Available online at www.sciencedirect.com
SCIENCE DIRECT
Marine Micropaleontology 58 (2006) 159–183
MARINE MICROPALEONTOLOGY
www.elsevier.com/locate/marmicro

Stable oxygen and carbon isotopes of live benthic foraminifera from the Bay of Biscay: Microhabitat impact and seasonal variability

C. Fontanier [a,*], A. Mackensen [b], F.J. Jorissen [a], P. Anschutz [c], L. Licari [d], C. Griveaud [a]

[a] *Department for the Study of Recent and Fossil Bio-Indicators, Angers University, UPRES EA 2644, 2 Boulevard Lavoisier, 49045 Angers Cedex, France*
[b] *Alfred Wegener Institute for Polar and Marine Research, Columbustrasse, D-27515 Bremerhaven, Germany*
[c] *Department of Geology and Oceanography, Bordeaux University, CNRS UMR 5805, Avenue des Facultés, 33405 Talence Cedex, France*
[d] *CEREGE, Europole de l'Arbois-BP80, 13545 Aix-en-Provence Cedex 4, France*

Received 7 June 2005; received in revised form 3 September 2005; accepted 21 September 2005

Abstract

We determined the stable oxygen and carbon isotopic composition of live (Rose Bengal stained) benthic foraminifera (>150 μm size fraction) of seven taxa sampled along a downslope transect between 140 to 2000 m water depth in the Bay of Biscay. At the five stations, *Hoeglundina elegans*, *Cibicidoides pachydermus*, *Uvigerina peregrina*, *Uvigerina mediterranea* preferentially occupy shallow infaunal niches, whereas *Melonis barleeanus* and *Uvigerina elongatastriata* occupy an intermediate infaunal microhabitat, and *Globobulimina* spp. live in a deep infaunal niche close to the zero oxygen boundary.

When compared with $\delta^{18}O$ values of calcite formed in equilibrium with bottom waters, *U. peregrina* forms its test in close equilibrium with bottom water $\delta^{18}O$. All other foraminiferal taxa calcify with a constant offset to calculated equilibrium calcite. There is no systematic relationship between the foraminiferal microhabitat depth and the $\Delta\delta^{18}O$ between foraminiferal and equilibrium calcite. We calculated correcting factors for the various taxa, which are needed for constructing multispecies-based oxygen isotope records in paleoceanographic studies of the study area.

The $\delta^{13}C$ values of foraminiferal taxa investigated in this study do neither record bottom water $\delta^{13}C_{DIC}$ in a 1:1 relationship nor with a constant offset, but appear to be mainly controlled by microhabitat effects. The increase of $\delta^{13}C$ values of shallow infaunal taxa with increasing water depth reflects the decrease of the exported flux of organic carbon along the bathymetric transect and early diagenetic processes in the surface sediment. This is particularly the case for the shallow infaunal *U. peregrina*. The $\delta^{13}C$ values of deep infaunal *Globobulimina* spp. are much less dependent on the exported organic matter flux. We suggest that the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. can shed light on the various pathways of past degradation of organic detritus in the benthic environments.

At a station in 550 m water depth, where periodic eutrophication of sediment surface niches was demonstrated previously, we performed a two-year seasonal survey of the isotopic composition of foraminiferal faunas. No marked seasonal changes of the stable carbon isotopic composition of shallow, intermediate and deep infaunal foraminiferal taxa were observed. Thus, the $\delta^{13}C$ values of foraminiferal individuals belonging to the >150 μm fraction may result from rather long-term calcification processes lasting for several weeks or months, which limit the impact of ephemeral ^{12}C enrichment of shallow infaunal niches on the isotope chemistry of adult individuals during eutrophic periods. Only highly opportunistic taxa reproducing or calcifying during

* Corresponding author. Tel.: +33 2 4173 5381; fax: +33 2 4173 5352.
E-mail address: christophe.fontanier@univ-angers.fr (C. Fontanier).

0377-8398/$ - see front matter
doi:10.1016/j.marmicro.2005.09.004

phytoplankton bloom periods and the subsequent deposits of phytoplankton remains in the benthic environment may exhibit a particularly low $\delta^{13}C$, indicative of such short productive periods.

Keywords: stable oxygen and carbon isotopes; benthic foraminifera; microhabitat; seasonality; exported organic matter flux

1. Introduction

Knowledge about the stable isotope composition of benthic foraminiferal tests has been strongly improved during the last about two decades of studies on live foraminiferal faunas (Woodruff et al., 1980; Grossman, 1984a,b, 1987; Mackensen and Douglas, 1989; McCorkle et al., 1990, 1997; Mackensen et al., 1993, 2000; McCorkle and Keigwin, 1994; Rathburn et al., 1996, 2000, 2003; Corliss et al., 2002; Mackensen and Licari, 2004; Schmiedl et al., 2004; Holsten et al., 2004). The $\delta^{18}O$ of many benthic foraminifera has been considered to be in equilibrium with the $\delta^{18}O$ of bottom water, or to have a constant offset (e.g. Shackleton and Opdyke, 1973; Shackleton, 1977). Therefore, by recording the $\delta^{18}O$ changes in oceanic water masses, benthic foraminiferal oxygen isotopes provide a fundamental tool to reconstruct fluctuations in global ice volume and deep ocean temperature during the Quaternary, to construct reliable time scales and to improve paleoceanographic reconstructions going back further in time than the Pleistocene and Holocene Epochs (e.g., Imbrie et al., 1992; see also review by Rohling and Cooke, 1999; Zachos et al., 2001; Katz et al., 2003).

Carbon isotopes in foraminiferal carbonate tests have been widely used as proxies of paleoproductivity and/or water mass configuration (e.g. Duplessy et al., 1984; Curry et al., 1988; Mackensen et al., 2001; McCorkle et al., 1997; Bickert and Mackensen, 2004; Curry and Oppo, 2005). There is a consensus that the carbon isotope signature of infaunal benthic foraminifera is strongly influenced by the ambient pore water $\delta^{13}C$ (e.g., Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1984a, 1984b, 1987; McCorkle et al., 1985; Zahn et al., 1986; McCorkle et al., 1990, 1997; Wefer and Berger, 1991; Loubere et al., 1995; Corliss et al., 2002; Mackensen et al., 2000; Mackensen and Licari, 2004; Schmiedl et al., 2004, Holsten et al., 2004). Usually, the profile of ambient pore water $\delta^{13}C$ shows a rapid isotopic depletion with depth in the sediment, caused by the decomposition of sedimentary organic matter (Grossman, 1984a,b, 1987; McCorkle et al., 1985). Foraminiferal taxa calcifying in the pore water of the sediment interval in which they preferentially live, should therefore mirror this depletion, and may show a so-called "microhabitat effect". Only strictly epifaunal taxa would form their test in direct contact with bottom water and thus may provide a measure for the past isotopic composition of oceanic bottom water masses (e.g. Woodruff et al., 1980; Graham et al., 1981; Zahn et al., 1986; Grossman, 1987; Wefer and Berger, 1991). All available evidence shows that the interpretation of carbon isotopes in benthic foraminiferal tests in relation with the chemical properties of bottom and interstitial waters requires an exhaustive knowledge of the ecology of the investigated taxa (microhabitat, population dynamics, food preferences) and an understanding of geochemical processes affecting the carbonate and stable isotope chemistry of interstitial waters (McCorkle et al., 1990, 1997; Mackensen et al., 1993, 2000; McCorkle and Keigwin, 1994; Rathburn et al., 1996, 2000; Corliss et al., 2002; Mackensen and Licari, 2004; Schmiedl et al., 2004; Holsten et al., 2004). For example, as suggested by Mackensen et al. (1993), a pulsed phytodetritus supply to the sediment–water interface may have a significant impact on the $\delta^{13}C$ of benthic foraminifera preferentially living on the sediment. Mackensen et al. (1993) showed that *Fontbotia wuellerstorfi* (=*Cibicides wuellerstorfi*), which generally is regarded as a strictly epifaunal taxon, responds to seasonal input of organic matter at the sediment–water interface. It obviously calcifies within this phytodetritus deposit and thus reflects the very low $\delta^{13}C$ values within the so-called fluffy layer. Consequently, $\delta^{13}C$ values of *C. wuellerstorfi* tests do not always strictly reflect bottom water $\delta^{13}C_{DIC}$ values in a 1 : 1 manner.

In this study, we concentrate on oxygen and carbon isotopes in carbonate tests of live benthic foraminifera collected in the Bay of Biscay. Fontanier et al. (2002) showed that the density and composition of foraminiferal faunas along a bathymetric transect from shelf to mesobathyal environments is mainly controlled by the mean annual exported organic matter flux from the surface waters to the sea floor. Dissolved oxygen concentration and redox levels at and below the sediment–water interface play a secondary role. Together, these factors control the microhabitat of some intermediate and deep infaunal taxa (e.g. *Melonis barleeanus*, *Globobulimina affinis*). Furthermore, Fontanier et al. (2003, in press) showed that phytodetritus deposits

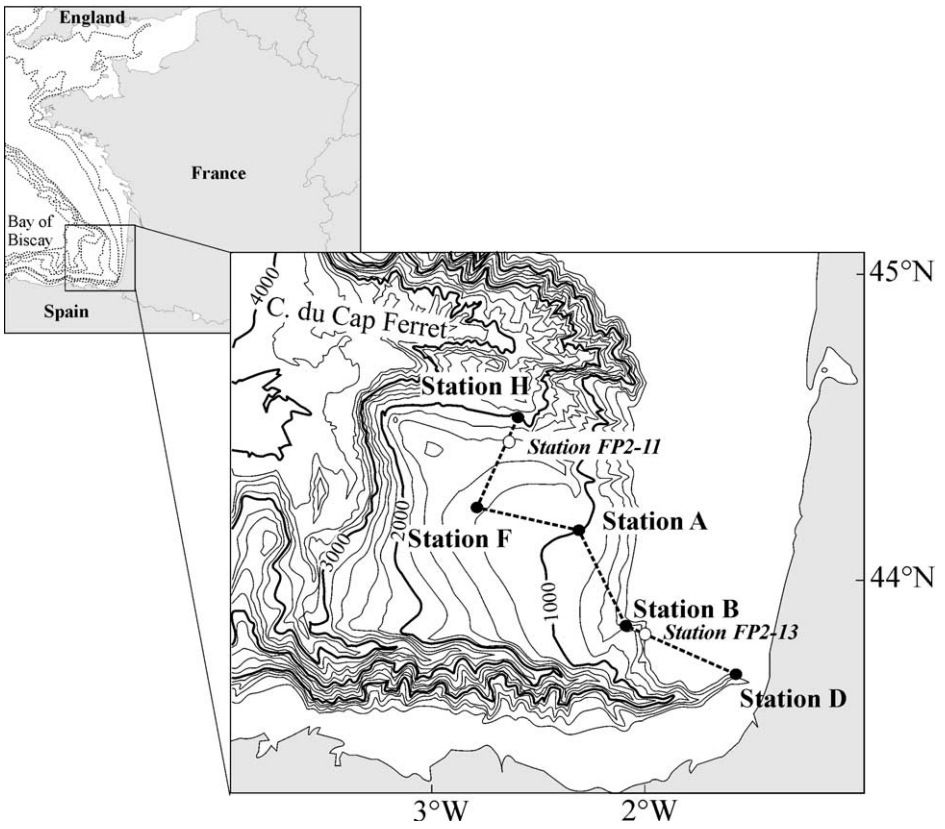

Fig. 1. Study area, bathymetry and geographical position of our 5 stations (D, B, A, F and H) where we sampled foraminiferal faunas and collected samples from water column and sediment–water interface for isotopic measurements. Stations FP2-11 and FP2-13 were only investigated for water isotopic chemistry (see Table 3).

related to spring and autumn surface water blooms induce seasonal changes of the composition and density of foraminiferal faunas at continental margin stations at ~550 m and ~1000 m water depth. Reactive foraminiferal taxa occupying shallow infaunal microhabitats exhibit marked density increases in eutrophic periods. This especially holds for *Epistominella exigua*, *Reophax guttiferus*, *Uvigerina peregrina*, *Uvigerina mediterranea* at 550 m depth and *Nuttallides pusillus*, *U. peregrina* and *U. mediterranea* at 1000 m depth (Fontanier et al., 2003, in press). Deeper in the sediment, intermediate and deep infaunal foraminiferal taxa, such as *M. barleeanus* and *Globobulimina* spp., show only minor seasonal changes in density. This can be explained by the much larger stability of their deep infaunal microhabitat. Here, we concentrate on the

Table 1
Main characteristics of the five stations in our study area

Station	Depth (m)	Latitude	Longitude	Sampling date	Cruises	Cores	Temperature (°C)	Salinity (PSU)	Bottom water oxygenated (μmol/l)	Zero oxygen boundary (mm)	Jz (g C/m^2/year)
D	140	43°4193N	1°3410W	Oct-97	1	1	12.5	35.50	220	8	31.4
B	~550	43°4998N	2°2304W	Oct-97–Apr-00	10	15*	11.0	35.60	205–221	17–26	9.3
A	1012	44°0978N	2°2027W	Oct-97	1	1	9.5	35.75	196	18	5.6
F	1264	44°1710N	2°4495W	Jan-98	1	1	8.0	35.50	211	63	4.6
H	1993	44°1710N	2°4495W	Oct-98	1	1	4.0	35.00	263	60	3.2

Temperature and salinity data come from Ogawa and Tauzin (1973), Durrieu de Madron et al. (1999) and CTD measurements performed during PROTAGO and FORPROX II programs (respectively done in February 2003 and May 2004). Bottom water dissolved oxygen concentration was calculated 5 mm above sediment–water interface (Fontanier et al., 2002). Jz represents exported organic carbon flux calculated using a mean annual primary production value of 150 g C/m^2 /year and according to the formula proposed by Berger and Wefer (1990) and improved by Herguera (1992). The asterisk indicates that 5 duplicate cores are available at Station B (Fontanier et al., 2003).

Table 2
Isotopic measurements for all foraminiferal taxa studied in our study area (*Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Uvigerina elongatastriata, Melonis barleeanus* and *Globobulimina* spp.)

