



Glacial cold-water coral growth in the Gulf of Cádiz: Implications of increased palaeo-productivity

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ABSTRACT

A set of 40 Uranium-series datings obtained on the reef-forming scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* revealed that during the past 400 kyr their occurrence in the Gulf of Cádiz (GoC) was almost exclusively restricted to glacial periods. This result strengthens the outcomes of former studies that coral growth in the temperate NE Atlantic encompassing the French, Iberian and Moroccan margins dominated during glacial periods, whereas in the higher latitudes (Irish and Norwegian margins) extended coral growth prevailed during interglacial periods. Thus it appears that the biogeographical limits for sustained cold-water coral growth along the NE Atlantic margin are strongly related to climate change. By focussing on the last glacial–interglacial cycle, this study shows that palaeo-productivity was increased during the last glacial. This was likely driven by the fertilisation effect of an increased input of aeolian dust and locally intensified upwelling. After the Younger Dryas cold event, the input of aeolian dust and productivity significantly decreased concurrent with an increase in water temperatures in the GoC. This primarily resulted in reduced food availability and caused a widespread demise of the formerly thriving coral ecosystems. Moreover, these climate induced changes most likely caused a latitudinal shift of areas with optimum coral growth conditions towards the northern NE Atlantic where more suitable environmental conditions established with the onset of the Holocene.

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1. Introduction

Along the NE Atlantic margin cold-water corals occur in a belt that extends from northern Norway (Barents Sea, 70°N; Lindberg et al., 2007) down to NW Africa (off Mauritania, 16°N; Colman et al., 2005). These ecosystems vary strongly with respect to their appearance, structure and coral vitality. Large flourishing *Lophelia*-reefs occur along the Norwegian margin. With a horizontal dimension of several hundred meters to kilometres they developed to the largest known living cold-water coral reefs worldwide (Fosså et al., 2005). Along the Irish margin cold-water corals are associated with coral mounds that vary in height from a few metres up to >380 m being often densely covered by living coral colonies (Wheeler et al., 2007, and refs. therein). Further to the south, cold-water corals mainly occur as isolated colonies or accumulations of fossil corals in the Bay of Biscay (Reveillaud et al., 2008), on seamounts (Duineveld et al., 2004) and

within canyons along the Iberian margin (Tyler et al., 2009), and on coral mounds along the NW African margin (Wienberg et al., 2009).

Along with the geographic distribution, a distinct stratigraphic pattern regarding the development of cold-water coral ecosystems along the NE Atlantic margin has been observed during the last glacial–interglacial cycle. Reefs of Holocene age on the Norwegian shelf started to develop after the retreat of glaciers at the termination of the last glacial (Freiwald et al., 2004). The Irish coral mounds seem to be restricted to interglacials with a very few exceptions (Dorschel et al., 2005; Eisele et al., 2008) and the latest re-establishment of cold-water coral ecosystems appears to have been started after the Younger Dryas (YD) cold reversal (Frank et al., 2009). To the south along the French, Iberian and Moroccan margins, corals are suggested to have been widely distributed during the last glacial (Schröder-Ritzrau et al., 2005; Wienberg et al., 2009). In actual fact, although the Gulf of Cádiz (GoC) was recently identified to be an important cold-water coral site in the temperate NE Atlantic, this area is at present mainly characterised by so-called ‘coral graveyards’ with only very few living corals (Foubert et al., 2008; Wienberg et al., 2009). Such current depauperation of live coral ecosystems might be explained by the recent warm and oligotrophic

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conditions in the GoC forcing reduced food availability (Wienberg et al., 2009). In addition, tidal currents and internal waves that have been identified to be important hydrodynamic processes for supplying food particles to and through the coral thickets (White et al., 2005, 2007) nowadays do not seem to play a major role in the GoC (Wienberg et al., 2009). However, the widespread occurrence of fossil corals suggests more favourable oceanographic conditions in the past. Indeed, initial datings revealed that cold-water corals have been common in the GoC during the last glacial (Wienberg et al., 2009).

The present study aims to refine and extend this observed stratigraphic pattern of coral occurrence along the NE Atlantic margin by 40 Uranium-series datings of reef-forming scleractinian cold-water corals from sediment cores retrieved in various areas of the GoC. Moreover, it is intended to relate the prosperity and/or demise of cold-water corals in the GoC to a distinct environmental and oceanographic setting that altered along with climate change. Thus, we aim to identify the main forcing factors triggering the development of cold-water coral ecosystems in the GoC.

2. Regional setting

The GoC is situated west of the Strait of Gibraltar, and thus connects the open North Atlantic Ocean and the Mediterranean Sea (Fig. 1). It is bordered by the Iberian Peninsula and the NW African coasts and extends from Cape St. Vincent at the southwestern tip of Portugal down to the Moroccan Atlantic margin at 33°N (Mauritzen et al., 2001). The Iberian continental shelf widens from ~15 km west of Faro to ~50 km further to the east (Garcia-Lafuente and Ruiz, 2007), which is similar to the width of the Moroccan shelf (<60 km; Mittelstaedt, 1991).

