $\delta^{13}C$ of foraminifera occurring in the bioturbated interval. However, several individuals of *Melonis barleeanus* collected in the direct vicinity of the holothurian exhibited lower $\delta^{13}C$ values, suggesting a potential influence of macrofaunal activity on the carbon isotopes of some intermediate and deep infaunal taxa calcifying in the deep sediment. The comparison of $\Delta\delta^{13}C$ between *Uvigerina peregrina*, *M. barleeanus* and *Globobulimina* spp. with values recorded at shallower stations suggests that the focusing of organic matter in an intermediate state of decay, at our canyon station, has a weak impact on the biogeochemical processes deeper in the sediment. The $\delta^{13}C$ of *U. peregrina* and the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina affinis* appears definitively more sensitive to labile organic matter supplies than to the advection of low-quality, organic matter.

INTRODUCTION

Most recent studies on stable oxygen and carbon isotopes of live benthic foraminifera demonstrate clearly that the $\delta^{13}C$ and $\delta^{18}O$ of deep-sea foraminifera are constrained by several biological parameters (e.g., microhabitat, growth) and by the physicochemical properties of bottom and pore water (e.g., temperature, oxygenation, organic matter deposits, methane). On the one hand, it is commonly accepted that infaunal benthic foraminifera calcify in the pore water from the sediment interval in which they preferentially live and, therefore, record the ambient pore-water $\delta^{13}C$, following a so-called microhabitat effect (e.g., Woodruff and others, 1980; Belanger and others, 1981; Grossman, 1984a; 1984b; 1987; McCorkle and others, 1985; McCorkle and others, 1990; McCorkle and others, 1997; Corliss and others, 2002; Rathburn and others, 2003; Hill and others, 2004; Mackensen and Licari, 2004; Schmiedl and others, 2004; Holsten and others, 2004). The ambient pore-water $\delta^{13}C$ is largely influenced by the introduction of isotopically light carbon due to the aerobic and/or anaerobic degradation of organic matter in the sediment. Therefore, the carbon isotopic composition of foraminiferal tests would ultimately be controlled by the organic carbon flux at the sediment water interface and the oxygenation in the benthic environment (e.g., McCorkle and others, 1990; McCorkle and others, 1997; Holsten and others, 2004; Filipsson and others, 2004; Eberwein and Mackensen, 2006; Corliss and others, 2006). In contrast, the $\delta^{18}O$ values of foraminifera are controlled by a fractionation dependent on the bottom water temperature. Constant offsets are generally recorded between species (e.g., McCorkle and others, 1990; McCorkle and others, 1997; Corliss and others, 2002; Mackensen and Licari, 2004; Schmiedl and others, 2004). Moreover, both $\delta^{18}O$ and $\delta^{13}C$ are assumed to be constrained by complex metabolic processes that change during ontogeny, juveniles presenting lighter isotopic compositions than adults (e.g., Schmiedl and others, 2004).

A recent study of live foraminiferal faunas from Cap-Ferret Canyon allowed us to clarify the ecological characteristics of benthic foraminiferal faunas collected at a station in the lower part of a submarine canyon (Bay of Biscay, eastern Atlantic Ocean, Station I; Fontanier and others, 2005). At this 2800-m-deep station, where organic matter in an intermediate state of decay focuses (Fontanier and others, 2005), foraminiferal communities are charac-

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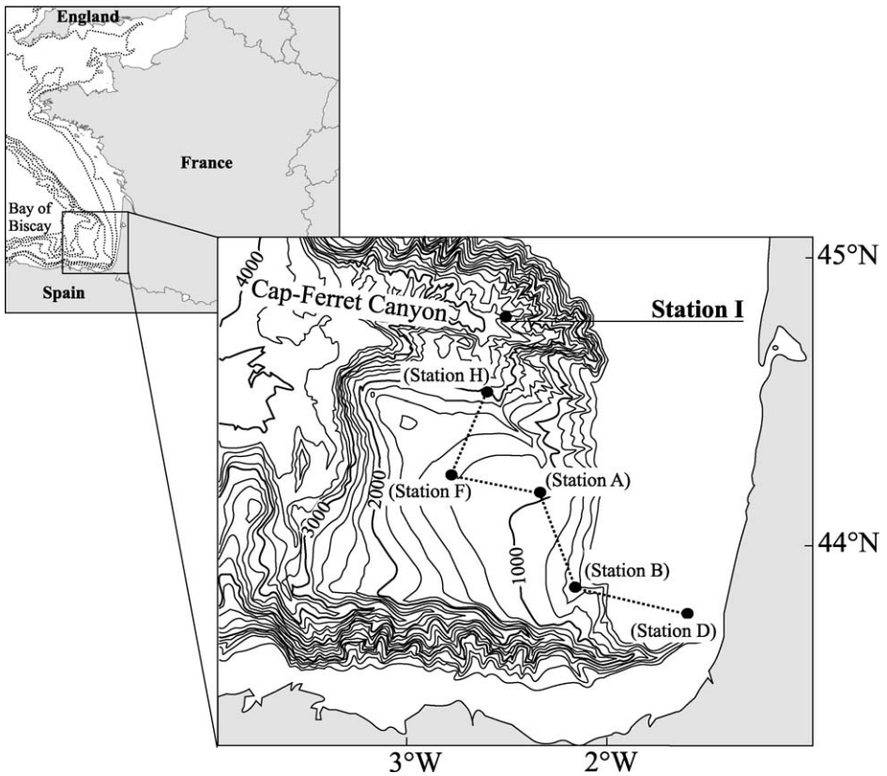

FIGURE 1. Study area, including the bathymetry (m) and geographical position of our Station I in the Cap-Ferret Canyon, where we sampled foraminiferal faunas. The locations of Stations D, B, A, F and H, which were studied in Fontanier and others (2006a), are also shown (see Discussion).

terized by a high density of intermediate and deep infaunal taxa (e.g., *Melonis barleeanus*, *Chilostomella oolina* and *Globobulimina affinis*). The well-stratified vertical distribution of these species follows the succession of several fundamental redox boundaries in the first centimeters of the sediment (zero oxygen boundary, zone of precipitation of iron and manganese oxides and oxyhydroxides) and appears to be related to the input of low-quality organic matter in the topmost sediment. On only one occasion (April 2000, core B), the microhabitat stratification within the sediment was unclear. This unusual observation was obviously related to the downcore presence of a deep active burrow occupied by a 3-cm-long holothurian (Fontanier and others, 2005).

In this paper, we deal with the carbon and oxygen isotopes of live benthic foraminiferal taxa collected at this 2800-m-deep station (Fig. 1). Eight taxa are investigated: *Cibicides wuellerstorfi*, *Bulimina inflata*, *Uvigerina peregrina*, *Melonis barleeanus*, *Pullenia quinqueloba*, *Chilostomella oolina*, *Globobulimina affinis* (all calcitic) and *Hoeglundina elegans* (aragonitic). First, we will investigate the relationship between the foraminiferal vertical distribution (e.g., microhabitat) and the isotopic signature ($\delta^{18}C$, $\delta^{13}C$) of investigated taxa for three different sampling periods (January 1999, June 1999 and April 2000). We will especially study the influence of the large holothurian burrow on foraminiferal $\delta^{13}C$ values in one of the replicate cores collected in April 2000 (core B). Next, we will compare our results with isotope values obtained from adjacent and shallower open slope environments (Fontanier and others, 2006a). Our data should complete the 140–2000 m depth bathymetric transect described by Fontanier and others (2006a). More specifically, we will compare the benthic foraminiferal isotopic signatures ($\delta^{13}C$) with the exported organic matter fluxes along a bathymetric transect from 140 to 2800 m depth, keeping in mind that low quality organic matter focuses at our canyon station.