Taxa depth in sediment (cm)	No. of individuals	*Hoeglundina elegans*		No. of individuals	*Cibicidoides pachydermus*		No. of individuals	*Uvigerina meditrranea*	
		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$
Station D, October 1997									
0–0.25									
0.35–0.75									
1–2.5									
Station B, October 1997									
0–0.25				14	0.13	1.08	15	–0.60	1.91
0–0.50							30	–1.09	1.85
0.25–0.5									
1–1.5									
Station B, October 1997*									
1.5–2									
Station B, January 1998									
0–0.25				10	0.29	1.03	10	–0.57	1.75
0.5–0.75									
0.75–1									
1–1.5									
Station B, January 1998*									
0–0.25									
Station B, June 1998									
0–1				10	0.21	1.28	10	–0.48	1.79
1.5–1.75									
0–2									
Station B, July 1998									
0–0.25				10	0.42	1.21	15	–0.46	1.97
0.5–0.75									
3–3.5									
Station B, October 1998									
0–0.25				9	0.38	1.31	10	–0.55	1.77
0.25–0.5				6	0.37	1.07			
1–1.5									
1.5–2									
3–3.5									
Station B, December 1998									
0–0.25							12	–0.71	1.75
0–0.75									
0–1				5	0.23	0.90			
0.75–1							10	–0.51	1.74
1–1.5							10	–0.41	1.88
1–2.5									
2–2.5									
4–5									
Station B, January1999									
0–0.25				10	0.53	1.31	13	–0.63	2.00
1–1.5									
4–5									
Station B, April 1999									
0.25–0.5									
0.75–1							15	–0.48	2.05
0–2									
1–1.5									
1–2									
Station B, April 1999*									
0.25–0.5							13	–0.54	1.94
0.25–0.75									
1–1.5				1	0.24	1.07			
1–2									
1.5–2									
2–2.5									
Station B, June 1999									
0–0.25							14	–0.53	1.97
0–0.50				11	0.36	1.23			
0.25–0.5							15	–0.49	2.00
0.75–1							14	–0.49	2.11
1–1.5							14	–0.34	2.13

Table 2 (*continued*)

Taxa depth in sediment (cm)	No. of individuals	*Hoeglundina elegans*		No. of individuals	*Cibicidoides pachydermus*		No. of individuals	*Uvigerina meditrranea*	
		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$
Station B, June 1999									
1.5–2							6	–0.40	1.93
1.5–2.5									
2–2.5									
Station B, June 1999*									
0–0.25							15	–0.57	2.05
0–1				8	0.31	1.16			
0–1.5									
1–1.5									
1.5–2									
1.5–2.5									
Station B, April 2000									
0–0.25							15	–0.56	1.93
0.25–0.5							17	–0.41	2.00
0.5–0.75							14	–0.49	2.03
0.75–1							15	–0.57	1.99
1–1.5							15	–0.43	2.00
1.5–2							15	–0.40	2.10
2–2.5							11	–0.59	1.92
Station B, April 2000*									
0–0.25							16	–0.43	1.94
0–0.50				8	0.18	1.33			
1–1.5									
1–2									
1–2.5									
Station A, October 1997									
0–0.25							6	–0.08	2.07
0–0.75				6	0.56	1.28			
0.25–0.5							12	–0.17	1.93
0.5–0.75							10	–0.09	2.17
0.5–1									
0.75–1	10	1.77	2.57				10	–0.25	2.07
1–1.5	7	1.78	2.49						
1.5–2									
5.5–6.5									
Station F, January 1998									
0–0.25									
0.5–0.75	6	1.79	2.69						
4–5									
Station H, October 1998									
0–0.25	12	1.89	3.48						
0.25–0.5	14	1.73	3.48						
0.5–0.75	15	1.90	3.66						
5–7									

Taxa depth in sediment (cm)	No. of individuals	*Uvigerina peregrina*		No. of individuals	*Uvigerina elongatastriata*		No. of individuals	*Melonis barleeanus*		No. of individuals	*Globobulimina affinis*	
		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$
Station D, October 1997												
0–0.25	15	–1.78	1.66									
0.35–0.75										3	–2.26	1.83
1–2.5										6	–2.06	1.83
Station B, October 1997												
0–0.25	20	–1.51	1.65									
0–0.50	30	–1.69	1.72				10*	–1.44	1.32			
0.25–0.5							15	–1.35	1.28			
1–1.5				20	–1.51	2.53				15	–1.52	1.98
Station B, October 1997*												
1.5–2				11	–1.34	1.89						

(continued on next page)

Table 2 (*continued*)

Taxa depth in sediment (cm)	No. of individuals	*Uvigerina peregrina*		No. of individuals	*Uvigerina elongatastriata*		No. of individuals	*Melonis barleeanus*		No. of individuals	*Globobulimina affinis*	
		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$
Station B, January 1998												
0–0.25												
0.5–0.75	10	–1.38	1.74									
0.75–1										8	–1.38	1.24
1–1.5				10	–1.45	2.00	12	–1.39	1.24			
Station B, January 1998*												
0–0.25				13	–1.63	2.13						
Station B, June 1998												
0–1	12	–1.15	1.63				12	–1.71	1.12			
1.5–1.75										11	–1.68	1.84
0–2				13	–1.50	1.91						
Station B, July 1998												
0–0.25	10	–1.20	1.55									
0.5–0.75							3	–1.36	0.90			
3–3.5										6	–1.78	1.99
Station B, October 1998												
0–0.25	6	–1.41	1.22									
0.25–0.5	10	–1.35	1.31									
1–1.5							16	–1.54	1.26			
1.5–2				16	–1.45	2.29						
3–3.5										4	–1.49	1.94
Station B, December 1998												
0–0.25												
0–0.75	10	–1.18	1.81									
0–1												
0.75–1												
1–1.5	10	–1.08	1.75									
1–2.5				16	–1.47	1.84						
2–2.5							10	–1.58	1.08			
4–5										10	–1.40	2.05
Station B, January1999												
0–0.25	9	–1.32	1.59									
1–1.5				15	–1.40	2.97	10	–1.53	1.26			
4–5										16	–1.53	1.92
Station B, April 1999												
0.25–0.5							5	–1.61	1.26			
0.75–1												
0–2	12	–1.11	1.75									
1–1.5				10	–1.88	1.78						
1–2										12	–1.61	2.14
Station B, April 1999*												
0.25–0.5												
0.25–0.75	11	–1.24	1.84									
1–1.5												
1–2				10	–1.50	2.88						
1.5–2							15	–1.48	1.31			
2–2.5										13	–1.37	2.14
Station B, June 1999												
0–0.25												
0–0.50	12	–1.05	1.83									
0.25–0.5												
0.75–1												
1–1.5												
1.5–2												
1.5–2.5				16	–1.51	1.93						
2–2.5										14	–1.54	2.11
Station B, June 1999*												
0–0.25												
0–1												
0–1.5	10	–1.30	1.77									
1–1.5							14	–1.54	1.32			
1.5–2				15	–1.44	1.88						
1.5–2.5										11	–1.49	2.00

Table 2 (*continued*)

Taxa depth in sediment (cm)	No. of individuals	*Uvigerina peregrina*		No. of individuals	*Uvigerina elongatastriata*		No. of individuals	*Melonis barleeanus*		No. of individuals	*Globobulimina affinis*	
		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$		$\delta^{13}C$	$\delta^{18}O$
Station B, April 2000												
0–0.25	18	–1.24	1.78									
0.25–0.5												
0.5–0.75												
0.75–1												
1–1.5				15	–1.35	2.00						
1.5–2							15	–1.65	1.33			
2–2.5										12	–1.48	2.08
Station B, April 2000*												
0–0.25	13	–1.19	1.78									
0–0.50												
1–1.5							15	–1.67	1.42			
1–2				13	–1.67	1.93						
1–2.5										10	–1.69	2.07
Station A, October 1997												
0–0.25												
0–0.75												
0.25–0.5												
0.5–0.75												
0.5–1	18	–0.83	1.89									
0.75–1												
1–1.5	15	–0.93	1.98									
1.5–2	13	–0.86	1.87									
5.5–6.5										20	–1.16	2.23
Station F, January 1998												
0–0.25	10	–0.58	2.24									
0.5–0.75	14	–0.63	2.18									
4–5										(4)	(–1.32)	(2.57)
Station H, October 1998												
0–0.25												
0.25–0.5	15	–0.63	3.03									
0.5–0.75												
5–7										5	–2.28	3.43

Numbers of individuals used for measurements are also presented. Asterisks indicate duplicate cores available at Station B. Shaded boxes correspond to isotopic measurements performed on individuals belonging to 63–150 μm size fraction. Values between parentheses are related to isotopic measurements performed on doubtfully stained individuals that are not considered alive at the time of sampling, and which may have died several weeks to months before.

isotopic signatures of seven benthic foraminiferal taxa: *Cibicidoides pachydermus*, *Hoeglundina elegans*, *U. mediterranea*, *U. peregrina*, *Uvigerina elongatastriata*, *M. barleeanus* and *Globobulimina* spp. Along a bathymetric transect (Fontanier et al., 2002), we will compare the benthic foraminiferal isotopic signatures ($\delta^{18}C$, $\delta^{13}C$) with physico-chemical properties (temperature, oxygenation) of bottom and pore waters and the exported organic matter flux in the Bay of Biscay (Fig. 1; Tables 1, 2 and 3). The estimated exported organic matter flux from the surface waters to the sea floor shows a significant gradient from high values in shallow environments (Station D, 140 m deep) to very low values deeper in the basin (Station H, 1964 m) (Fontanier et al., 2002). The organic supply is supposed to have a major impact on the $\delta^{13}C$ signal of the dissolved inorganic carbon (DIC) of bottom and interstitial waters, and should provoke consistent downslope changes of the $\delta^{13}C$ isotopic signature of benthic foraminifera. In addition, we expect a significant increase of benthic foraminiferal $\delta^{18}O$ values with increasing depth as a direct result of a temperature decrease. Based on 10 successive samplings at Station B (550 m) between October 1997 and April 2000 (Fontanier et al., 2003), we investigate whether $\delta^{13}C$ and $\delta^{18}O$ values in benthic foraminiferal tests are stable over time, or perhaps influenced by the seasonal supply of food to the sediment–water interface. This seasonal investigation gives new insights into the isotopic response of benthic foraminiferal communities to the deposition of phytodetritus in continental margin environments.

2. Study area

2.1. Hydrological settings

The water masses that fill the Bay of Biscay are derived from a branch of the north Atlantic drift. The

Table 3
Isotopic measurements for water samples collected during FORPROX II program (May 2004)

Site	Station D		Station FP2–13		Station B		Station A		Station F		Station FP2–11		Station H	
Latitude	43°42'N		43°45'N		43°50'N		44°10'N		44°17'N		44°27N		44°32'N	
Longtitude	1°34'W		2°00'W		2°03'W		2°20'W		2°45'W		2°39'W		2°37'W	
Depth (m)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)
0							1.25 ± 0.02	0.44 ± 0.03						
25					1.11 ± 0.02	0.57 ± 0.03								
50					1.25 ± 0.05	1.53 ± 0.02								
75			0.99 ± 0.05	0.55 ± 0.00										
100							1.00 ± 0.00	0.56 ± 0.00						
150							1.98 ± 0.03	0.55 ± 0.03						
200							1.01 ± 0.02	0.56 ± 0.03						
300							0.88 ± 0.05	0.52 ± 0.01						
400							1.68 ± 0.01	0.54 ± 0.02						
550							0.75 ± 0.06	0.48 ± 0.00						
800							0.87 ± 0.04	0.52 ± 0.01						
1000							0.92 ± 0.00	0.53 ± 0.00						
1200									1.01 ± 0.06	0.50 ± 0.01				
1400											0.97 ± 0.04	0.40 ± 0.01		
1600											1.03 ± 0.02	0.25 ± 0.02		
1940													1.03 ± 0.02	0.25 ± 0.02
Supernatant water	0.77 ± 0.04	0.44 ± 0.03			0.84 ± 0.01	0.54 ± 0.00	0.87± 0.03	0.54 ± 0.00			0.99 ± 0.03	0.24 ± 0.00	0.98 ± 0.04	0.33 ± 0.01
Reference values	$\delta^{13}C_{DIC}$ (VPDB)	$\delta^{18}O_{e.c.}$ (VSMOW)			$\delta^{13}C_{DIC}$ (VPDB)	$\delta^{18}O_{e.c.}$ (VSMOW)	$\delta^{13}C_{DIC}$ (VPDB)	$\delta^{18}O_{e.c.}$ (VSMOW)	$\delta^{13}C_{DIC}$ (VPDB)	$\delta^{18}O_{e.c.}$ (VSMOW)			$\delta^{13}C_{DIC}$ (VPDB)	$\delta^{18}O_{e.c.}$ (VSMOW)
	0.77	1.31			0.84	1.73	0.87	2.09	1.01	2.42			0.98	3.28

Seven stations (among which our five stations) were sampled for water column and supernatant water. Isotopic values are graphically presented in Fig. 2. Last line includes isotopic values that we considered as reliable references for bottom water chemistry at our five stations; $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$ (PDB)) was calculated from $\delta^{18}O$ (SMOW) with the method of McCorkle et al. (1997).

current velocity of the various water masses is less than 10 cm s^{-1} (Tréguer et al., 1979). The surface waters that enter from the north, along the Irish shelf-break, leave the area near Cape Finisterre after only two years of slow transit. The surface water patterns are strongly tributary to the seasonal variations of the thermocline and mixed layer (Tréguer et al., 1979; Lampert, 2001), and the seasonal changes of the riverine discharge (Lampert, 2001). Surface currents (velocity and directions) are widely influenced by local wind regimes (Boucher, 1985).

The five open-slope stations of our study area are positioned between 140 and 1993 m water depth (Table 1). Station D (140 m depth) is situated at the boundary between surface waters (≤150 m depth) and the North Atlantic Central Water (Ogawa and Tauzin, 1973). According to CTD data performed in February 2003, temperature at 140 m depth is 12.5 °C and salinity is close to 35.50 PSU. Bottom water dissolved oxygen concentration measured in October 1997 is 220 μmol/l (Fontanier et al., 2002). Station B (550 m depth) is situated in the Northern Atlantic Central Waters (NACW). Bottom water has a salinity of 35.60 PSU and a temperature of about 11.0 °C and its dissolved oxygen concentration ranges from 205 to 221 μmol/l for the ten samplings performed between September 1997 and April 2000 (Fontanier et al., 2002, 2003). Station A (1012 m deep) is in the Mediterranean Waters (MW) that spread between 800 and 1200 m depth in our study area (Ogawa and Tauzin, 1973). The Mediterranean Waters are generally characterized by high salinities between 35.80 and 35.85 PSU and a minimum bottom water oxygenation value of 3.8 mL/l or 170 μmol/l (Le Floch, 1968). At station A, temperature is about 9.5 °C and salinity is about 35.75 PSU (Durrieu de Madron et al., 1999). In October 1997, bottom water dissolved oxygen concentration was 196 μmol/l (Fontanier et al., 2002). Station F (1264 m deep) is positioned in transitional waters resulting from the mixing between the MW and the upper layers Northern Atlantic Deep Waters (Ogawa and Tauzin, 1973). Data collected in the Cap Ferret Canyon close to the study area (Fig. 1) suggest that the temperature at Station F is about 8 °C and salinity would be close to 35.50 PSU (Durrieu de Madron et al., 1999). The oxygen concentration measured in January 1998 is 211 μmol/l (Fontanier et al., 2002). Station H (1993 m deep) is bathed by North Atlantic Deep Water (NADW) (senso lato). NADW originates from the Labrador Sea and Norwegian Sea and has been described off Brittany, north of our study area (Vangrieshem, 1985). Although Station H is geographically rather close to the Cap Ferret Canyon, it is an open-slope environment with muddy sediments. Water temperature is about 4 °C and salinity is close to 35.00 PSU. Bottom water oxygenation is 263 μmol/l in October 1998 (Fontanier et al., 2002).

2.2. Primary production

Primary production in the surface waters from the Bay of Biscay is dominated by an intense spring bloom (Tréguer et al., 1979; Laborde et al., 1999; Lampert, 2001). It starts at the end of boreal winter (March) and lasts for about two months until May (Laborde et al., 1999, Fontanier et al., 2003). Diatoms (*Chaetoceros* spp. and *Nitzschia* spp.) are the dominant phytoplankton components of spring blooms (Tréguer et al., 1979). In summer, coccolithophorid blooms are related to active up-welling cells at the French shelf-break (Fernandez et al., 1993; Antoine et al., 1996; Froidefond et al., 1996; Beaufort and Heussner, 1999). In autumn, a short fall bloom may occur, that is generally characterized by sub-surface primary production maxima consisting of dinoflagellates (*Gonyaulax* spp.) and small amounts of diatoms (Tréguer et al., 1979). However, Schiebel et al. (2001), who studied a BIOTRANS site (47°N/20°W), did not observe such a fall bloom. Phytoplankton biomass increases that are exceptionally observed in surface and sub-surface waters in boreal autumn could be due to mechanical mixing of residual summer deep chlorophyll production into the surface waters with very limited new phytoplankton production (personal communication, Joanna Waniek, 2004).

Only few quantitative data are available about the primary production in the study area. Tréguer et al. (1979) estimate a production between 0.4 and 1.9 g C/m^2/day for the spring bloom of 1973 in the Bay of Biscay. Primary production measurements during the autumn of 1972 indicate a bloom with values of 0.3–0.4 g C/m^2/day (Le Corre and Treguer, 1976). This range of primary production values agrees with recent data obtained in the Cap Ferret region during five ECOFER campaigns: 0.7–1.2 g C/m^2/day in spring (May 1990 and 1991) and 0.3 g C/m^2/day in autumn (October 1990; Laborde et al., 1999). Total annual primary production in the Bay of Biscay has been estimated between 145 and 170 g C/m^2/year (Laborde et al., 1999).

3. Materials and methods

At each station of the study area, cores were collected with a classical Barnett multitube corer (Barnett et al., 1984). At Station B, we studied 15 cores collected between October 1997 and April 2000. Live foraminif-

eral faunas of all investigated cores have already been described by Fontanier et al. (2002, 2003, in press). Most cores were sliced down to 10 cm depth for faunal analysis. Sampling and storage protocols are presented in Fontanier et al. (2002, 2003). All stable isotopic analyses were performed on foraminifera stained with Rose Bengal (Walton, 1952). Only completely stained specimens have been selected for isotopic measurements. The methodology of oxygenation measurements performed on bottom and pore waters is described in Chaillou et al. (2002).

Isotopic measurements were performed on individuals belonging to seven dominant taxa of the >150 μm size fraction: *C. pachydermus*, *H. elegans*, *U. mediterranea*, *U. peregrina, U. elongatastriata, M. barleeanus, Globobulimina* spp. Only two isotope measurements were successfully performed on benthic foraminifera belonging to the 63–150 μm size fraction. Table 2 gives the numbers of specimens analyzed and the stable isotopic composition as determined with a Finnigan MAT 251 isotope ratio gas mass spectrometer directly coupled to an automated carbonate preparation device (Kiel II) and calibrated via NIST 19 international standard to the VPDB (Vienna Pee Dee Belemnite) scale. All values are given in δ-notation versus VPDB (Table 2). The precision of the measurements at 1σ based on repeated analyses of an internal laboratory standard (Solnhofen limestone) over a one-year period was better than ± 0.08‰ and ± 0.06‰ for oxygen and carbon isotopes, respectively.

In May 2004, we collected samples from the water column with a Niskin bottle at different sites of the study area (Fig. 1) and sampled supernatant and clear water overlying the sediment–water interface from multitube cores at four of the stations (D, B, A, H). For determination of the stable carbon isotope ratio of DIC and the stable oxygen isotope ratio of water, water samples were filled into 50 mL glass vials, sealed with wax under 4 °C air temperature, and kept cool until further treatment on shore. The DIC samples

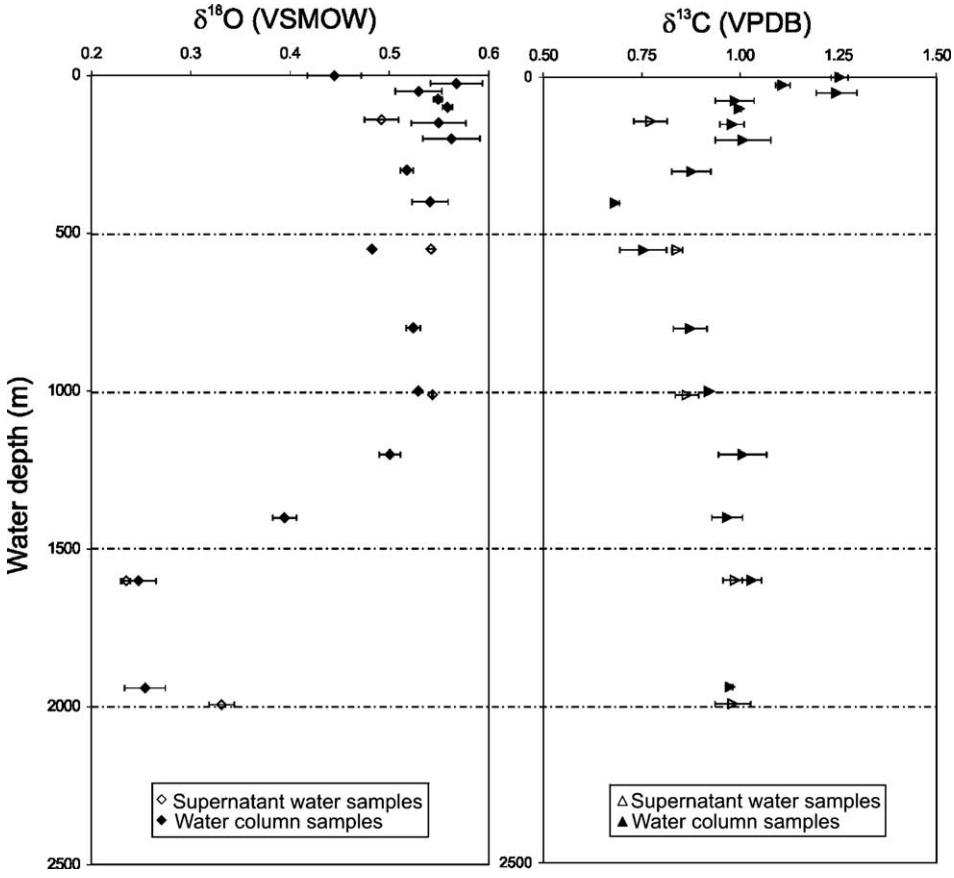

Fig. 2. δ^{18}O and δ^{13}C measurements for water samples collected during FORPROX II program (May 2004). We investigated seven stations (among which our five stations) to get water column and supernatant water samples. Empty diamonds and triangles correspond with supernatant water samples. Vertical bars represent standard errors calculated when several isotopic measurements are available for the same water sample.

additionally were poisoned with a saturated solution of $HgCl_2$. Isotopic values measured in supernatant water are considered to be representative for the bottom water at the stations. We systematically refer to these values in the Results and Discussion sections. At Station F (1264 m), however, we use the oxygen and carbon isotopic values from 1200 m depth, about 60 m above sea floor (Table 3, Fig. 2). DIC was extracted from seawater with phosphoric acid in an automatic preparation line (Finnegan Gasbench I) coupled online with a Finnigan MAT 252 mass spectrometer to determine its $^{13}C/^{12}C$ ratio. All samples were run at least in duplicate. Results are reported in δ-notation relative to the VPDB-scale with an external reproducibility of $\pm 0.1‰$ at 2σ. For the oxygen isotope determination of water, 7 mL of water were equilibrated in 13 mL headspace with CO_2 gas using an automated equilibration device, online connected with a Finnigan MAT Delta-S mass spectrometer. At least two replicates (including preparation and measurement) were run for each oxygen isotope determination. Results are reported in δ-notation relative to the SMOW scale with an external reproducibility of $\pm 0.03‰$ at 1σ.

The $\delta^{18}O$ of calcite in equilibrium with bottom water for a given temperature T (K) ($=\delta^{18}O_{e.c.}$) can be calculated with the following equation (McCorkle et al., 1997):

$$\delta^{18}O_{e.c.}(\mathrm{SMOW}) = \left(\exp^{\left(\left(2.7\times10^3/T^2\right)-\left(2.89/10^3\right)\right)} \times \left(\delta^{18}O_w + 10,000\right)\right) - 1000,$$

where $\delta^{18}O_w$ is the oxygen isotopic composition of bottom water relative to SMOW (Table 3). This equation is derived from the expression for the calcite–water fractionation factor determined by O'Neil et al. (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 the equation (Friedman and O'Neil, 1977):

$$\delta^{18}O\ (\mathrm{PDB}) = \left(0.97006 \times \delta^{18}O\ (\mathrm{SMOW})\right) - 29.94$$

For comparison we calculated $\delta^{18}O_{e.c.}$ using fractionation factors of Kim and O'Neil (1997):

$$\delta^{18}O_{e.c.}(\mathrm{SMOW}) = \left(\exp^{\left(\left(18.03\times10^3/T\right)-\left(32.42/10^3\right)\right)} \times \left(\delta^{18}O_w + 10000\right)\right) - 1000$$

In the study area, $\delta^{18}O_{e.c.}$ values calculated after Kim and O'Neil (1997) range from 0.83‰ to 2.61‰ along the bathymetric transect with an offset of about 0.5‰ to values calculated after Friedman and O'Neil (1977). After Kim and O'Neil (1997), the $\delta^{18}O$ values of *M. barleeanus* and *C. pachydermus* are close to $\delta^{18}O_{e.c.}$ values, whereas all other taxa exhibit very significant offsets (Fig. 3). In order to easily compare our data with the most relevant data sets of Rathburn et al. (1996), McCorkle et al. (1997), and Schmiedl et al. (2004), we here decided to use the methodology based on fractionation factors of Friedman and O'Neil (1977). However, it is important to keep in mind that, at low temperatures, there is a significant difference in calcu-

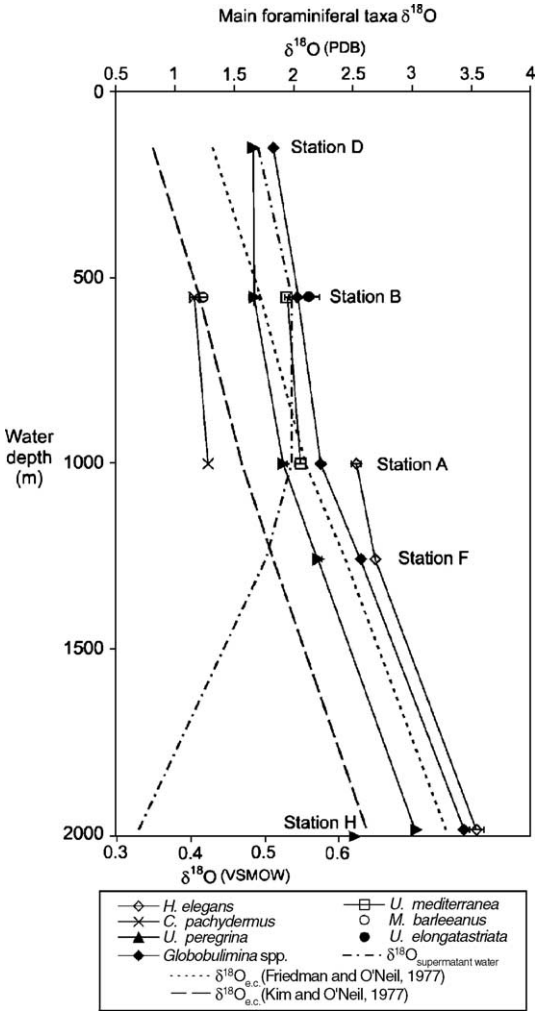

Fig. 3. $\delta^{18}O$ isotopic signatures of main foraminiferal taxa (*Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Uvigerina elongatastriata, Melonis barleeanus* and *Globobulimina* spp.) along our 5 stations bathymetric transect. The dotted line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with the method of McCorkle et al. (1997). The dashed line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with the method of Kim and O'Neil (1997) (see in Discussion). Vertical bars represent standard errors calculated when several isotopic measurements are available for the same station. The $\delta^{18}O$ of supernatant water in VSMOW scale are also presented.

lated $\delta^{18}O_{e.c.}$ values between the Friedman and O'Neil (1977) and Kim and O'Neil (1997) calculations. It is essential to be aware of this difference, when offsets between individual species of benthic foraminifera and equilibrium calcite are discussed.

4. Results

4.1. $\delta^{18}O$ and $\delta^{13}C_{DIC}$ in the water column

From the surface water to 1940 m depth, the $\delta^{18}O$ VSMOW of the water column shifts from +0.55‰ to +0.25‰ (Fig. 2). The calculated $\delta^{18}O_{e.c.}$ of calcite precipitated in equilibrium with bottom water $\delta^{18}O$ increases by almost 2‰, from +1.31‰ to +3.28‰ VPDB (Table 3). This $\delta^{18}O_{e.c.}$ gradient corresponds to a temperature decrease of 8.5 °C. Maximum $\delta^{13}C_{DIC}$ values of 1.25‰ are recorded at the surface; values then decrease until a minimum of 0.68‰ at about 400 m depth, and increase again to about 1.0‰ at 1200 to 2000 m water depth (Fig. 2). The $\delta^{13}C_{DIC}$ of bottom water at our stations ranges from +0.77‰ to +0.98‰ with the lowest value recorded at station D (140 m deep) in the upper Northern Central Atlantic Water (Fig. 2, Table 3). With the exception of the $\delta^{13}C_{DIC}$ obtained at station D, all isotopic values of waters directly overlying the sediment correspond fairly well with those obtained in the water column at the same water depth.