MATERIAL AND METHODS

Station I (~2800 m depth) is situated on the northern flank of Cap-Ferret Canyon (Fig. 1). It is bathed by the lower Northeastern Atlantic Deep Water (NEADW; van Aken, 2000). The bottom water is ~34.95 psu and ~2.9°C (Durrieu de Madron and others, 1999; van Aken, 2000). In the eastern Bay of Biscay, the lower NEADW is a complex mixture (van Aken, 2000) of Iceland-Scotland Overflow Water (ISOW: 12.9% of contribution, $[O_2]$ = 283.3 μmol/l), Labrador Sea Water (LSW: 21.7%, $[O_2]$ = 279 μmol/l), Lower Deep Water (LDW: 62.6% of contribution, $[O_2]$ = 245.3 μmol/l) and Mediterranean Sea Water (MSW: 2.8% of contribution, $[O_2]$ = 177 μmol/l). Taking into account the oxygen concentration in each water mass and the respective water mass contribution to the lower NEADW, a calculation gives a value of bottom-water oxygenation of about 255 μmol/l in our study area and an apparent oxygen utilization (AOU) of 77 μmol/l. Later, we will use this AOU value to calculate the $\delta^{13}C_{DIC}$ of bottom water (the lower

TABLE 1. Isotope analyses for all foraminiferal taxa studied at our station (*Hoeglundina elegans*, *Cibicides wuellerstorfi*, *Bulimina inflata*, *Uvigerina peregrina*). Numbers (nbr) of individuals used for measurements are also presented. All isotope measurements on the material collected in April 2000 (cores A and B) were performed at the LSCE laboratory (Gif-sur-Yvette, France). Isotope analyses of foraminifera sampled in January and June 1999 were measured at the Laboratory of CEREGE (Aix-en-Provence, France).

Taxa Depth in the sediment (cm)	Nbr of individuals	*Hoeglundina elegans* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Cibicides wuellerstorfi* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Bulimina inflata* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Uvigerina peregrina* $\delta^{13}C$	$\delta^{18}O$
Station I, January1999												
0.5-0.75				1	1.12	2.63						
Station I, June 1999												
0-0.75										4	-0.03	3.34
0.5-0.75	1	2.27	4.04									
0.75-1.5										4	-0.10	3.39
Station I, April 2000 Core A												
0-0.25				2	1.06	2.72						
Station I, April 2000 Core B												
0-0.25	1	1.77	4.00				3	-0.45	3.16	2	-0.77	3.07
	1	1.91	3.89									
0.25-0.5	1	1.76	4.05				1	-0.57	3.25	3	-0.88	3.22
0.5-1										3	-0.55	3.17
0.5-0.75							2	-0.22	3.27			
							1	-0.49	3.15			
1-2	1	1.60	3.82				3	-0.81	3.09			
	1	2.06	3.93									
2-2.5	1	1.84	3.80									
	1	1.75	4.11									
2-3										2	-0.54	3.29
2.5-3				1	0.90	2.50						
3-3.5	1	1.79	3.91									
	1	1.99	3.87									
4-5	1	1.79	4.07									
	3	1.95	3.88									
4-7										2	-0.31	3.28
5-6							2	-0.64	3.19			
							2	-0.30	3.20			
5-7	2	1.84	4.00									
	2	1.76	3.93									
8-9	1	1.71	4.02									

NEADW) in our study area. Station I is characterized by a rapid accumulation of fine-grained sediments and by significant input of reworked, low-quality organic matter (Fontanier and others, 2005). As suggested by Durrieu de Madron and others (1999) and Heussner and others (1999), the lower part of Cap-Ferret Canyon is an inactive canyon environment without recent turbidite deposition.

At Station I, four cores were collected with a standard Barnett multitube corer (Barnett, 1984). One core was sampled in January 1999, a second one in June 1999 and two replicate cores (cores A and B) were collected in April 2000. The live (stained) foraminiferal faunas of all cores have already been described in Fontanier and others (2005). All cores were sliced horizontally down to 10 cm depth for faunal analysis: every 0.25 cm for the first centimeter of the sediment, every 0.5 cm between 1–4 cm, and every 1.0 cm between 4–10 cm. Detailed sampling and storage protocols are presented in Fontanier and others (2005). As mentioned above, in core B (April 2000), a live holothurian (genus *Molpadia*) was found in its burrow between 4–7 cm depth.

All stable isotopic analyses were performed on rose-Bengal-stained foraminifera (Walton, 1952). Although foraminifera can stain for some time after their death, this period is short (days to months) for specimens living in the topmost, well-oxygenated sediment (Corliss and Emerson, 1990). It cannot be precluded, however, that specimens found in deeper, hypoxic sediment intervals (*Chilostomella oolina*, *Melonis barleeanus*, *Globobulimina affinis*) remain partly or imperfectly stained for a longer period, months to years (Corliss and Emerson, 1990). Therefore, only perfectly stained specimens were selected for isotopic measurements. Bernhard (2000) further explains the limitations of the rose-Bengal staining method. Isotopic measurements were performed on individuals belonging to eight dominant species of the >150-μm-size fraction (*Cibicides wuellerstorfi*, *Hoeglundina elegans*, *Uvigerina peregrina*, *Bulimina inflata*, *Melonis barleeanus*, *Pullenia quinqueloba*, *Chilostomella oolina* and *Globobulimina affinis*). Tables 1 and 2 present the investigated material and the results of the isotopic measurements. Fifteen stable isotope analyses were performed on foraminifera, which were sampled in January 1999 and June 1999 at the Laboratory of CEREGE (Aix-en-Provence) with a Finnigan Delta Advantage mass spectrometer coupled to an automated carbonate preparation device. Isotopic ratios were calibrated to an international scale (VPDB). External precision was controlled with regular analyses of the standard NBS-19 and is better than 0.03‰ and 0.05‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. The other 47 isotope analyses were performed at the LSCE laboratory (Gif-sur-Yvette) on individuals picked in both cores A and B, which were sampled in April 2000. In order to compare data obtained at CEREGE and LSCE, an inter-laboratory calibration for $\delta^{13}C$ and $\delta^{18}O$ measurements was conducted on MARGO standard samples (from Gif-sur-Yvette). Values obtained at CEREGE ($\delta^{13}C = 2.06 \pm 0.02$‰; $\delta^{18}O = -1.93$‰ ± 0.03‰; $n = 40$) are in good agreement with measurements from the LSCE laboratory ($\delta^{13}C = 2.09$‰; $\delta^{18}O = -1.91$‰). Finally, we performed 3 isotope analyses on *Cibicides wuellerstorfi*, 15 analyses on *Hoeglundina elegans*, 7 analyses on *Uvigerina peregrina*, 7 analyses on

TABLE 2. Isotope analyses for all foraminiferal taxa studied at our station (*Pullenia quinqueloba*, *Melonis barleeanus*, *Chilostomella oolina*, *Globobulimina affinis*). Numbers (nbr) of individuals used for measurements are also presented. All isotope measurements on the material collected in April 2000 (cores A and B) were performed at the LSCE laboratory (Gif-sur-Yvette, France). Isotope analyses of foraminifera sampled in January and June 1999 were measured at the Laboratory of CEREGE (Aix-en-Provence, France).