4.2. Benthic foraminiferal $\delta^{18}O$ values along the bathymetric transect

Foraminiferal taxa that were analyzed from two or more stations along the bathymetric transect show a systematic trend of increasing $\delta^{18}O$ values with increasing water depth (Fig. 3). *H. elegans* presents the heaviest $\delta^{18}O$ values of all taxa (Table 2, Fig. 3), which is systematically higher than calculated $\delta^{18}O_{e.c.}$ by about +0.32‰ ($\Delta\delta^{18}O = \delta^{18}O_{H.\ elegans} - \delta^{18}O_{e.c}$). From 140 to 1993 m depth, the $\delta^{18}O$ of *Globobulimina* spp. and *U. peregrina* increases by 1.60‰ and 1.37‰, respectively. The $\delta^{18}O$ values of *Globobulimina* spp. are close to $\delta^{18}O_{e.c.}$ (except at Station D). The average offset to equilibrium calcite ($\Delta\delta^{18}O$) is only +0.25‰. The $\delta^{18}O$ of *U. peregrina* is slightly lower than $\delta^{18}O_{e.c.}$ with a mean offset of −0.07 ‰, which is very close to calculated equilibrium with bottom water. Rather surprisingly, at station D, the $\delta^{18}O$ both of *Globobulimina* spp. and *U. peregrina* are higher than $\delta^{18}O_{e.c.}$. *U. mediterranea* $\delta^{18}O$ values deviate just slightly from equilibrium values ($\Delta\delta^{18}O$=+0.09‰). Measured at just one station (Station B), *U. elongatastriata* documents a positive deviation from $\delta^{18}O_{e.c.}$ ($\Delta\delta^{18}O$=+0.41‰). *M. barleeanus* and *C. pachydermus* have the lowest isotopic values of all species with $\Delta\delta^{18}O$ values of about −0.49‰ and −0.69‰ compared to $\delta^{18}O_{e.c.}$, respectively.

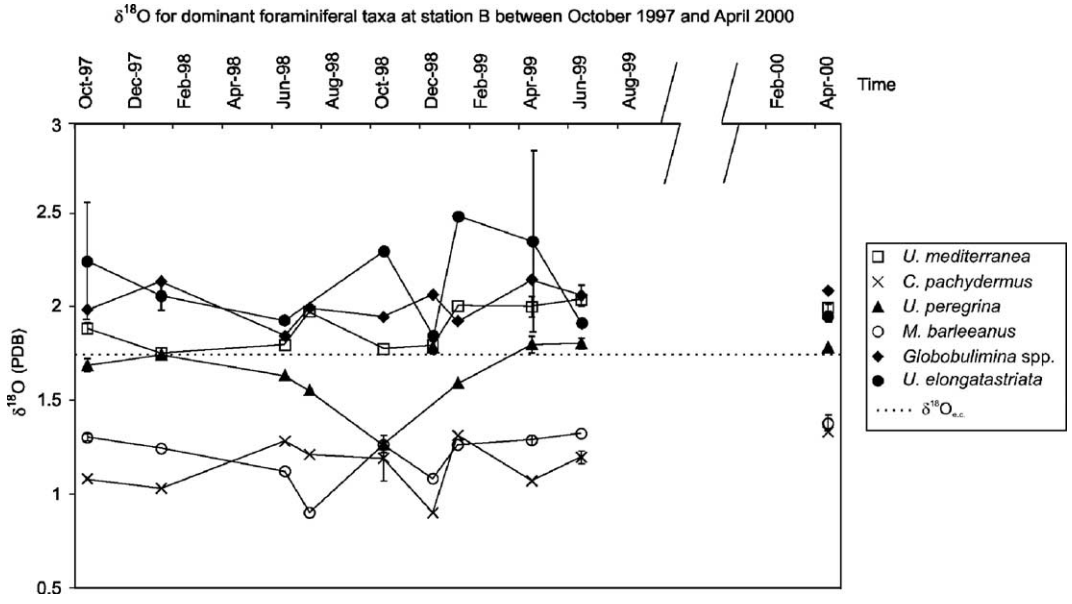

Fig. 4. Seasonal changes of the $\delta^{18}O$ for the main foraminiferal taxa (*Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Uvigerina elongatastriata, Melonis barleeanus* and *Globobulimina* spp.) at Station B (~550 m depth). Vertical bars represent standard errors calculated when duplicate cores and/or several isotopic measurements are available for the same sampling date. The dotted line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with the method of McCorkle et al. (1997).

4.3. Seasonal changes of benthic foraminiferal $\delta^{18}O$ values at Station B

Seasonal changes of the $\delta^{18}O$ values of *C. pachydermus*, *U. mediterranea*, *U. peregrina*, *M. barleeanus*, *U. elongatastriata* and *Globobulimina spp.* at Station B are depicted in Fig. 4. The $\delta^{18}O$ of all species appears to be rather constant over the two and a half years' sampling period. When compared to a putatively constant $\delta^{18}O_{e.c.}$ at Station B (1.73‰), we observe that *U. peregrina*, with the exception of October 1998, and to minor extent *U. mediterranea* $\delta^{18}O$ values are close to $\delta^{18}O_{e.c.}$ with average $\Delta\delta^{18}O$ values of $-0.07‰ \pm 0.05$ ‰ and $0.17‰ \pm 0.04‰$, respectively. *Globobulimina* spp. and *U. elongatastriata* have $\delta^{18}O$ values higher than equilibrium calcite with an average offset of $0.28‰ \pm 0.03‰$ and $0.43‰ \pm 0.12‰$, respectively. *M. barleeanus* and *C. pachydermus* have isotope values lower than $\delta^{18}O_{e.c.}$ with offsets of $-0.52‰ \pm 0.04‰$ and $-0.57‰ \pm 0.04‰$, respectively. Note the rather strong variability of $\delta^{18}O$ values of *U. elongatastriata* with a standard error of 0.12‰.

4.4. Benthic foraminiferal $\delta^{13}C$ values along the bathymetric transect

The $\delta^{13}C$ values of *H. elegans*, *C. pachydermus*, *U. mediterreanea and U. peregrina* increase with increasing water depth (Fig. 5). $\delta^{13}C$ values of *H. elegans* range from 1.77‰ to 1.84‰. The $\delta^{13}C$ of *C. pachydermus* and *U. mediterreanea* shifts from +0.30‰ to +0.56‰, and from −0.53‰ to −0.15‰, respectively, between 550 and 1000 m water depth. Along the complete bathymetric transect *U. peregrina* $\delta^{13}C$ decreases from −1.78‰ to −0.62‰. Only *Globobulimina* spp. exhibits a different trend. Its $\delta^{13}C$ increases from −2.16‰ to −1.16‰ between 140 and 1000 m depth and then decreases again progressively to −2.28‰ down to 1993 m. For most taxa there is no constant offset between their $\delta^{13}C$ isotopic signature and the bottom water $\delta^{13}C_{DIC.}$ Only the difference between the isotopic signature of *H. elegans* and $\delta^{13}C_{DIC}$ is more or less constant with an average value of $+0.85‰ \pm 0.04‰$. From 550 to 1000 m depth, the $\Delta\delta^{13}C$ between *C. pachydermus* and bottom water $\delta^{13}C_{DIC}$ and between *U. mediterranea* and bottom water $\delta^{13}C_{DIC}$ decrease significantly. A similar tendency can be observed for $\Delta\delta^{13}C$ between *U. peregrina* and bottom water $\delta^{13}C_{DIC}$ along the whole bathymetric transect, which decreases continuously from −1.61‰ at Station H (~2000 m) to about −2.55‰ at Station D (140 m). For *Globobulimina* spp., $\Delta\delta^{13}C_{Globobulimiona\ spp.} - \delta^{13}C_{DIC}$ is −2.93‰ at Station D and 3.26‰ at Station H, and is lowest at Station A (−2.03‰).

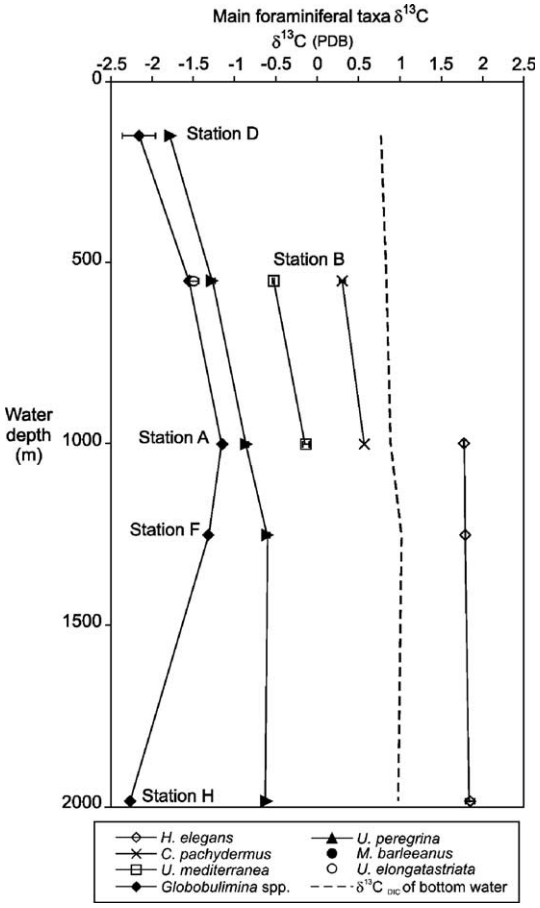

Fig. 5. $\delta^{13}C$ isotopic signatures of the main foraminiferal taxa (*Hoeglundina elegans*, *Cibicidoides pachydermus*, *Uvigerina peregrina*, *Uvigerina mediterranea*, *Uvigerina elongatastriata*, *Melonis barleeanus* and *Globobulimina* spp.) along our 5 stations' bathymetric transect. The dotted 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.

4.5. Seasonal changes of $\delta^{13}C$ signatures of foraminiferal taxa at station B

The $\delta^{13}C$ of all taxa appears very stable over the 2.5 years sampling period (Fig. 6). The offsets between foraminiferal isotopic signatures and $\delta^{13}C_{DIC}$ are very constant. Average $\Delta\delta^{13}C$ is lowest for *C. pachydermus* ($-0.55‰ \pm 0.04‰$) and attains values of $-1.39‰ \pm 0.04‰$ for *U. mediterranea*, $-2.11‰ \pm 0.05‰$, $-2.34‰ \pm 0.03‰$, $-2.37‰ \pm 0.04‰$ and $-2.40‰ \pm 0.03‰$ for *U. peregrina*, *U. elongatastriata, M. barleeanus* and *Globobulimina* spp., respectively.

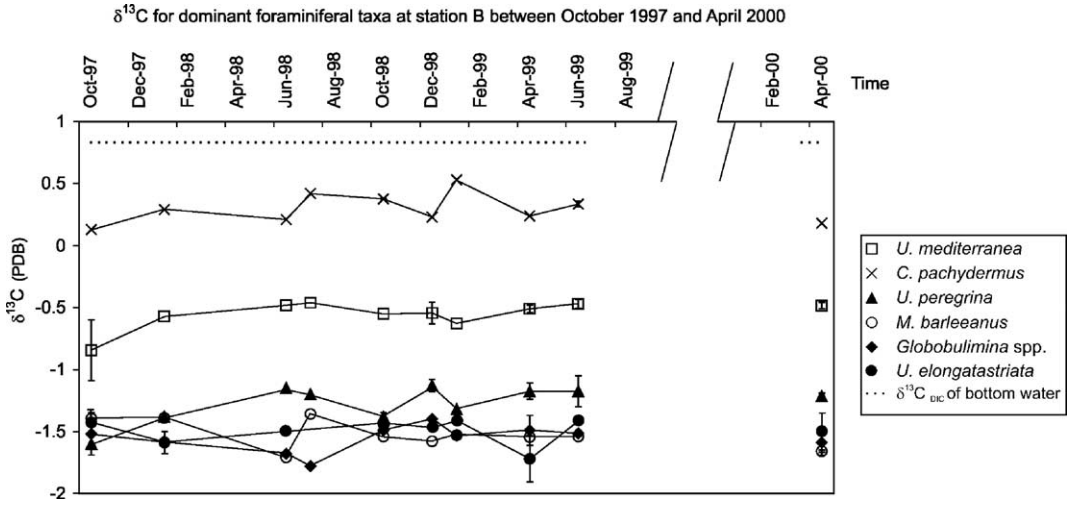

Fig. 6. Seasonal changes of the $\delta^{13}C$ for the main foraminiferal taxa (*Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Uvigerina elongatastriata, Melonis barleeanus* and *Globobulimina* spp.) at Station B (~550 m depth). Vertical bars represent standard errors calculated when duplicate cores and several isotopic measurements are available for the same sampling date. Dotted line represents the $\delta^{13}C$ of dissolved inorganic carbon of bottom water. At first approximation, the $\delta^{13}C$ of bottom water is supposed to be constant throughout the years of investigation ($\delta^{13}C_{DIC}$ (PDB)=~0.84‰).

4.6. $\delta^{18}O$ and $\delta^{13}O$ changes in relation to the vertical distribution of foraminiferal taxa

Fig. 7a–b shows the foraminiferal isotopic signatures at stations A and B in relation to the sediment interval where the live foraminiferal individuals have been sampled. We also present the density (number of individuals per 50 cc) for the analyzed foraminiferal taxa, to show the foraminiferal vertical distribution in relation to the sediment–water interface and the zero oxygen boundary. The description of foraminiferal microhabitats is more fully presented in Fontanier et al. (2002, 2003). *C. pachydermus* and *H. elegans* live in very shallow infaunal and oxic microhabitats close to the sediment–water interface (Fig. 7a–b). *U. mediterranea* and *U. peregrina* occupy shallow infaunal niches. *M. barleeanus* and *U. elongastriata* thrive in intermediate infaunal niches just above the zero oxygen boundary (Fig. 7a). *Globobulimina* spp. is a deep infaunal taxon that preferentially appears around and below the zero oxygen boundary (Fig. 7a–b). To sum up, Table 4 presents average living depth (ALD) for all taxa for the 5 stations of our bathymetric transect. Methods of calculation of ALD and results are in Fontanier et al. (2002, 2003).