Taxa Depth in the sediment (cm)	Nbr of individuals	*Pullenia quinqueloba* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Melonis barleeanus* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Globobulimina affinis* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Chilostomella oolina* $\delta^{13}C$	$\delta^{18}O$
Station I, January1999												
3-5				6	-0.87	2.31						
				5	-1.31	2.89						
Station I, June 1999												
2.5-3				7	-1.23	2.84						
3-3.5				5	-1.16	2.84						
4-5							4	-1.49	3.66	10	-2.09	3.46
							10	-1.51	3.73			
5-6							8	-1.53	3.60	15	-2.02	3.43
							5	-1.58	3.69			
6-7							5	-1.58	3.64			
Station I, April 2000 Core A												
1-3				4	-1.48	2.87						
3-3.5							3	-1.84	3.49			
4-5							4	-1.99	3.52			
5-6							3	-2.02	3.43			
							3	-2.01	3.63			
6-7							5	-1.89	3.66			
7-8							20µg	-1.94	3.64			
Station I, April 2000 Core B												
1-2				2	-0.90	2.85						
2-2.5				3	-1.17	2.89						
2.5-3				2	-1.19	2.89						
4-5	2	-1.99	3.31	3	-1.57	2.99						
5-6	3	-1.54	3.38									
	2	-2.03	3.36									
6-7				3	-1.47	2.73	2	-1.89	3.73			
				2	-1.59	2.71						
7-8				2	-1.27	2.90	2	-2.05	3.52			

Bulimina inflata, 12 analyses on *Melonis barleeanus*, 3 analyses on *Pullenia quinqueloba*, 2 analyses on *Chilostomella oolina* and 13 analyses on *Globobulimina affinis*.

As indicated by McCorkle and others (1997), Rathburn and others (1996), and Schmiedl and others (2004), the $\delta^{18}O$ of calcite in equilibrium (= $\delta^{18}Oe.c.$) with bottom water for a given temperature T (°K) can be calculated with the following equation, proposed by Friedman and O'Neil (1977):

$$\delta^{18}\text{Oe.c.(SMOW)} = \left(e^{\left(\left(2.78 \times 10^3/T^2\right) - \left(2.89/10^3\right)\right)} \times \left(\delta^{18}\text{Ow} + 1000\right)\right) - 1000,$$

where $\delta^{18}Ow$ is the oxygen isotopic composition of bottom water on the SMOW scale (here, VSMOW scale). This equation is derived from the expression for the calcite-water fractionation factor determined by O'Neil and others (1969), incorporating a revised estimate of the CO_2-water fractionation factor (1.0412 rather than 1.0407) as discussed by Friedman and O'Neil (1977). The SMOW-PDB conversion is calculated according to the equation (Friedman and O'Neil, 1977)

$$\delta^{18}\text{Oe.c.(PDB)} = \left(0.97006 \times \delta^{18}\text{Oe.c.(SMOW)}\right) - 29.94.$$

The $\delta^{18}Ow$ of bottom water at Station I was estimated based on water column measurements performed off Ireland (Frew and others, 2000). There, the oxygen isotopic composition of the lower NEADW at 2800 m depth is + 0.225‰ VSMOW. This later value allowed us to calculate the bottom-water $\delta^{18}Oe.c.$ value, which is equal to +3.46‰ PDB.

In order to obtain the $\delta^{13}C$ of dissolved inorganic carbon in bottom water ($\delta^{13}C_{DIC}$), we used Kroopnick's equation that links apparent oxygen utilization in bottom water (AOU) with $\delta^{13}C_{DIC}$ (Kroopnick, 1985):

$$\delta^{13}C_{DIC} = 1.54 - 0.0074 \times \text{AOU},$$

where AOU is defined as the difference between the saturation dissolved oxygen concentration in bottom water and the measured dissolved oxygen concentration [O_2(meas.)],

$$\text{AOU} = O_2(\text{sat}) - O_2(\text{meas.}).$$

At Station I, we calculated AOU using a mean bottom-water oxygenation of 255 µmol/l (see above for the explanation of the calculation of bottom water oxygenation). The AOU in the lower NEADW is equal to 77 µmol/l, and the $\delta^{13}C_{DIC}$ of bottom water is consequently +0.97‰ PDB.

RESULTS

Benthic Foraminiferal $\delta^{13}C$ and $\delta^{18}O$ for the Three Sampling Periods

Figure 2 presents the benthic foraminiferal $\delta^{13}C$ and $\delta^{18}O$ for the three sampling periods (January 1999, June 1999, April 2000). Note that intraspecific comparisons between sampling periods are sometimes based on a limited data set. Therefore, some observations must be considered with utmost care. For April 2000, two replicate cores were available. For each investigated taxon, mean $\delta^{13}C$ and $\delta^{18}O$

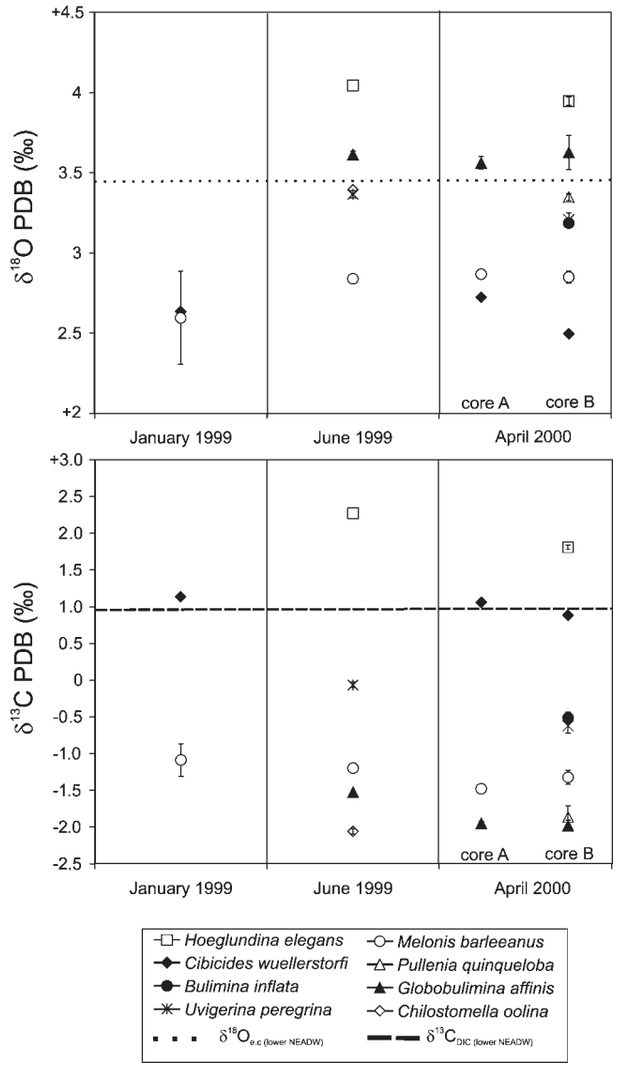

FIGURE 2. $\delta^{13}C$ and $\delta^{18}O$ of foraminiferal taxa for the four investigated cores. For April 2000, two duplicate cores (core A and core B) are available. Vertical bars represent standard errors. Dotted and dashed lines represent, respectively, the supposed constant $\delta^{18}O$e.c. and $\delta^{13}C_{DIC}$ values for bottom water (the lower NEADW).

values with standard errors are presented. $\delta^{18}O$ and $\delta^{13}C$ values recorded for *Cibicides wuellerstorfi* in January 1999 are close to the measurements performed in April 2000. $\delta^{13}C$ values recorded for *Melonis barleeanus* in January 1999 are heavier compared to April 2000 (+0.3‰). When comparing the isotopic composition of the material collected in June 1999 and April 2000, the $\delta^{18}O$ values are quite similar (see in particular *M. barleeanus* and *Globobulimina affinis*). However, $\delta^{13}C$ values tend to be systematically heavier in June 1999 compared to April 2000, with a mean offset of about +0.5‰ for *Hoeglundina elegans*, *Uvigerina peregrina* and *G. affinis* and a slight increase of +0.1‰ for *M. barleeanus*. When comparing the two replicate cores of April 2000, *M. barleeanus* and *G. affinis* exhibit invariable $\delta^{18}O$ values. This is also the case for the $\delta^{13}C$ values. The $\delta^{18}O$ of *C. wuellerstorfi* differs by only ~0.2‰ between both cores.

$\delta^{18}O$ and $\delta^{13}O$ Changes in Relation to the Vertical Distribution of Foraminiferal Taxa

Figures 3–6 depict the vertical distribution of foraminiferal taxa investigated in this study and their oxygen and carbon isotope values. Fontanier and others (2005) earlier described the microhabitat patterns for all cores. To summarize, the first centimeter of the sediment is commonly occupied by shallow infaunal species, such as *Hoeglundina elegans*, *Cibicides wuellerstorfi*, *Uvigerina peregrina* and *Bulimina inflata* (Figs. 3–5). *Melonis barleeanus* and *Pullenia quinqueloba* behave as intermediate infaunal taxa that commonly thrive below an oxygen threshold of about 50 μmol/l (Figs. 3–5). Deeper in the sediment, deep infaunal *Chilostomella oolina* and *Globobulimina affinis* occur at the zero oxygen boundary and in the anoxic sediments below (Figs. 2 and 3). As mentioned above, it should be kept in mind that a 3-cm-large holothurian lived in a burrow between 4–7 cm depth in core B, which was collected in April 2000. This probably explains why the foraminiferal microhabitat stratification in the sediment (Fig. 6) is unclear in core B (April 2000) compared to core A (April 2000). For example, in the bioturbated core B, individuals of *U. peregrina*, *C. wuellerstorfi* and *H. elegans* are found down to 8 cm depth, although they preferentially live in the first centimeter of sediment in core A.

In the cores from June 1999 and April 2000 (core A), for which the most complete isotopic data sets are available, individuals of the same foraminiferal taxon do not exhibit significant changes of $\delta^{18}O$ and $\delta^{13}C$ over successive sediment intervals. For example, *Globobulimina affinis* shows rather stable $\delta^{18}O$ and $\delta^{13}C$ values between 3–8 cm depth in the core A (Fig. 5). This is also the case for *Melonis barleeanus*, *Uvigerina peregrina* and *Chilostomella oolina*, for which oxygen and carbon isotope values are more or less the same in all depth intervals (Fig. 4).

In June 1999, the shallow infaunal taxa *Hoeglundina elegans* (aragonitic) and *Uvigerina peregrina* (calcitic) show the most positive $\delta^{13}C$ values (respectively +2.27‰ and −0.06‰). Intermediate infaunal *Melonis barleeanus* exhibits a mean value of −1.20‰, whereas the deep infaunal taxa *Globobulimina affinis* and *Chilostomella oolina* have the lowest $\delta^{13}C$ of all species (respectively −1.53‰ and −2.06‰). For the other cores (January 1999 and April 2000), the shallow infaunal *Cibicides wuellerstorfi* appears to have a $\delta^{13}C$ value close to that of the bottom water (about 1.0‰). There are no obvious trends in the $\delta^{18}O$ values of foraminiferal taxa in relation to microhabitat preferences.

In April 2000, a large data set is available for the bioturbated core (core B; Fig. 6). Measurements were performed on individuals living either in the direct vicinity of the active burrow occupied by the holothurian or far away from it close to the sediment-water interface. In general, there is no obvious change of $\delta^{13}C$ and $\delta^{18}O$ in relation to the presence of the burrow. This is particularly clear for *Hoeglundina elegans*, for which we have numerous measurements throughout the core. Its mean $\delta^{13}C$ value is +1.82‰ with a standard error of ±0.03‰, and its mean $\delta^{18}O$ is +3.95 ±0.02‰. In addition, *Bulimina inflata* and *Uvigerina peregrina* exhibit stable $\delta^{13}C$ and $\delta^{18}O$ values with

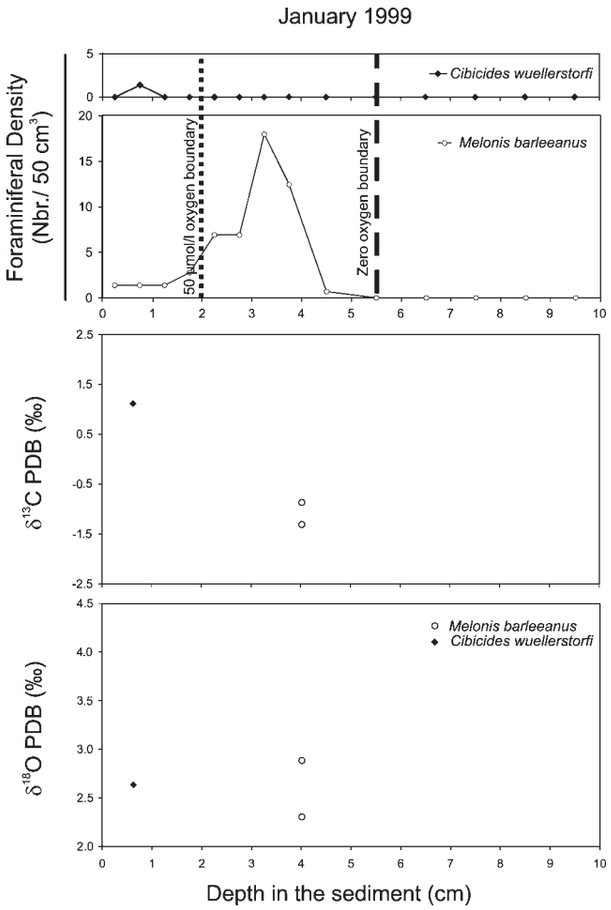

FIGURE 3. $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the investigated foraminiferal taxa at Station I in January 1999. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. The dotted line represents the boundary where oxygen concentration falls to 50 µmol/l. The dashed line depicts the zero oxygen boundary in the sediment.

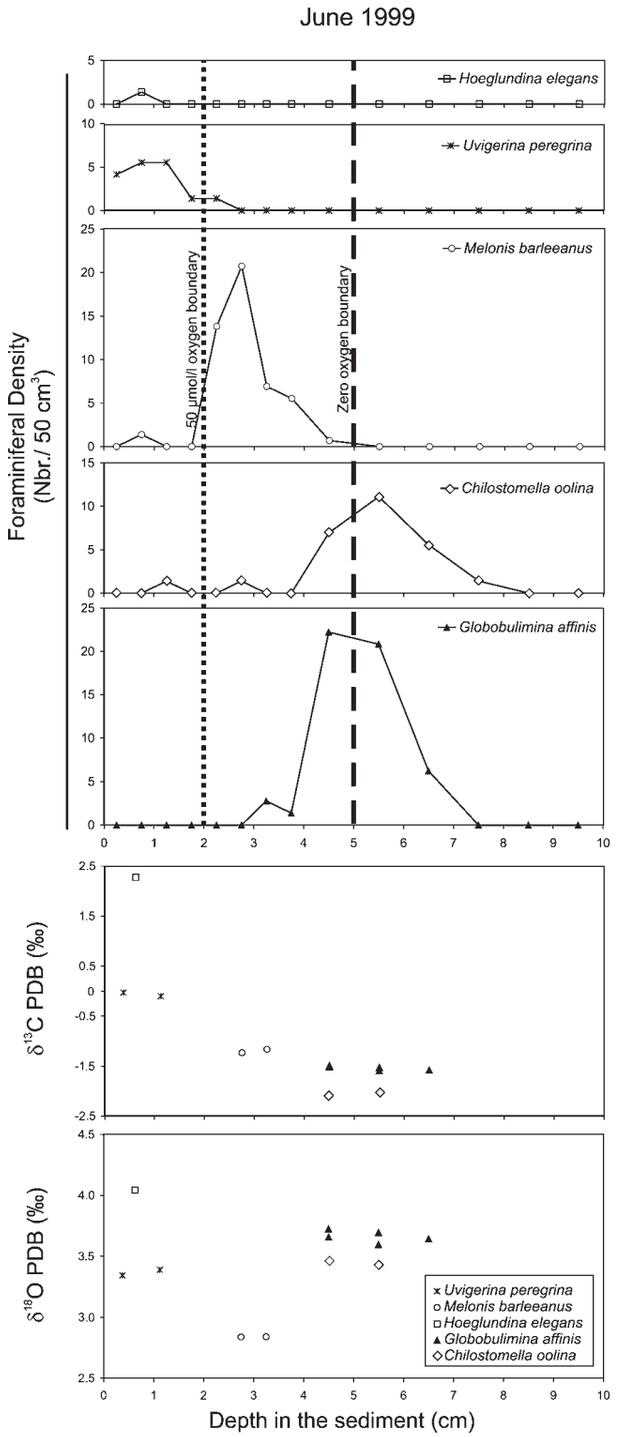

FIGURE 4. $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the investigated foraminiferal taxa at Station I in June 1999. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. The dotted line represents the boundary where oxygen concentration falls to 50 µmol/l. The dashed line depicts the zero oxygen boundary in the sediment.