At station B, where the most complete isotopic data set is available, most investigated taxa do not exhibit significant changes of $\delta^{18}O$ and $\delta^{13}C$ with depth in the sediment. For example, *U. mediterranea* shows surprisingly stable $\delta^{18}O$ and $\delta^{13}C$ values with depth (Fig. 7a). Only *U. elongatastriata* shows some $\delta^{18}O$ values characterized by high standard errors. At Station A, we can observe the same pattern, although isotopic measurements are less numerous than at Station B. If considering all stations, deep and intermediate infaunal taxa such as *Globobulimina* spp., *M. barleeanus* and *U. elongatastriata* exhibit systematically lower $\delta^{13}C$ values than more superficially living taxa. Very shallow infaunal *H. elegans* and *C. pachydermus* show heaviest values. *Uvigerina mediterreanea* and *U. peregrina* have intermediate $\delta^{13}C$ values. There are no obvious changes in the $\delta^{18}O$ signature of foraminiferal taxa in relation to microhabitat preferences.

5. Discussion

5.1. Intergeneric $\delta^{18}O$ variability along the bathymetric transect

All of the calcitic benthic foraminiferal taxa investigated in this study, i.e. *C. pachydermus*, *Uvigerina mediterreanea*, *U. peregrina*, and *Globobulimina* spp., biomineralise their test close to, or with a constant offset to isotopic equilibrium values, as calculated by using Friedman and O'Neil (1977) fractionation factors. This is very clear when we compare the $\delta^{18}O$ of *U. peregrina* and *Globobulimina* spp. with equilibrium calcite $\delta^{18}O$ ($\delta^{18}O_{e.c.}$) along the bathymetric transect (Fig. 3). The $\Delta\delta^{18}O$ values of taxa, i.e. the difference between taxon specific $\delta^{18}O$ and $\delta^{18}O_{e.c.}$ is constant

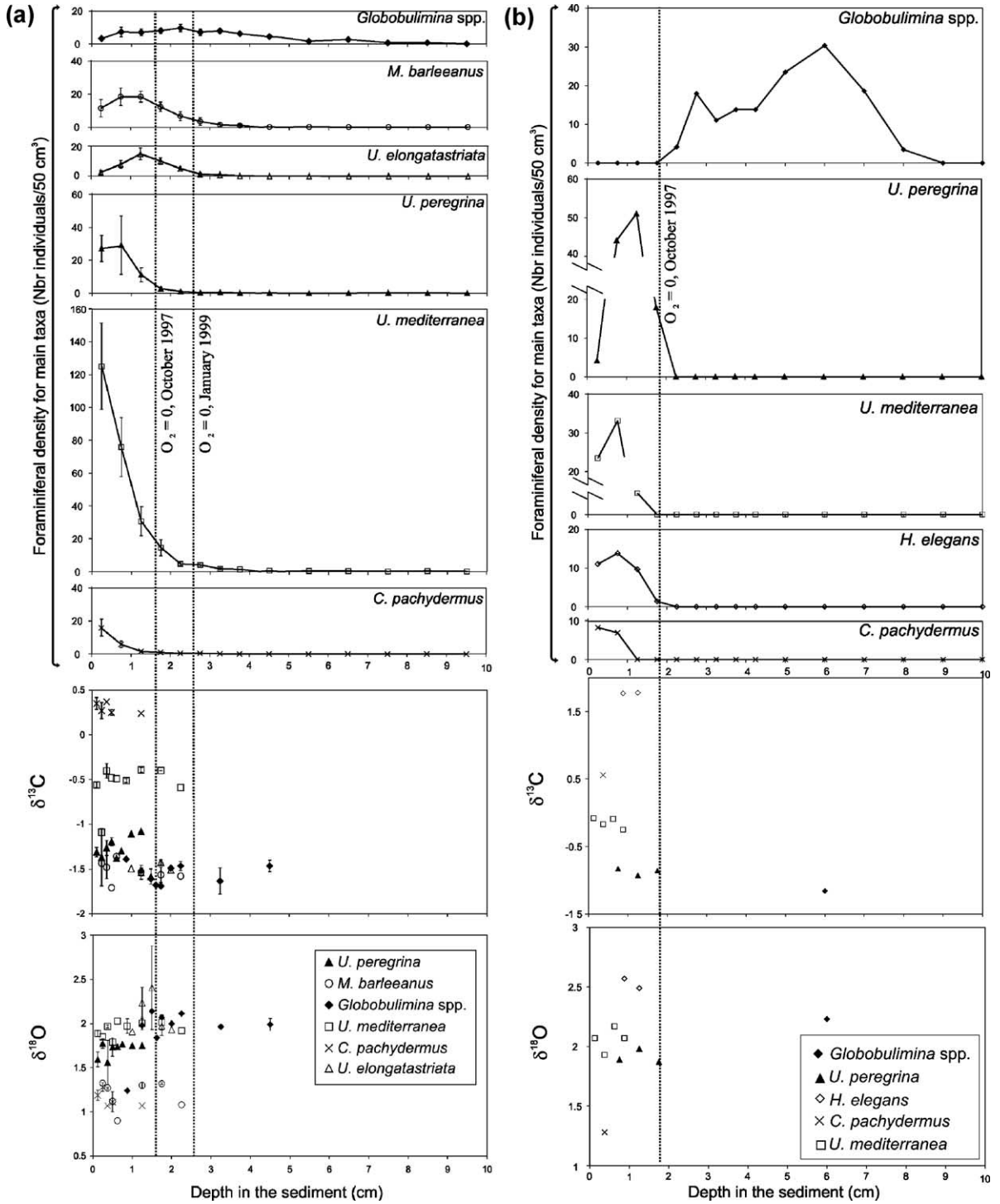

Fig. 7. a. $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the main foraminiferal taxa at Station B. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. b. Same, station A. The dotted line depicts the zero oxygen boundary in the sediment. For station B, All values for foraminiferal densities are the average of 12 cores. The two dotted lines indicating the zero oxygen boundary represent the minimum and maximum values observed during the 12 samplings. For isotopic values, vertical bars represent standard errors calculated when several isotopic measurements for the same depth interval are available.

Table 4
Average living depth (ALD_{10}) calculated for all present foraminiferal taxa along the bathymetric transect

Taxa	Stations, ALD_{10}					Microhabitat
	Station D	Station B	Station A	Station F	Station H	
Cibicidoides pachydermus		0.5	0.4		1.4	SI
Globobulimina spp.	2.2	2.8	4.7		6.1	DI
Hoeglundina elegans			0.8	0.5	0.6	SI
Uvigerina elongatastriata		1.5				II
Melonis barleeanus		1.3	1.7	1.4		II
Uvigerina mediterranea		0.8	0.6			SI
Uvigerina peregrina	0.4	0.8	1.1	0.9	0.7	SI/II
Oxygen penetration depth (cm)	0.8	1.7–2.6	2	6.4	6.3	

Values at Stations D, A, F and H are presented in Fontanier et al. (2002). At station B, ALD are average weighed values for 13 cores (Fontanier et al., 2003).

with increasing water depth, just reflecting the increasing thermodynamic fractionation with decreasing temperatures. However, it is also evident that significant offsets exist between $\delta^{18}O$ values of the different taxa. So-called vital effects may explain these constant differences (e.g. Urey et al., 1951; McCorkle et al., 1990; 1997). On the left-hand side of Fig. 8, we present the average $\Delta\delta^{18}O$ of each taxon compared with data from

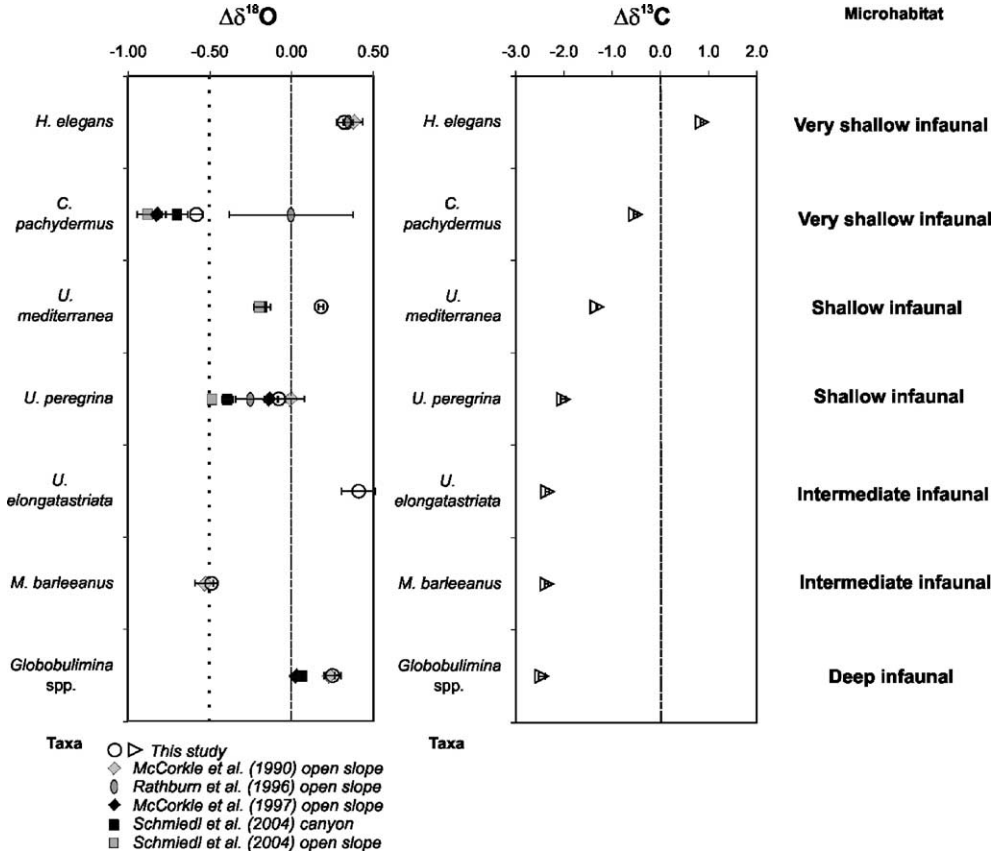

Fig. 8. $\Delta\delta^{18}O$ between foraminiferal taxa and $\delta^{18}O_{e.c.}$ ($\Delta\delta^{18}O = \delta^{18}O_{benthic\ foraminifera} - \delta^{18}O_{e.c.}$). $\Delta\delta^{13}C$ between foraminiferal taxa and $\delta^{13}C_{DIC}$ in our study area ($\Delta\delta^{13}C = \delta^{13}C_{benthic\ foraminifera} - \delta^{13}C_{DIC}$). The microhabitat description of the seven foraminiferal taxa is added on the right side of the figure. See Fontanier et al. (2002; 2003) for complementary explanation about foraminiferal microhabitat. Vertical bars represent standard errors calculated on the basis of 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 et al. (1997). The dotted line represents the putative $\Delta\delta^{18}O$ between foraminiferal taxa and $\delta^{18}O_{e.c.}$ calculated with the method of Kim and O'Neil (1997), which is equal to zero (see in Discussion). We have added $\Delta\delta^{18}O$ from McCorkle et al. (1990, 1997) and Schmiedl et al. (2004).

McCorkle et al. (1990, 1997), Rathburn et al. (1996) and Schmiedl et al. (2004). Readers should keep in mind that some analyses from Rathburn et al. (1996) and McCorkle et al. (1990, 1997) were conducted on single individuals or very low numbers of specimens than were analyzed for this study. *U. peregrina* deviates by just −0.08‰ from $\delta^{18}O_{e.c.}$. This offset is lower than −0.25‰ as determined by Rathburn et al. (1996) or the mean $\Delta\delta^{18}O$ of −0.40‰ determined by Schmiedl et al. (2004) but in the range of mean $\Delta\delta^{18}O$ values between −0.02‰ and −0.12‰ determined by McCorkle et al. (1990; 1997). The $\Delta\delta^{18}O$ of *U. mediterranea* is about +0.18‰, which differs from the mean value of −0.18‰ determined by Schmiedl et al. (2004) in the western Mediterranean Sea. The $\delta^{18}O$ of *Globobulimina* spp. is slightly higher than bottom water $\delta^{18}O_{e.c.}$ with an average $\Delta\delta^{18}O$ of +0.25‰, a value close to +0.22‰ as presented by McCorkle et al. (1990) but higher than +0.06‰ as given by Schmiedl et al. (2004). Schmiedl et al. (2004) consider *Globobulimina* spp. as calcifying close to equilibrium with bottom water $\delta^{18}O$, which is not the case in this study. *M. barleeanus* shows a significant shift of about −0.49‰, which is very close to an average value of −0.53‰ measured by McCorkle et al. (1990). *C. pachydermus* $\Delta\delta^{18}O$ values are −0.58‰. This shift is lower than the $\Delta\delta^{18}O$ average value determined by McCorkle et al. (1997) (~−0.83‰) and Schmiedl et al. (2004) (−0.70‰, −0.88‰). The value of -0.01 ± 0.39 determined by Rathburn et al. (1996) clearly deviates for all other observations.

5.2. Interspecific $\delta^{18}O$ variability related to microhabitat

The $\delta^{18}O$ of taxa here investigated do not vary systematically in relation to sediment depth. This is in agreement with observations by Rathburn et al. (1996) who analyzed live benthic foraminifera from Sulu and South China Seas. Moreover, the different microhabitat preferences of the species investigated do not seem to induce any systematic impact on the stable oxygen isotopes in their tests. The $\Delta\delta^{18}O$ of intermediate infaunal *M. barleeanus* is close to the $\Delta\delta^{18}O$ of shallow infaunal *C. pachydermus*, whereas the $\Delta\delta^{18}O$ of shallow infaunal *U. peregrina* is lower. Therefore, our data do not confirm observations of Schmiedl et al. (2004), who describe $\delta^{18}O$ offsets between taxa directly related to microhabitat preferences of foraminifera, with heavy values, close to equilibrium calcite, for deep infaunal taxa and increasingly lighter values for intermediate to shallow infaunal species. This tendency is probably partially due to the fact that Schmiedl et al. (2004) studied only five different taxa. Of these taxa, *U. peregrina* and *U. mediterranea* occupy roughly the same microhabitat, whereas the two *Globobulimina* species studied by Schmiedl et al. (2004) have an identical $\delta^{18}O$. In this study we, in addition, analyzed the two intermediate infaunal species *U. elongatastriata* and *M. barleeanus* that both occupy a microhabitat between that of *Uvigerina* and *Globobulimina* species. The high value of *U. elongatastriata* and consistently low values of *M. barleeanus* clearly show that the pattern of increasing $\delta^{18}O$ with microhabitat depth suggested by Schmiedl et al. (2004) cannot be retained. There is no apparent systematic relationship between $\delta^{18}O$ and microhabitat depth.