depth. Only the intermediate infaunal *Melonis barleeanus* presents lower $\delta^{13}C$ values in the depth interval where the holothurian settled (between 4–7 cm depth). There, its $\delta^{13}C$ is close to −1.54‰, whereas it is −1.13‰ outside the active burrow. In spite of the presence of the holothurian, the $\delta^{13}C$ values are comparable to those observed in the other cores and correspond to the microhabitats occupied by the investigated taxa (except *M. barleeanus*) in the other cores, without an active burrow. The heaviest values are recorded for *H. elegans* and *Cibicides wuellerstorfi*, whereas intermediate $\delta^{13}C$ values are recorded in *U. peregrina* and *B. inflata*. The lightest $\delta^{13}C$ values are recorded by *Globobulimina affinis* and *Pullenia quinqueloba*.

DISCUSSION

Temporal Variability Recorded by $\delta^{18}O$ and $\delta^{13}C$ of Foraminiferal Tests

In the present study, we might wonder whether foraminiferal carbon isotopes measured for three different

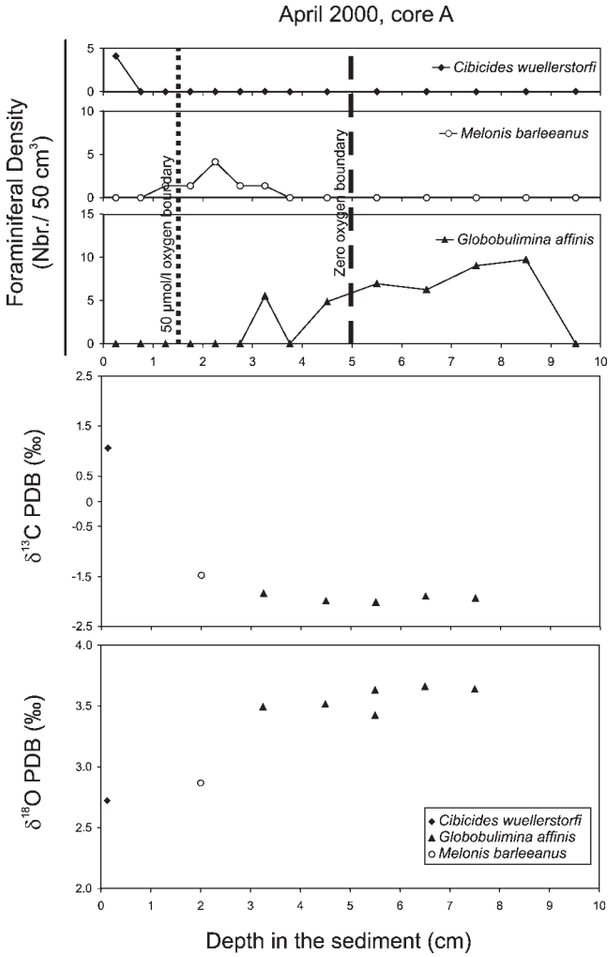

FIGURE 5. $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the investigated foraminiferal taxa at Station I in April 2000, core A. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. The dotted line represents the boundary where oxygen concentration falls to 50 µmol/l. The dashed line depicts the zero oxygen boundary in the sediment.

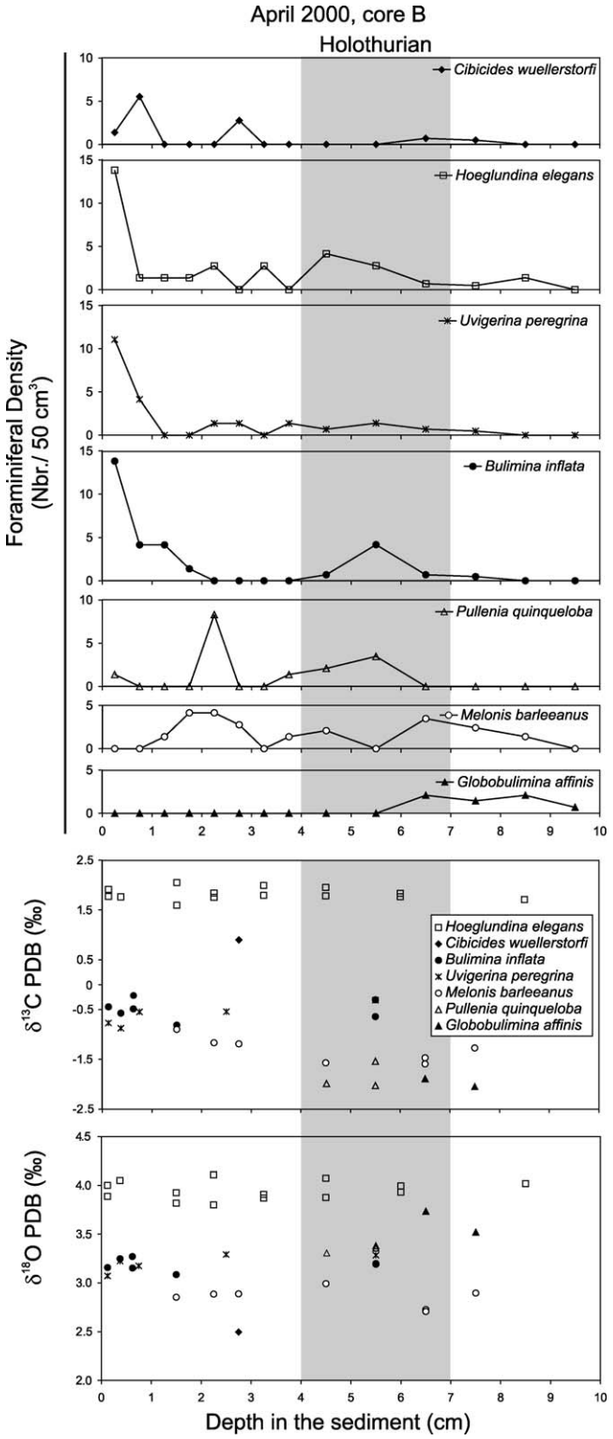

FIGURE 6. $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the investigated foraminiferal taxa at Station I in April 2000, core B. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. The gray shaded area represents the depth interval occupied by the live holothurian.

sampling periods have recorded a seasonal impact of organic matter supply to the sea floor. In the mesotrophic Bay of Biscay, a two-month-long spring bloom occurs between March and May (Tréguer and others, 1979; Laborde and others, 1999; Fontanier and others, 2003; 2006b). This bloom event is supposed to be responsible for the sudden input of phytodetritus to the sea floor in spring (April–June), triggering reproduction of the most responsive and/or opportunistic foraminiferal taxa. For example, at Station B (550 m depth) and Station A (1000 m depth), a boom in foraminiferal community is well recorded in surficial samples collected in June 1999 and April 2000 (Fontanier and others, 2003; 2006b). At Station I (the present study), Fontanier and others (2005) observed no clear increase in foraminiferal reproduction in response to hypothetical fresh organic matter deposits in eutrophic periods (June 1999 and April 2000). That is why a priori it seems improbable that the variability of foraminiferal $\delta^{13}C$ values between sampling periods, with heavier values

recorded in June 1999, is related to a seasonal variability of phytodetritus input. In our results, it appears that the foraminiferal $\delta^{18}O$ is almost constant throughout the investigation period, whereas the $\delta^{13}C$ values are minimal in April 2000 for most investigated taxa (both cores). The depletion of most $\delta^{13}C$ values in April 2000 (both cores) compared to June 1999 and January 1999 could, however, be related to the temporary increase of organic matter degradation in the topmost sediment. The mineralization is corroborated by the uncommonly low oxygen concentration recorded at the sediment-water interface (~123 μmol/l) and limited penetration of oxygen in April 2000 (Fontanier and others, 2005; Fig 6a). It should be kept in mind, however, that the data set is much larger in April (47 analyses) than in January (3 analyses) and June (12 analyses). Therefore, the observed isotopic depletion in April 2000 could be an artifact due to the low number of isotope measurements performed for the June and January samples. A more complete seasonal survey with extra sampling periods is obviously necessary to clarify the impact of seasonal organic matter export on the foraminiferal $\delta^{13}C$ values.

Interspecific $\delta^{18}O$ Differences

For all investigated calcitic taxa (*Cibicides wuellerstorfi*, *Uvigerina peregrina*, *Bulimina inflata*, *Melonis barleeanus*, *Pullenia quinqueloba*, *Chilostomella oolina* and *Globobulimina affinis*), we calculated the average $\Delta\delta^{18}O$ values (the difference between the taxon specific $\delta^{18}O$ and the calculated $\delta^{18}O_{e.c.}$), in order to clarify whether these species biomineralize their test close to or with a constant offset to isotopic equilibrium values (Fig. 7). Since $\Delta\delta^{18}O$ values are rather constant for the three sampling periods (Fig. 2), we calculate an average value for each taxon using all measurements performed for the four cores. Significant offsets between $\delta^{18}O$ values of the different taxa are usually explained by so-called vital effects (e.g., Urey and others, 1951; McCorkle and others, 1990; 1997). *Uvigerina peregrina* deviates by only −0.21‰ from $\delta^{18}O_{e.c.}$. This offset is close to −0.30‰ as determined by Rathburn and others (1996). It is smaller than the mean $\Delta\delta^{18}O$ of −0.40‰ determined by Schmiedl and others (2004) but is larger than values between −0.02 and −0.12‰ determined by McCorkle and others (1990; 1997). Our offset is also higher than the mean value (−0.08‰) determined in the Bay of Biscay along a bathymetric transect of five open-slope stations (Fontanier and others, 2006a; Fig. 1). Differences between these studies might be partially due to several morphotypes within the species *Uvigerina peregrina*, which is sometimes split into different taxa (*Uvigerina pigmea*, *U. peregrina parva*, *U. peregrina*, *U. hollicki*, *U. bifurcata*). The morphotypes might have significantly different isotopic values that could result in differences between studies (Schönfeld and Altenbach, 2005). *Melonis barleeanus* shows a significant offset of about −0.65‰, which is close to the average value of −0.53‰ measured by McCorkle and others (1990) and slightly larger than the value of −0.49‰ determined for shallower open-slope stations by Fontanier and others (2006a). The $\delta^{18}O$ of *Globobulimina affinis* is slightly higher than calculated bottom-water $\delta^{18}O_{e.c.}$, with an average $\Delta\delta^{18}O$ of +0.15‰, a value close to +0.22‰, recorded by McCorkle and others (1990), and +0.25‰, determined in the shallower open-slope stations by Fontanier and others (2006a). It is higher than the +0.06‰ that was determined by Schmiedl and others (2004). *Chilostomella oolina* is very close to bottom-water $\delta^{18}O$ ($\Delta\delta^{18}O$ = −0.02‰). This value is close to the average values of +0.09‰ and −0.08‰ presented respectively by McCorkle and others (1997) and Rathburn and others (1996) but lower than the value of +0.32‰ determined by McCorkle and others (1990). In our study area, *C. oolina* appears to be the species calcifying its test nearest to equilibrium with bottom water. The mean $\Delta\delta^{18}O$ of *Cibicides wuellerstorfi* is −0.84‰, a value close to the −0.90‰ that was published by McCorkle and others (1997). No comparable data are available in the literature about the $\delta^{18}O$ values of *Pullenia quinqueloba* and *Bulimina inflata*. For *Hoeglundina elegans*, an aragonitic taxon, we also calculate $\Delta\delta^{18}O$ to compare with other available data (Grossman, 1984b, Rathburn and others, 1996). *H. elegans* shows an average $\Delta\delta^{18}O$ of about +0.49‰, which is close to the value of +0.41‰ determined by Grossman (1984b) and higher than the value of +0.35‰ presented by Rathburn and others (1996). It should be kept in mind that the above-mentioned $\Delta\delta^{18}O$ values from McCorkle and others (1990; 1997), Rathburn and others (1996) and Schmiedl and others (2004) were calculated based on bottom water $\delta^{18}Ow$ extrapolated from atlases or other publications. Only in Fontanier and others (2006a) were values of $\delta^{18}Ow$ directly measured on the bottom water overlying the sediment-water interface. In the present paper, $\delta^{18}Ow$ were extracted from water column measurements performed off Ireland (Frew and others, 2000). These methodological differences might explain part of the $\Delta\delta^{18}O$ discrepancies between studies.

As demonstrated by Rathburn and others (1996), McCorkle and others (1997; 1990) and Fontanier and others (2006a), the $\delta^{18}O$ of taxa is not controlled by microhabitat preferences. This is clearly the case in our study area, where heavy $\delta^{18}O$ values can be found for either the shallow infaunal *Uvigerina peregrina* or the deep infaunal *Globobulimina affinis*, whereas the intermediate infaunal *Melonis barleeanus* has a very low $\delta^{18}O$ (Fig. 6).

Interspecific $\delta^{13}C$ Differences

Our results clearly suggest that the $\delta^{13}C$ of foraminiferal taxa is strongly constrained by their microhabitat preferences (Fig. 7). The deeper in the sediment the microhabitat is the lower the $\delta^{13}C$ values are. Such observations are in agreement with numerous previous studies that showed that foraminifera might record the pore water $\delta^{13}C_{DIC}$ of the sediment interval where they preferentially live (e.g., Woodruff and others, 1980; Belanger and others, 1981; Grossman, 1987; McCorkle and others, 1990; Rathburn and others, 1996; McCorkle and others, 1997; Rathburn and others, 2003; Hill and others, 2004; Mackensen and Licari, 2004; Schmiedl and others, 2004; Holsten and others, 2004: Fontanier and others, 2006a). As has been observed previously (e.g., Graham and others, 1981; Duplessy and others, 1984; McCorkle and Keigwin, 1994; McCorkle and others, 1997; Eberwein and Mackensen, 2006), only *Cibicides wueller-*