5.3. Intrageneric $\delta^{18}O$ variability

It is noticeable that significant $\delta^{18}O$ differences exist between species belonging to the same genus. This is clearly the case for uvigerinids (*U. mediterranea*, *U. peregrina*, *U. elongatastriata*). For example, we record an average shift of about 0.25‰ between *U. mediterranea* and *U. peregrina*. This difference cannot be explained by a putative microhabitat effect since both taxa occupy roughly the same sediment depth interval. The data rather confirm the suggestion of Woodruff et al. (1980) that the use of *Uvigerina* spp. for oxygen isotope stratigraphic framework and paleoceanographic studies without a precise identification at the species-level and its according vital effect is irrelevant and can induce significant errors. In Table 5, we propose correction factors that can be used to adjust isotopic data for our foraminiferal taxa in comparison to *U. peregrina*, which constructs its test in close equilibrium with bottom water $\delta^{18}O$, as calculated according to Friedman and O'Neil (1977).

Table 5
$\Delta\delta^{18}O$ between *Uvigerina peregrina* and other dominant foraminiferal taxa in our study area

$\Delta\delta^{18}O$ between *Uvigerina peregrina* and XXX	Correction factor
Hoeglundina elegans	−0.40
Cibicidoides pachydermus	0.50
Uvigerina mediterranea	−0.26
Uvigerina elongatastriata	−0.49
Melonis barleeanus	0.41
Globobulimina spp.	−0.33

$\Delta\delta^{18}O$ values may be used as correcting factors for future paleoceanographic studies in order to construct, a complete and improve oxygen isotope stratigraphic frameworks.

5.4. Interspecific $\delta^{13}C$ variability related to microhabitat

Pore water $\delta^{13}C_{DIC}$ within the sediment decreases from a value close to bottom water $\delta^{13}C_{DIC}$ at the sediment–water interface to much lighter values in deeper sediments. This is a result of progressive degradation of organic matter buried in deeper sediments and the related release of ^{12}C by aerobic and anaerobic bacterial degradation. (e.g. Grossman, 1984a, 1987; McCorkle et al., 1985, 1990; McCorkle and Emerson, 1988; Sackett, 1989). In this study, low $\delta^{13}C$ values of taxa living deeper in the sediment further confirm that infaunal benthic foraminifera record the $\delta^{13}C_{DIC}$ of pore waters (e.g. Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1987; McCorkle et al., 1990, 1997; Rathburn et al., 1996; Mackensen and Licari, 2004; Schmiedl et al., 2004; Holsten et al., 2004). So-called microhabitat effects refer to carbonate precipitation in isotopically distinct growth environments. Because *C. pachydermus* and *U. mediterranea* live, respectively, in very shallow and shallow infaunal niches (e.g. Fontanier et al., 2002, 2003), both species have $\delta^{13}C$ values close to bottom water $\delta^{13}C_{DIC}$ (Fig. 8). Heavier values of very shallow infaunal *C. pachyderma* (=*C. pachydermus*) in comparison to other shallow and deep infaunal species are also observed in cores from the Sulu and China Seas by Rathburn et al. (1996) as well as in material from the western Mediterranean Sea by Schmiedl et al. (2004). The same is found in foraminiferal faunas from the North Carolina continental margin where *C. pachyderma* has a higher $\delta^{13}C$ value than shallow infaunal *U. peregrina* and deep infaunal *M. barleeanum* and *Globobulimina* spp. (McCorkle et al., 1990, 1997). The $\delta^{13}C$ of *U. peregrina* is surprising since it has a relatively light $\delta^{13}C$ value despite its shallow infaunal microhabitat close to *U. mediterranea* (Table 4). The offset between both taxa equals 0.70‰, which is the same value as determined by Schmiedl et al. (2004). Several phenomena can explain this offset. First, *U. peregrina* may occupy a microhabitat slightly deeper than that of *U. mediterranea* (Fontanier et al., 2002; Schmiedl et al., 2004). Second, in spite of a rather similar microhabitat, *U. peregrina* may calcify deeper in the sediment than *U. mediterranea*. Next, *U. peregrina* may biomineralise a large part of its test in eutrophic periods when its shallow infaunal niche is temporarily enriched in ^{12}C by the rapid degradation of phytodetritus in a shallow bioturbation zone. *U. peregrina* is indeed described in the Bay of Biscay as a very reactive taxon that appears to preferentially reproduce and show rapid growth during eutrophic periods (spring and autumn bloom) (Fontanier et al., 2003, in press). And finally, it is also feasible that complex vital effects are responsible for the different $\delta^{13}C$ signature of both *Uvigerina* species, as has been suggested earlier for other taxa (e.g. Rathburn et al., 1996; Schmiedl et al., 2004). *M. barleeanus, U. elongatastriata* and *Globobulimina* spp., which generally occupy intermediate and deep infaunal microhabitats, close to the zero oxygen boundary (Fontanier et al., 2002, 2003), have generally the lowest $\delta^{13}C$ of all our species (Fig. 8). A very low $\delta^{13}C$ of deep infaunal *Globobulimina* species has been observed in numerous other studies (e.g. Grossman, 1984a; Grossman, 1987; McCorkle et al., 1990, 1997; Schmiedl et al., 2004).

At stations A and B, all investigated species show rather constant $\delta^{13}C$ values throughout the depth interval in the sediment where they were found (Fig. 7a–b). It is conceivable that each taxon might record a pore water $\delta^{13}C_{DIC}$ of a rather narrow sediment layer where it performs the major part of its metabolic activity and related calcification. However, it can also be envisaged that the final isotopic signal is a composite of the life history of the individual and presents an average value of a much wider depth interval in which the foraminiferal specimen lives and calcifies (Rathburn et al., 1996; Mackensen and Licari, 2004; Holsten et al., 2004).

5.5. Interspecific $\delta^{13}C$ variability along the bathymetric transect

Along the bathymetric transect investigated in this study there appears to be a relation between the $\Delta\delta^{13}C$ of *U. peregrina* ($\Delta\delta^{13}C = \delta^{13}C_{benthic\ foraminifera} - \delta^{13}C_{DIC}$) and the organic carbon flux to the sea floor (Fig. 9a). We used the equation of Berger and Wefer (1990), improved by Herguera (1992) to estimate the exported organic carbon supplies (Jz) (Table 1). The estimated organic matter fluxes decrease with water depth, probably causing a significant decrease with water depth of the intensity of organic degradation on and within the topmost oxic sediments. As a major consequence, the oxygen zero boundary in the sediment deepens along the bathymetric transect (Fontanier et al., 2002). This should result in steep pore water $\delta^{13}C_{DIC}$ profiles in shallow environments and much less marked $\delta^{13}C_{DIC}$ profiles in deeper and more oligotrophic settings (McCorkle et al., 1985, 1997; McCorkle and Emerson, 1988; Loubere et al., 1995). In other words, the organic carbon flux at the sediment–water interface should play a fundamental role controlling the shallow infaunal foraminiferal $\delta^{13}C$, since it may induce drastic pore water $\delta^{13}C_{DIC}$ decreases in the upper sediment layers

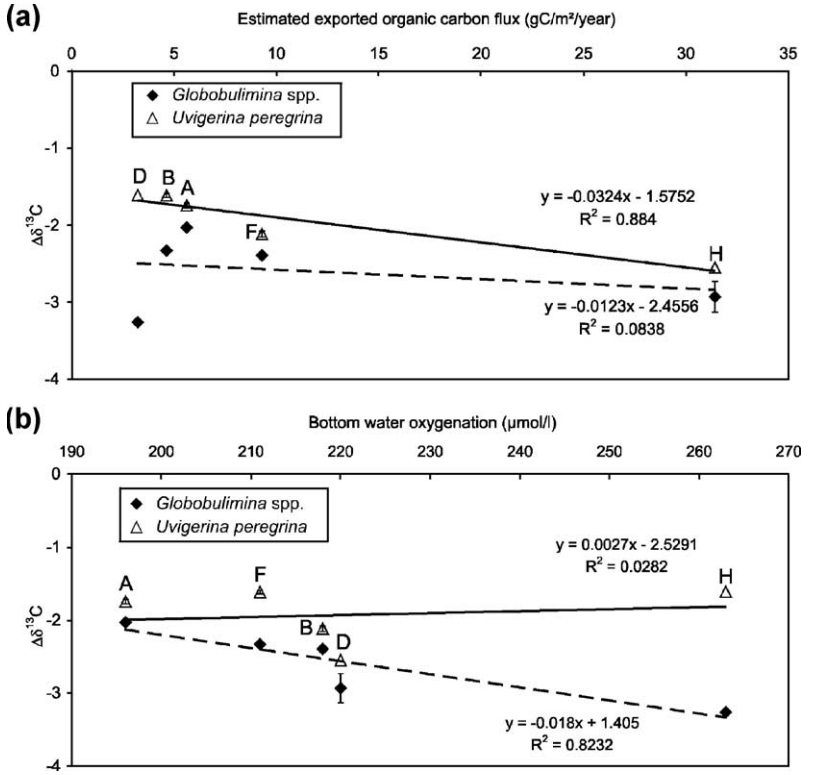

Fig. 9. a. $\Delta\delta^{13}C$ between the $\delta^{13}C$ of *Uvigerina peregrina* and the $\delta^{13}C_{DIC}$ bottom water and $\Delta\delta^{13}C$ between the $\delta^{13}C$ of *Globobulimina* spp. and the $\delta^{13}C_{DIC}$ bottom water versus exported organic carbon flux (Jz). b. $\Delta\delta^{13}C$ between the $\delta^{13}C$ of *U. peregrina* and the $\delta^{13}C_{DIC}$ bottom water and $\Delta\delta^{13}C$ between the $\delta^{13}C$ of *Globobulimina* spp. and the $\delta^{13}C_{DIC}$ bottom water versus bottom water oxygenation. Vertical bars represent standard errors calculated when we have duplicate cores at the same station and several isotopic measurements for the same depth interval are available. Simple linear regressions were systematically performed. For each regression, the equation and the "r^2" are presented.

in areas with high labile organic matter supply, and much less marked pore water $\delta^{13}C_{DIC}$ depletion in the topmost sediment layers in areas with low organic matter supply.

On the contrary, the $\Delta\delta^{13}C$ of *Globobulimina* spp. appears not to be correlated with Jz (Fig. 9a). For this taxon, a correlation with bottom water oxygenation can be observed (Fig. 9b). Such a relation between the $\delta^{13}C$ of *Globobulimina* spp. and bottom water oxygenation has been shown by McCorkle et al. (1990, 1997). The data presented here certainly need supplementary data integrating a larger range of bottom oxygenation measurements and *Globobulimina* spp. $\delta^{13}C$. However, these first results agree rather well with the data of McCorkle et al. (1997). It appears that bottom water oxygenation influences the intensity of organic matter degradation in the surface sediments down to the zero oxygen boundary, with a more intensive oxic degradation in sediments underlying better oxygenated bottom waters. Such a dependency would apparently also influence the related pore water $\delta^{13}C_{DIC}$ values at the depth of maximal oxygen penetration. A slight increase of bottom water oxygenation at the sediment–water interface could result in an enhanced ^{12}C release into the "more" oxygenated superficial sediment and at the upper part of dysoxic layers. This might finally induce a stronger depletion of pore water $\delta^{13}C_{DIC}$ at the zero oxygen boundary where *Globobulimina* spp. is commonly found.

Fig. 10 shows the vertical distribution of *U. peregrina* and *Globobulimina* spp. in cores collected along our bathymetric transect, the average $\delta^{13}C$ signature of both taxa and the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. for each station. Both foraminiferal taxa are supposed to calcify their test in close equilibrium with pore water $\delta^{13}C$ of the sediment interval in which they preferentially live. *U. peregrina* thrives in shallow infaunal niches in the first centimeter of the sediment whereas *Globobulimina* spp. lives around and below the zero oxygen boundary (Table 4, Fig. 7a–b). As previously shown, the $\delta^{13}C$ of *U. peregrina* increases with water depth as a result of the decrease of organic matter flux to the sediment surface. At Station D, where the exported organic carbon input is