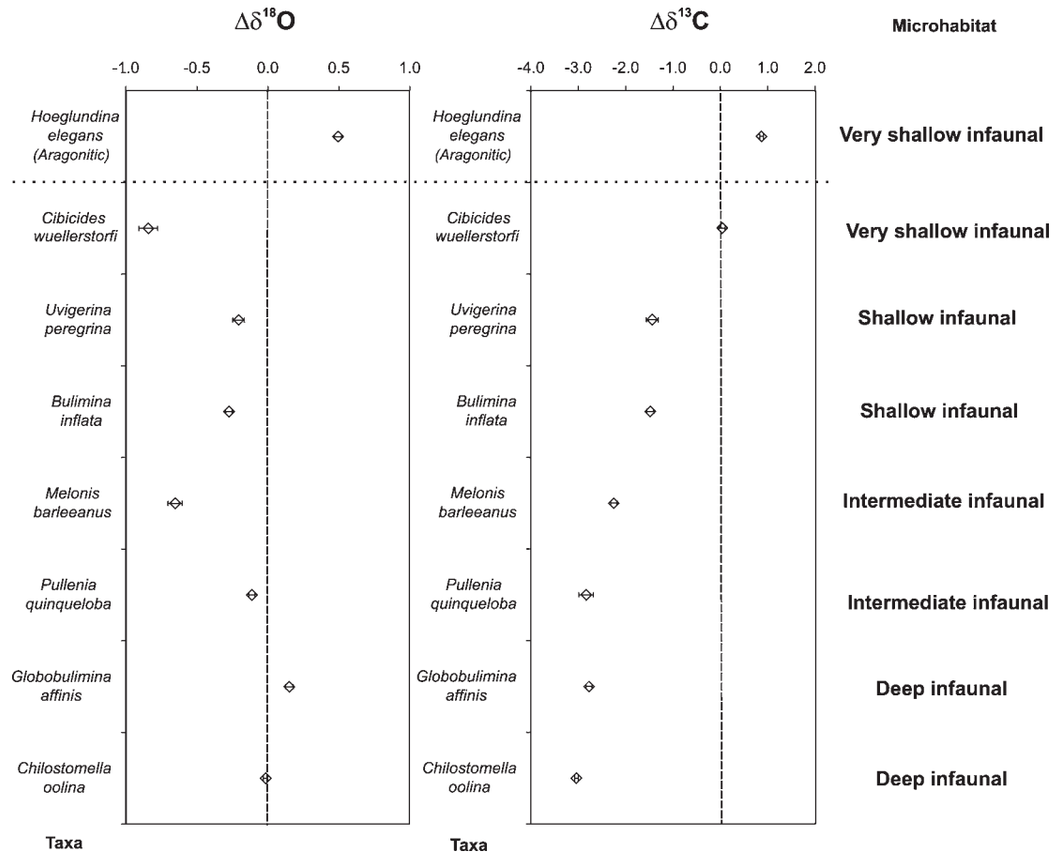

FIGURE 7 $\Delta\delta^{18}O$ between foraminiferal taxa and $\delta^{18}O_{e.c.}$ ($\Delta\delta^{18}O = \delta^{18}O_{benthic\ foraminifera} - \delta^{18}O_{e.c.}$). $\Delta\delta^{13}C$ between foraminiferal taxa and $\delta^{13}C_{DIC}$ in our study area ($\Delta\delta^{13}C = \delta^{13}C_{benthic\ foraminifera} - \delta^{13}C_{DIC}$). The microhabitat description of the eight foraminiferal taxa is added on the right side of the figure. See Fontanier and others (2005) for complementary explanation about foraminiferal microhabitat. Horizontal bars represent standard errors calculated based on all measurements performed on foraminiferal material in our study area. The $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) was calculated with the method of McCorkle and others (1997). Readers should keep in mind that *Hoeglundina elegans* is an aragonitic taxon.

storfi, a very shallow and epifaunal species, seems to record the $\delta^{13}C_{DIC}$ of bottom water.

Impact of the Presence of a Live Holothurian

Theoretically, the $\delta^{13}C_{DIC}$ of pore water decreases from a value close to bottom-water $\delta^{13}C_{DIC}$ at the sediment-water interface to much lighter values in deeper sediments. The gradient results from the progressive degradation of organic matter buried in deeper sediments and the related release of isotopically light carbon (e.g., Grossman, 1984a; Grossman, 1987; McCorkle and others, 1985; McCorkle and Emerson, 1988; Sackett, 1989; McCorkle and others, 1990). This theoretical $\delta^{13}C_{DIC}$ gradient in the topmost sediment, however, will probably be modified by the presence of a macrofaunal burrow and related bio-irrigation. In this case, bottom waters with a $\delta^{13}C_{DIC}$ heavier than that of pore waters might be introduced through the burrow into the deep and anoxic sediment layers. On the other hand, an active macrofaunal organism occupying such a burrow might concentrate organic matter in its vicinity, a process that could provoke $\delta^{13}C_{DIC}$ depletion of the surrounding pore waters as a consequence of increased degradation of organic detritus. Therefore, a benthic foraminifer that calcified a substantial part of its test in a temporarily bioturbated microhabitat could record a mixed pore-water $\delta^{13}C_{DIC}$ that mimics that of the theoretical gradient.

The presence of a living holothurian in the deep part of the core B collected at our Station I in April 2000 allowed us to assess the impact of intermittent bioturbation on foraminiferal carbon isotopes. The 3-cm-long holothurian (genus *Molpadia*) was found in life position between 4–7 cm depth. Selective feeding of *Molpadia blakei* was investigated by Wigham and others (2003) in the abyssal northeast Atlantic Ocean. The genus *Molpadia* belongs to a group of deep infaunal holothurians that are able to feed on low-quality organic detritus. Wigham and others (2003) showed that gut sediments of *Molpadia blakei* are characterized by refractory chloropigments, whereas carotenoid or un-degraded chlorophyll pigments are absent. Like most infaunal molpadids, *Molpadia* is probably not selective in its organic matter intake, ingesting mainly low-quality organic compounds (Ian Hudson, communication, 2005). Our isotope results show that most living foraminifera found in the direct vicinity of the holothurian exhibit $\delta^{13}C$ values close to

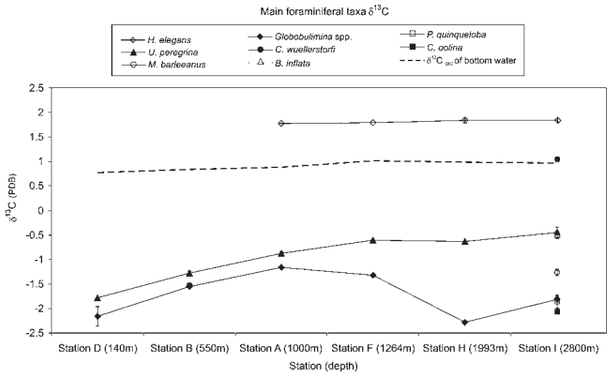

FIGURE 8. $\delta^{13}C$ isotopic signatures of the main foraminiferal taxa (*Hoeglundina elegans*, *Cibicides wuellerstorfi*, *Uvigerina peregrina*, *Bulimina inflata*, *Pullenia quinqueloba*, *Melonis barleeanus*, *Chilostomella oolina* and *Globobulimina* spp.) along a six-station bathymetric transect in the Bay of Biscay. The dotted line represents the $\delta^{13}C$ of dissolved inorganic carbon of bottom water. Vertical bars represent standard errors calculated when several isotopic measurements are available for the same station. Note that Station I lies in a canyon where organic matter is focused.