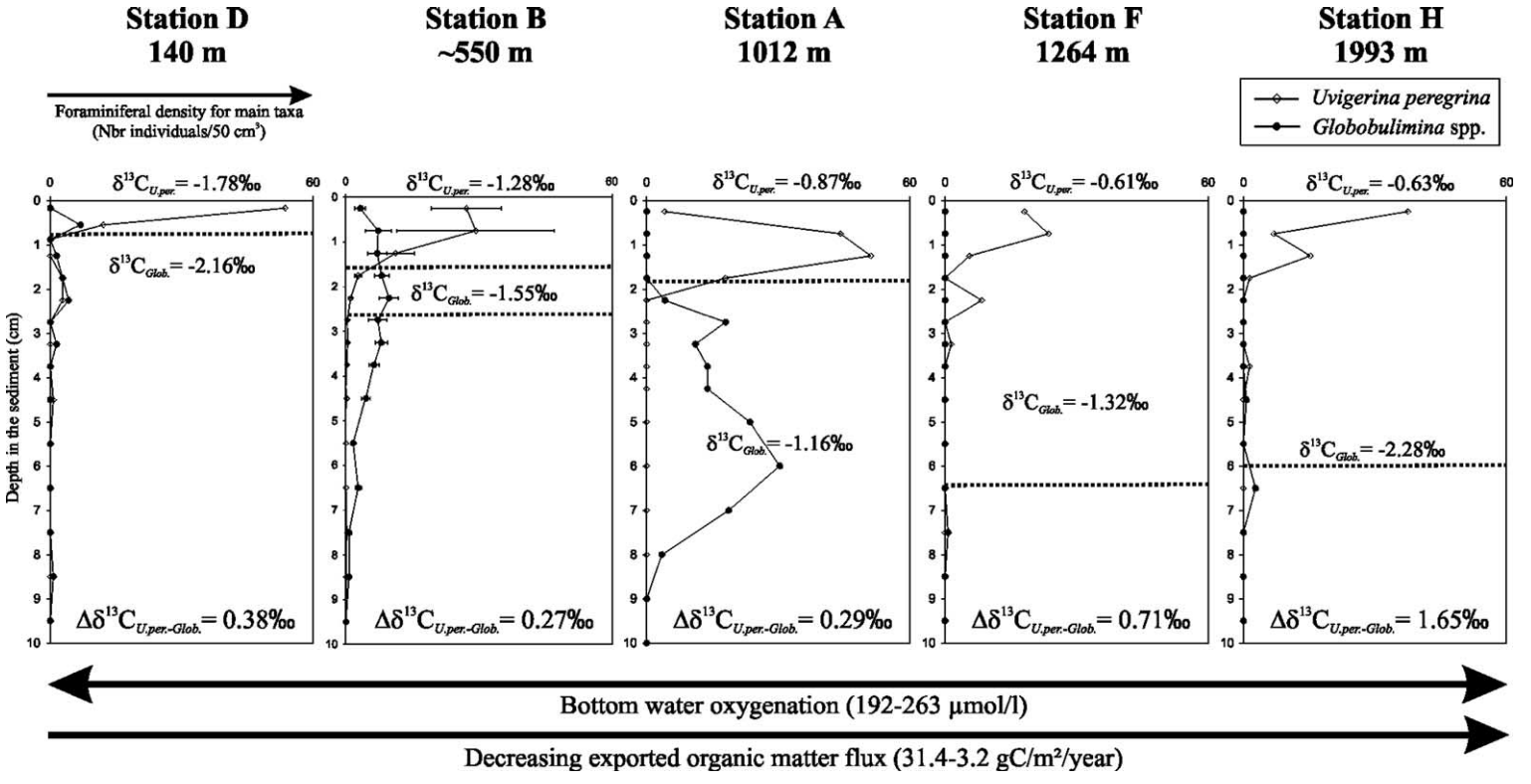

Fig. 10. Synthetic scheme showing the carbon isotopic signatures of *Globobulimina* spp. and *Uvigerina peregrina* along a bathymetric transect in the Bay of Biscay. Both foraminiferal taxa are supposed to record pore water $\delta^{13}C_{DIC}$ of the sediment interval where they preferentially live (microhabitat effect) (see text for further explanation). The vertical density profiles of *Globobulimina* spp. and *U. peregrina* are added. Foraminiferal densities are expressed in number of individuals per 50 cm^3. The $\delta^{13}C$ of *U. peregrina* and *Globobulimina* spp. and the $\Delta\delta^{13}C$ between both taxa are presented for the 5 stations.

much higher than at all other stations, $\delta^{13}C$ depletion is strong in the first centimeter as a direct result of the elevated release of ^{12}C-enriched CO_2 by aerobic degradation. Downslope, pore water $\delta^{13}C$ depletion in the first centimeter of sediment will become weaker as a result of decreasing organic carbon flux. Therefore, in oligotrophic areas, the $\delta^{13}C$ profile of pore water should be much less steep in the uppermost sediment in comparison with eutrophic and shallow environments. Such a scenario, which would need to be confirmed by modeling the relationship between exported organic matter flux and $\delta^{13}C$ pore water, can explain why the $\Delta\delta^{13}C$ between shallow infaunal *U. peregrina* and deep infaunal *Globobulimina* spp. is minimal in eutrophic areas, but shows an important increase towards more oligotrophic areas. If true, this could mean that the $\Delta\delta^{13}C$ can give us information about the importance of organic matter degradation in the topmost oxygenated sediment layer (McCorkle et al., 1997; Mackensen and Licari, 2004; Schmiedl et al., 2004; Holsten et al., 2004).

5.6. Paleoceanographic applications

In view of the relation between $\Delta\delta^{13}C$ of shallow infaunal *U. peregrina* and the exported organic carbon flux at our well-oxygenated stations, it appears that the isotopic chemistry of foraminiferal tests could be used to reconstruct benthic carbon oxidation rate in the sediment and related paleoproductivity from surface waters on the basis of a past sedimentary record. The use of $\Delta\delta^{13}C$ between *U. peregrina* and an epifaunal taxon that would biomineralise its test close to bottom water $\delta^{13}C$ would be a good proxy to estimate the variation of exported organic carbon paleoflux ("paleo-Jz") to the sediment–water interface (e.g. McCorkle et al., 1997). *C. wuellerstorfi*, which commonly is regarded as a preferentially epifaunal species, is widely used as proxy of bottom water $\delta^{13}C$. However, several papers show that *C. wuellerstorfi* is not exclusively living at the sediment surface, but spreads also in shallow infaunal microhabitats (e.g. Jorissen et al., 1998; Wollenburg and Mackensen, 1998). In addition its $\delta^{13}C$ values may be influenced by pulsed seasonally high organic matter fluxes (Mackensen et al., 1993). Similar to the suggestion of using bolivinids from the California Continental Borderland (Holsten et al., 2004), we propose the use of $\delta^{13}C$ differences between *U. peregrina* and *Globobulimina* spp. as a proxy of the rate of aerobic remineralisation of organic matter in the top sediment of well-oxygenated basins. If infaunal foraminifera calcify their test in accordance with their preferred microhabitat and living depth, the use of other taxa, such as intermediate infaunal and purely epifaunal species, could help to reconstruct paleo-profiles of pore water $\delta^{13}C_{DIC}$ in oxygenated sediment, and to better understand the fate of organic carbon transported to the sea floor in the past.

5.7. Seasonal changes of benthic foraminifera $\delta^{13}C$ and $\delta^{18}O$

In the present data set, samples from October 1997, April 1999, June 1999 and April 2000 have been collected during or shortly after phytoplankton bloom events (Fontanier et al., 2003, in press). High benthic foraminiferal standing stocks dominated by reactive and/or opportunistic taxa are recorded in shallow infaunal microhabitat of the cores collected at those sampling dates at Station B (550 m) and Station A (1000 m) (Fontanier et al., 2003, in press). *U. peregrina* and *U. mediterranea* are the most abundant species in these eutrophic periods in the >150 μm fraction, whereas *E. exigua* and *N. pusillus* dominate the 63–150 μm fraction as strictly opportunistic taxa. The rapid changes of faunal composition in the smaller fraction between successive sampling periods (some weeks to months) suggest that shallow dwelling taxa have rather rapid turnover rates and that a seasonal survey of foraminiferal isotopic signals will be relevant. Mackensen et al. (1993) suggested that epibenthic *F. wuellerstorfi* (=*C. wuellerstorfi*) responds to rapid and seasonal productivity changes by low $\delta^{13}C$ in eutrophic settings. Similarly, Corliss et al. (2002) who investigated the >150 μm size fraction, suggested that also the $\delta^{13}C$ of *H. elegans* reflects phytodetritus seasonal deposits in the North Atlantic by a decrease of about 0.3‰ in spring bloom compared to more oligotrophic periods. Therefore, we would expect to observe lower $\delta^{13}C$ in eutrophic periods for opportunistic and reactive foraminiferal taxa living in shallow infaunal microhabitat such as *U. peregrina* and *U. mediterranea* as a direct result of a temporal ^{12}C enrichment of surficial niches and/or a synchronous enhanced calcification rate of these species. However the $\delta^{13}C$ values of foraminiferal taxa we analyzed do not exhibit any clear seasonal trend in relation to plankton bloom events (Fig. 6, Table 2). Even if shallow infaunal *C. pachydermus, U. peregrina* and *U. mediterranea* exhibit slightly lower isotopic signatures in October 1997, which would agree with an impact of a putative fall bloom on carbon isotopic signatures of these taxa (shift of about 0.4‰ in comparison to oligotrophic periods), they do not show any decrease of $\delta^{13}C$ during spring blooms (April 1999,

June 1999, April 2000). Also the *M. barleeanus*, *Globobulimina* spp., *U. elongatastriata*, all being intermediate to deep infaunal taxa, show only small $\delta^{13}C$ changes without any seasonal trend. If we assume that (1) temporal ^{12}C enrichment of surficical niches is effective when phytodetritus is intensively degraded in shallow infaunal microhabitats, (2) growth rate and metabolism of reactive foraminiferal taxa is enhanced in such a setting, the absence of a clear response in adult individuals could mean that temporal ^{12}C enrichment is predominantly affecting the isotopic chemistry of newly recruited juveniles tests (*U. peregrina*, *U. mediterranea*) and of small opportunistic taxa (*E. exigua*, *N. pusillus*), belonging preferentially to the 63–150 μm size fraction. Such an ^{13}C depletion effect in test of individuals belonging to different size fractions has been assessed in two recent papers (Corliss et al., 2002; Schmiedl et al., 2004). We could only perform two isotopic measurements on juvenile foraminifera belonging to *U. mediterranea* and *U. peregrina* species (Table 2). It appears that the $\delta^{13}C$ values of these juveniles sampled in October 1997 at Station B (−1.09‰ and −1.69‰) are markedly lower than adult $\delta^{13}C$ signatures. Such an ontogenetic effect has just recently been demonstrated by Schmiedl et al. (2004) who depicted a progressive ^{13}C (and ^{18}O) depletion of *U. mediterranea* juveniles and pre-adults (100–300 μm) in comparison to adults (>300 μm) at two stations from the western Mediterranean Sea. On the contrary, Corliss et al. (2002) who performed a seasonal survey of $\delta^{13}C$ signatures of *H. elegans* and *U. peregrina* in the >150 μm fraction at two deep-sea stations from northwest Atlantic Ocean did not find any ontogenetic impact on the foraminiferal $\delta^{13}C$. In our study, we did not discriminate any size sub-fraction within the >150 μm size class. We think that the isotopic composition of *U. peregrina, U. mediterranea* specimens from the >150 μm fraction reflects a long-term averaged calcification process that is not systematically biased towards eutrophic periods. It is evident that isotopic measurements on individuals from the 63–150 μm fraction are necessary to better approach seasonal changes of the $\delta^{13}C$ of benthic foraminifera in relation to organic matter deposits and changing growth rates.

6. Conclusions

The Bay of Biscay is a mesotrophic basin characterized by a typical mid-latitudes primary production regime with a strong spring bloom. On a bathymetric transect the oxygen and carbon isotopic composition of the seven benthic foraminiferal taxa, *H. elegans, C. pachydermus, U. peregrina, U. mediterranea, M. barleeanus, U. elongatastriata* and *Globobulimina* spp., were determined:

- *U. peregrina* forms its test in close equilibrium with bottom water $\delta^{18}O$, as determined by using fractionation factors of Friedman and O'Neil, 1977. All other foraminiferal taxa biomineralise their tests with a rather constant offset to calcite formed in equilibrium with bottom water $\delta^{18}O$. There is no systematic relationship between foraminiferal microhabitat and the offset of foraminiferal $\delta^{18}O$ and equilibrium calcite $\delta^{18}O$.
- The downslope increase of $\delta^{13}C$ values of shallow infaunal taxa reflects the decrease of exported organic carbon flux along the bathymetric transect and the less intense early diagenetic processes in the surficial sediment. This is especially the case for the shallow infaunal *U. peregrina*. The $\delta^{13}C$ signatures of deep infaunal *Globobulimina* spp. are much less dependent on the exported organic matter flux and could be more influenced by small changes of bottom water oxygenation. Therefore, $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. can shed light on the various pathways of past degradation of organic detritus in the sediment.
- The $\delta^{13}C$ signatures of foraminiferal taxa are not correlated to bottom water $\delta^{13}C_{DIC}$ and appear to be mainly controlled by "microhabitat effects". Intergeneric offsets in uvigerinids are significant and could be explained by various processes such as vital effect, microhabitat preferences, and opportunistic behavior.
- At Station B in 550 m water depth, temporal variability of $\delta^{13}C$ values of shallow, intermediate and deep infaunal foraminiferal taxa is low and does not seem to be related to seasonal export of phytodetritus. The $\delta^{13}C$ of all foraminiferal individuals belonging to the >150 μm fraction may result from rather long-term calcification processes (several weeks or months), which limit the impact of ephemeral ^{12}C enrichment of shallow infaunal niches during eutrophic periods on the isotope chemistry of adult individuals.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT and the FORPROX II programs. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship

during all campaigns. We thank Günter Meyer and Katrin Blancke for their technical help to perform isotopic measurements in Bremerhaven (AWI). We also thank Elisabeth Michel for scientific discussions about isotopes and also Clémentine Griveaud, Mélissa Gaultier and Claude David for their technical and practical works on foraminiferal faunas. We also thank Tony Rathburn and Ellen Thomas for their useful suggestions as reviewers.

Appendix A. Taxonomic references

Uvigerina peregrina Cushman, 1923; illustrated in Van der Zwaan et al. (1986), pl. 1, Figs. 1–6.

Uvigerina mediterranea Hofker, 1932; illustrated in Van der Zwaan et al. (1986), pl. 5, Figs. 1–7.

Uvigerina elongatastriata (Colom), 1952; illustrated in Van der Zwaan et al. (1986), pl. 6, Figs. 1–8.

Melonis barleeanus (Williamson), 1958; illustrated in Van Leeuwen (1989), pl. 13, Figs. 1–2.

Cibicidoides pachydermus (Rzehac), 1886; illustrated in Jones (1994), pl. 94, Fig. 9.

Hoeglundina elegans (d'Orbigny), 1826; illustrated in Phleger et al. (1953), pl. 9, Figs. 24–25.

References

Antoine, D., Andre, J.M., Morel, A., 1996. Ocean primary production: 2. Estimation at global scale from satellite (coastal zone color scanner) chlorophyll. Global Biogeochemical Cycles 10, 57–70.

Barnett, P.R.O., Watson, J., Connely, D., 1984. A multiple corer for taking virtually undisturbed sample from shelf, bathyal and abyssal sediments. Oceanologica Acta 7, 399–408.

Beaufort, L., Heussner, S., 1999. Coccolithophorids on the continental slope of the Bay of Biscay — production, transport and contribution to mass fluxes. Deep-Sea Research II 46, 2146–2174.

Belanger, P.E., Curry, W.B., Matthews, R.K., 1981. Coretop evaluation of benthic foraminiferal isotopic ratios for paleoceanographic interpretations. Palaeoceanography, Palaeoclimatology, Palaeoecology 33, 205–220.

Berger, W.H., Wefer, G., 1990. Export productivity: seasonality and intermittency, and paleooceanographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 89, 245–254.

Bickert, T., Mackensen, A., 2004. Last glacial to Holocene changes in South Atlantic deep water circulation. In: Wefer, G., Mulitza, S., Ratmeyer, V. (Eds.), The South Atlantic in the Late Quaternary — Reconstruction of Material Budget and Current Systems. Springer, Berlin, pp. 599–620.