the $\delta^{13}C$ values commonly found for the same taxa in unbioturbated cores (Fig. 6). Their $\delta^{13}C$ are constant along the core and close to the mean values recorded in unbioturbated cores. This is particularly the case for *Hoeglundina elegans* and *Uvigerina peregrina* (Fig. 6), for which we have consistent data. In the Bay of Biscay, these taxa are commonly described as shallow infaunal taxa (Fontanier and others, 2002; 2005). The high and unvarying values of their $\delta^{13}C$ downcore to 9 cm depth suggest that (1) individuals found around the holothurian calcified their test in their normal shallow infaunal microhabitat and not in the vicinity of the holothurian and (2) they were subsequently transported into these deeper sediment layers, probably due to the activity of holothurian. It is feasible that both taxa have a low calcification rate, which minimizes the impact of transport to a deeper sediment layer. It might even be possible that calcification stopped altogether in this deep hostile environment. After such a displacement, foraminifera might be able to migrate upward, back to their preferred microhabitat (shallow infaunal niches), where they would continue biomineralizing their test. As a last explanation, all (rose-Bengal stained) individuals of *Hoeglundina elegans* and *Uvigerina peregrina* found in the vicinity of the holothurian could be dead and would present a false staining. They might be passively transported from the shallow infaunal microhabitat to deeper sediment layers by macrofauna. Except for *Melonis barleeanus*, the $\delta^{13}C$ is lighter (a mean offset of $-0.41‰$) in individuals picked in the depth intervals with the holothurian compared to individuals living above and below this sediment interval. *M. barleeanus* is systematically found in deeper niches, and is obviously adapted to survive and biomineralize in deeper sediment layers (Fontanier and others, 2005). The isotopic depletion of *M. barleeanus* near the living holothurian suggests that these individuals have calcified in pore waters that are more depleted in ^{13}C than those of their normal unbioturbated microhabitat. This local depletion could reflect an important metabolic release of light carbon by the holothurian through the mineralization of more or less refractory organic compounds.

Interspecific $\delta^{13}C$ Variability Along a Bathymetric-Transect

Because the $\Delta\delta^{13}C$ between shallow, intermediate and deep infaunal foraminiferal taxa appears to mimic the pore-water $\delta^{13}C_{DIC}$ gradient in topmost sediment, it is commonly assumed that carbon isotopes of benthic foraminifera could be used to measure the importance of organic matter degradation in the topmost oxygenated sediment layer (McCorkle and others, 1997; Mackensen and Licari, 2004; Schmiedl and others, 2004; Holsten and others, 2004). In a recent study in the Bay of Biscay, Fontanier and others. (2006a) investigated the $\Delta\delta^{13}C$ between the shallow infaunal *Uvigerina peregrina* and the deep infaunal *Globobulimina* spp. along a five-station bathymetric transect between 150–2000 m depth on an open slope (Stations D, B, A, F and H; Fig. 1). Their results show that the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. is minimal in eutrophic areas (Stations D and B), but show an important increase towards more oligotrophic areas (Station H; Fig. 8). This increase might be mainly related to (1) the theoretical decrease of vertically exported organic matter flux downslope, what obviously controls the $\delta^{13}C$ of shallow infaunal *U. peregrina*; (2) the related downward migration of the zero oxygen boundary, where *Globobulimina* spp. is assumed to preferentially calcify and record its $\delta^{13}C$, and (3) discrete changes of bottom water oxygenation (Fontanier and others, 2006a). Therefore, it appears that the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. could reflect the state of remineralization of fresh organic detritus at and below the sediment-water interface (Fontanier and others, 2006a). Our Station I allows us to complete this bathymetric transect. Organic matter deposits related to primary production appears to be minimal at this deep site, whereas bottom water oxygen concentration is in the range of the oxygenation of the other open-slope stations. However, Station I is positioned in Cap-Ferret Canyon, which differs from open-slope environments in its advected supply of particulate matter. The total organic carbon content in the uppermost sediment is 1.5% of sediment dry weight, and the ratio of enzymatically hydrolysable amino acids to total hydrolysable amino acids (EHAA/THAA) in the upper sediment is about 0.24 (Fontanier and others, 2005). As a consequence of the low-quality organic matter focused into this canyon, the depth of oxygen penetration ranges between 4–5.5 cm, slightly shallower than that in the adjacent and shallower open-slope Station H (2000 m depth) where oxygen penetrates to 6 cm.

Figure 8 shows that the results for Station I tend to follow the bathymetric trend expressed by the open-slope stations. At our Station I, we observe (1) a slight increase of the $\delta^{13}C$ of *Uvigerina peregrina*, probably as the result of the lower vertical flux of exported labile organic matter and (2) a rather large $\Delta\delta^{13}C$ between shallow, intermediate and deep infaunal taxa. The comparison between the $\delta^{13}C$ of *U. peregrina*, *Melonis barleeanus* and *Globobulimina* spp. at our Station I (~2800 m depth) and at another open-slope station where these taxa are also present (Station B,

~550 m depth) shows a clear difference. The $\delta^{13}C$ values of specimens of the same taxon are close to each other in the upper bathyal station, where exported organic matter flux is high and oxygen penetration is limited (~2 cm). The $\delta^{13}C$ deviates significantly, however, at Station I, where fresh organic matter flux related to primary production is supposed to be very low and where oxygen penetration is deep (~5 cm). The additional input, by lateral advection, of organic matter in an intermediate state of decay at Station I (compared to open-slope Station H, 2000 m depth) has apparently only a weak contribution to biogeochemical processes deeper in the sediment.

CONCLUSIONS

At our 2800-m-deep station from the lower canyon, the oxygen and carbon isotopic compositions of eight benthic foraminiferal taxa, *Hoeglundina elegans*, *Cibicides wuellerstorfi*, *Uvigerina peregrina*, *Bulimina inflata*, *Melonis barleeanus*, *Pullenia quinqueloba*, *Chilostomella oolina* and *Globobulimina* spp., were determined. Based on the results, a number of observations can be made:

- There is no systematic relationship between foraminiferal microhabitat and the offset between foraminiferal $\delta^{18}O$ and equilibrium calcite $\delta^{18}O$.
- The $\delta^{13}C$ signatures of most foraminiferal taxa are not correlated to calculated bottom water $\delta^{13}C_{DIC}$ and seem to be controlled by microhabitat effects. Only the $\delta^{13}C$ of *Cibicides wuellerstorfi* is very close to bottom-water $\delta^{13}C_{DIC}$.
- The presence of a living holothurian in a deep infaunal burrow did not cause $\delta^{18}O$ and $\delta^{13}C$ offsets in epifaunal and shallow infaunal foraminifera accidentally transported into the bioturbated interval. Only some individuals of *Melonis barleeanus* collected in the immediate vicinity of the holothurian exhibit lower $\delta^{13}C$ values, suggesting the potential role of macrofaunal activity on the carbon isotopes of intermediate and deep infaunal foraminiferal taxa that calcify in deeper sediment layers.
- The comparison of the $\Delta\delta^{13}C$ between *Uvigerina peregrina*, *Melonis barleeanus* and *Globobulimina affinis* with values recorded at shallower open-slope stations suggests that the focusing of organic matter in an intermediate state of decay in our canyon station has, at most, a weak impact on the biogeochemical processes deeper in the sediment. The $\delta^{13}C$ of *U. peregrina* and the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. appear definitively more sensitive to labile organic matter supplies to the sediment-water interface than to input of low-quality organic matter.

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APPENDIX 1
Taxonomic notes.

Hoeglundina elegans (d'Orbigny), 1826; illustrated in Phleger and others (1953), pl. 9, figs. 24, 25.

Cibicides wuellerstorfi (Schwager), 1866; illustrated in Jones (1994), pl. 93, figs. 8, 9.

Uvigerina peregrina Cushman, 1923; illustrated in van der Zwaan and others (1986), pl. 1, figs. 1–6.

Bulimina inflata Seguenza, 1862; illustrated in van Leeuwen (1989), pl. 8, fig. 4.

Melonis barleeanus (Williamson), 1958; illustrated in van Leeuwen (1989), pl. 13, figs. 1, 2.

Pullenia quinqueloba (Reuss), 1951; illustrated in Jones (1994), pl. 84, figs. 14, 15.

Globobulimina affinis (d'Orbigny), 1839; illustrated in Verhallen (1991), pl. 27, figs. 2, 3.

Chilostomella oolina Schwager, 1878; illustrated in Jones (1994), pl. 55, figs. 12–14, 17, 18.