Boucher, J., 1985. Caractéristiques physiques et biologiques. In: Laubier, L., Monniot, C. (Eds.), Peuplements Profonds du Golfe de Gascogne: Campagne BIOGAS. IFREMER, pp. 25–40.

Chaillou, G., Anschutz, P., Lavaux, G., Schäfer, J., 2002. The distribution of Mo, U and Cd in relation to major redox species in muddy sediments of the Bay of Biscay. Marine Chemistry 80, 41–59.

Corliss, B.H., McCorkle, D.C., Higdon, D.M., 2002. A time series study of the carbon isotopic composition of deep-sea benthic foraminifera. Paleoceanography 17. doi:10.1029/2001PA000664.

Curry, W.B., Oppo, D.W., 2005. Glacial water mass geometry and the distribution of $\delta^{13}C$ of $\sum CO_2$ in the western Atlantic Ocean. Paleoceanography 20, PA 1017. doi:10.1029/2004PA001021.

Curry, W.B., Duplessy, J.-C., Labeyrie, L.D., Shackleton, N.J., 1988. Changes in the distribution of $\delta^{13}C$ of deep water ΣCO_2 between the last glaciation and the Holocene. Paleoceanography 3, 317–341.

Duplessy, J.-C., Shackleton, N.J., Matthews, R.K., Prell, W., Ruddiman, W.F., Caralp, M.H., Hendy, C.H., 1984. ^{13}C record of benthic foraminifera in the last interglacial ocean: implications for the carbon cycle and the global deep water circulation. Quaternary Research 21, 225–243.

Durrieu de Madron, X., Castaing, P., Nyffeler, F., Courp, T., 1999. Slope transport of resuspended particulate matter on the Aquitanian margin of the Bay of Biscay. Deep-Sea Research II 46, 2003–2027.

Fernandez, E., Boyd, P., Holligan, P.M., Harbour, D.S., 1993. Production of organic and inorganic carbon within a large-scale coccolithophore bloom in the northeast Atlantic Ocean. Marine Ecology Program Series 9, 271–285.

Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. Deep-Sea Research I 49, 751–785.

Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P., Lafon, V., 2003. Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay. Deep-Sea Research I 50, 457–494.

Fontanier, C., Forissen, F.J., Anschutz, P., Chaillou, G., in press. Seasonal variability of benthic foraminiferal faunas at 1000 m depth in the Bay of Biscay. Journal of Foraminiferal Research.

Friedman, I., O'Neil, J.R., 1977. Compilation of stable isotope fractionations factors of geochemical interest (Geological Survey Professional Paper 440-KK). In: Fleischer, M. (Ed.), Data of Geochemistry, Sixth edition. U.S. Government Printing Office, Washington, DC, pp. 1–12.

Froidefond, J.M., Castaing, P., Jouanneau, J.M., 1996. Distribution of suspended matter in a coastal upwelling area. Satellite data and in situ measurements. Journal of Marine System 8, 91–105.

Graham, D.W., Corliss, B.H., Bender, M.L., Keigwin, L.D., 1981. Carbon and oxygen isotopic disequilibria of recent deep-sea benthic foraminifera. Marine Micropaleontology 6, 483–479.

Grossman, E.L., 1984a. Carbon isotopic fractionation in live benthic foraminifera — comparison with inorganic precipitate studies. Geochemica et Cosmochimica Acta 48, 1505–1512.

Grossman, E.L., 1984b. Stable isotope fractionation in live benthic foraminifera from the southern California borderland. Palaeoceanography, Palaeoclimatology, Palaeoecology 47, 301–327.

Grossman, E.L., 1987. Stable isotopes in modern benthic foraminifera: a study of vital effect. Journal of Foraminiferal Research 17, 48–61.

Herguera, J.C., 1992. Deep-sea foraminifera and biogenic opal: glacial to postglacial productivity changes in the western Pacific. Marine Micropaleontology 19, 79–98.

Holsten, J., Stott, L., Berelson, W., 2004. Reconstructing benthic carbon oxidation rates using $\delta^{13}C$ of benthic foraminifers. Marine Micropaleontology 53, 117–132.

Imbrie, J., Boyle, E.A., Clemens, S.C., Duffy, A., Howard, W.R., Kukla, G., Kutzbach, J., Martinson, D.G., McIntyre, A., Mix,

A.C., Molfino, B., Morley, J.J., Peterson, L.C., Pisias, N.G., Prell, W.L., Raymo, M.E., Shackleton, N.J., Toggweiler, J.R., 1992. On the structure and origin of major glaciation cycles: 1. Linear responses to Milankovitch forcing. Paleoceanography 7, 701–738.

Jones, R.W., 1994. The Challenger Foraminifera. The Natural History Museum. Oxford Science Publications.

Jorissen, F.J., Wittling, I., Peypouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cap Blanc, NW Africa: community structure and microhabitats. Deep-Sea Research I 45, 2157–2188.

Katz, M.E., Wright, J.D., Katz, D.R., Miller, K.G., Pak, D.K., Shackleton, N.J., Thomas, E., 2003. Early Cenonoiz benthic foraminiferal isotopes: species reliability and interspecies correction factors. Paleoceanography 18, 1024. doi:10.1029/2002PA000798.

Kim, S.T., O'Neil, J.R., 1997. Equilibrium and nonequilibrium oxygen isotope effects in synthetic carbonates. Geochimica et Cosmochimica Acta 61 (16), 3461–3475.

Laborde, P., Urrutia, J., Valencia, V., 1999. Seasonal variability of primary production in the Cap-Ferret Canyon area (Bay of Biscay) during the ECOFER cruises. Deep-Sea Research II 46, 2057–2079.

Lampert, L., 2001.Dynamique saisonnière et variabilité pigmentaire des populations phytoplanctoniques dans l'Atlantique Nord (Golfe de Gascogne). Ph.D. Thesis, Université de Bretagne occidentale, Brest, France.

Le Corre, P., Treguer, P., 1976. Caractéristiques Chimiques et Planctoniques du Golfe de Gascogne et du Proche Atlantique. Campagne POLYGAS A (20.10 au 04.11.1972) et PHYGAS 32 (24.04 au 08.05.1973). Résultats des Campagnes à la mer. CNEXO 9. 306 pp.

Le Floch, J., 1968. Sur la circulation de l'eau d'origine méditerranéenne dans le Golfe de Gascogne et ses variations à courte période. Cahiers Océanographiques XX 7, 653–661.

Loubere, P., Meyers, P., Gary, A., 1995. Benthic foraminiferal microhabitat selection, carbon isotope values, and association with larger animals: a test with *Uvigerina peregrina*. Journal of Foraminiferal Research 25, 83–95.

Mackensen, A., Douglas, R.G., 1989. Down-core distribution of live and dead benthic foraminifera in box cores from the Weddell Sea and the California continental borderland. Deep-Sea Research 36, 879–900.

Mackensen, A., Licari, L., 2004. Carbon isotopes of live benthic foraminifera from the South Atlantic Ocean: sensitivity to bottom water carbonate saturation state and organic matter rain rates. In: Wefer, G., Mulitza, S., Rathmeyer, V. (Eds.), The South Atlantic in the Late Quaternary — Reconstruction of Material Budget and Current Systems. Springer-Verlag, Berlin, pp. 623–644.

Mackensen, A., Hubberten, H.-W., Bickert, T., Fischer, G., Futterer, D.K., 1993. $\delta^{13}C$ in benthic foraminiferal tests of *Fontbotia wuellerstorfi* (Schwager) relative to $\delta^{13}C$ of dissolved inorganic carbon in Southern Ocean deep water: implications for Glacial ocean circulation models. Paleoceanography 6, 587–610.

Mackensen, A., Schumacher, S., Radke, J., Schmidt, D.N., 2000. Microhabitat preferences and stable carbon isotopes of endobenthic foraminifera: clue to quantitative reconstruction of oceanic new production. Marine Micropaleontology 40, 233–258.

Mackensen, A., Rudolph, M., Kuhn, K., 2001. Late Pleistocene deepwater circulation in the sub-antarctic eastern Atlantic. Global and Planetary Change 30, 195–226.

McCorkle, D.C., Emerson, S.R., 1988. The relationship between pore water carbon isotopic composition and bottom water oxygen concentration. Geochemica et Cosmochimica Acta 52, 1169–1178.

McCorkle, D.C., Keigwin, L.D., 1994. Depth profile of $\delta^{13}C$ in bottom water and core-top *C. wuellerstorfi* on the Ontong-Java Plateau and Emperor Seamounts. Paleoceanography 9, 197–208.

McCorkle, D.C., Emerson, S.R., Quay, P., 1985. Stable carbon isotope in marine porewaters. Earth and Planetary Science Letters 74, 13–26.

McCorkle, D.C., Keigwin, L.D., Corliss, B.H., Emerson, S.R., 1990. The influence of microhabitats on the carbon isotopic composition of deep-sea benthic foraminifera. Paleoceanography 5, 161–185.

McCorkle, D.C., Corliss, B.H., Farnham, C.A., 1997. Vertical distributions and stable isotopic compositions of live (stained) benthic foraminifera from the North Carolina and California continental margin. Deep-Sea Research I 44, 983–1024.

O'Neil, J.R., Clayton, R.N., Mayeda, T.K., 1969. Oxygen isotope fractionation in divalent metal carbonates. Journal of Chemical Physics 51, 5547–5558.

Ogawa, N., Tauzin, P., 1973. Contribution à l'étude hydrologique et géochimique du Golfe de Cap-Breton. Bulletin de l'Institut Géologique du Bassin d'Aquitaine, Bordeaux 14, 19–46.

Phleger, F.B., Parker, F.L., Peirson, J.F., 1953. North Atlantic foraminifera. In: Pettersson, H. (Ed.), Reports of the Swedish Deep-Sea Expedition 1947–1948., Sediment cores from the North Atlantic, vol. VII. Fasc. 1, Sweden.

Rathburn, A.E., Corliss, B.H., Tappa, K.D., Lohmann, K.C., 1996. Comparison of the ecology and stable isotopic compositions of living (stained) benthic foraminifera from the Sulu and South China Seas. Deep-Sea Research 43, 1617–1646.

Rathburn, A.E., Levin, L.A., Held, Z., Lohmann, K.C., 2000. Benthic foraminifera associated with cold methane seeps on the northern California margin: ecology and stable isotopic composition. Marine Micropaleontology 38, 247–266.

Rathburn, A.E., Perez, M.E., Martin, J.B., Day, S.A., Mahn, C., Gieskes, J., Ziebis, W., Williams, D., Bahls, A., 2003. Relationships between the distribution and stable isotopic composition of living benthic foraminifera and cold methane seep biogeochemistry in Monterey Bay, California. Geochemistry, Geophysics, Geosystems 4 (12), 1–28.

Rohling, E.J., Cooke, S., 1999. Stable oxygen and carbon isotopes in foraminiferal carbonate shells. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, pp. 239–258.

Sackett, W.M., 1989. Stable carbon isotope studies on organic matter in the marine environment. In: Fritz, A.P., Fontes, J.C. (Eds.), Handbook of Environmental Isotope Geochemistry, The Marine Environment, vol. 3. Elsevier, Amsterdam, pp. 139–169.

Schiebel, R., Waniek, J., Bork, M., Hemleben, C., 2001. Planktic foraminiferal production stimulated by chlorophyll redistribution and entrainment of nutrients. Deep-Sea Research I 48, 721–740.

Schmiedl, G., Pfeilsticker, M., Hemleben, C., Mackensen, A., 2004. Environmental and biological effects on the stable isotope composition of Recent deep-sea benthic foraminifera from the Mediterranean Sea. Marine Micropaleontology 51/1–2, 129–152.

Shackleton, N.J., 1977. Carbon-13 in *Uvigerina*: tropical rainforest history and the Equatorial Pacific carbonate dissolution cycles. In: Anderson, N.R., Malahoff, A. (Eds.), The Fate of Fossil Fuel CO_2 in the Oceans. Plenum, New York, pp. 401–427.

Shackleton, N.J., Opdyke, N.D., 1973. Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperature and ice volumes on a 10^5 year and 10^6 year scale. Quaternary Research 3, 39–55.

Tréguer, P., Le Corre, P., Grall, J.R., 1979. The seasonal variations of nutrients in the upper waters of the Bay of Biscay region and their relation to phytoplanctonic growth. Deep-Sea Research 26, 1121–1152.

Urey, H.C., Lowenstam, H.A., Epstein, S., McKinney, C.R., 1951. Measurement of paleotemperatures and temperatures of the Upper Cretaceous of England, Denmark and southeastern United States. Geological Society of America Bulletin 62, 399–416.

Van Leeuwen, R.J.W., 1989. Sea-floor distribution and Late Quaternary faunal patterns of planktonic and benthic foraminifers in the Angola Basin. Utrecht Micropaleontological Bulletins, vol. 38. Utrecht University, Netherlands.

Van der Zwaan, G.J., Jorissen, F.J., Verhallen, P.J.J.M., Von Daniels, C.H., 1986. Atlantic–European Oligocene to Recent *Uvigerina*; Taxonomy, Paleoecology and Paleobiogeography, Utrecht Micropaleontology Bulletin, vol. 35. Utrecht University, Netherlands.

Vangrieshem, A., 1985. Hydrologie et circulation profonde. In: Laubier, L., Monniot, C. (Eds.), Peuplements Profonds du Golfe de Gascogne: Campagne BIOGAS. IFREMER, pp. 43–70.

Walton, W.R., 1952. Techniques for recognition of living Foraminifera. Contribution of the Cushman Foundation for Foraminiferal Research 3, 56–60.

Wefer, G., Berger, W.H., 1991. Isotope paleontology: growth and composition of extant calcareous species. Marine Geology 199, 207–248.

Wollenburg, J., Mackensen, A., 1998. Living benthic foraminifers from the central Arctic Ocean: faunal composition, standing stock and diversity. Marine Micropaleontology 34, 153–185.

Woodruff, F., Savin, S.M., Douglas, R.G., 1980. Biological fractionation of oxygen and carbon isotopes by recent benthic foraminifera. Marine Micropaleontology 5, 3–11.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate change 65 Ma to Present. Science 292, 686–693.

Zahn, R., Winn, K., Sarnthein, M., 1986. Benthic foraminiferal $\delta^{13}C$ and accumulation rates of organic carbon: *Uvigerina peregrina* group and *Cibicidoides wuellerstorfi*. Paleoceanography 1, 27–42.