The deeper basin of the GoC is characterised by a widespread occurrence of diapiric ridges and mud volcanoes (Somoza et al., 2003). Many of these mud volcanoes were identified to be covered by fossil cold-water corals (Somoza et al., 2003; Wienberg et al., 2009). Further conspicuous topographic features in the GoC are hundreds of coral mounds that are 20–30 m in height, and 50–200 m in length, and that are covered by fossil corals. They are restricted to the Moroccan

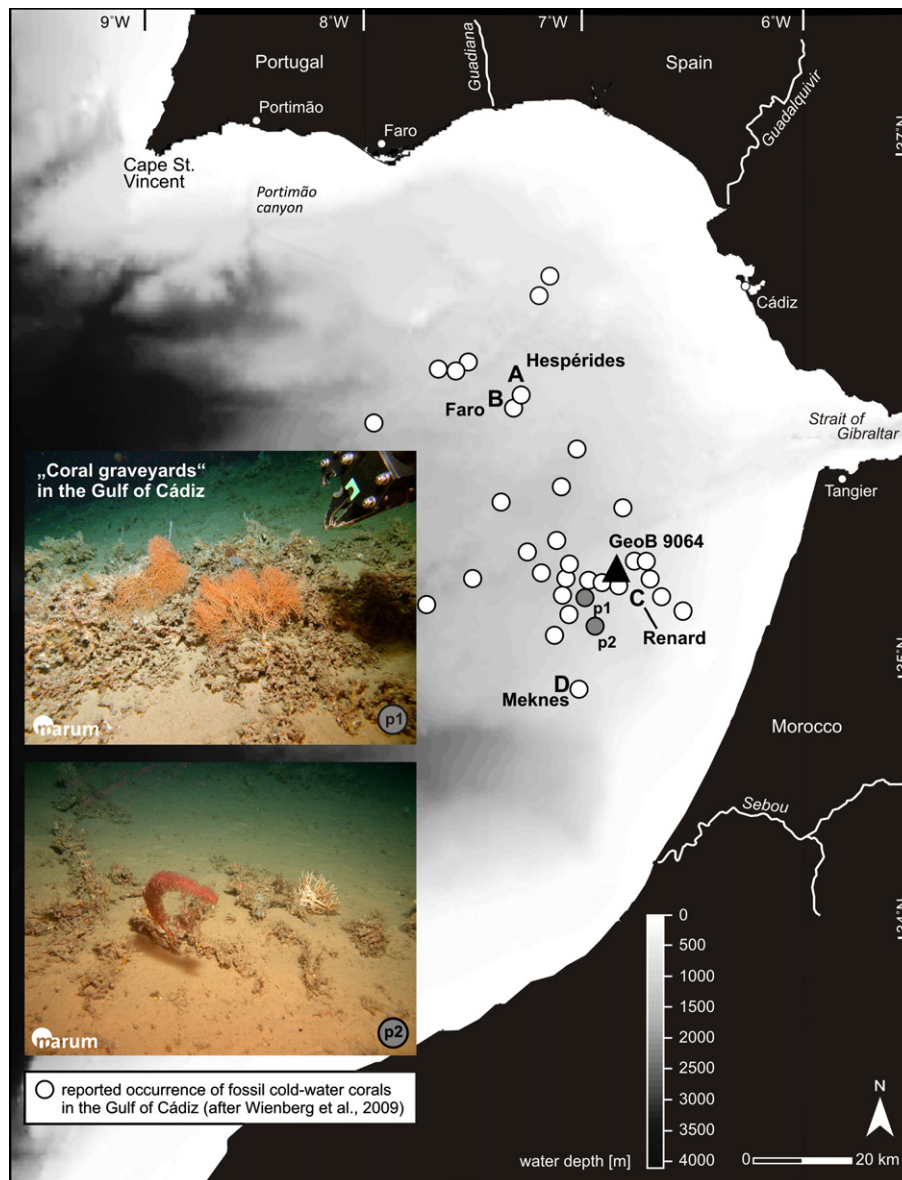


Fig. 1. Map of the Gulf of Cádiz (GoC) showing the coring sites (bathymetric data source: GEBCO). Reference sediment core GeoB 9064 (black triangle) and coral-bearing sediment cores (A–D). A: Hespérides mud volcano (GeoB 9018), B: Faro mud volcano (GeoB 9031, GeoB 9032), C: Renard Ridge (GeoB 9070, GeoB 12101, GeoB 12102, GeoB 12103, GeoB 12104, M2004-02), D: north of Meknes mud volcano (GeoB 12106). Indicated are the reported occurrences of fossil cold-water corals (after Wienberg et al., 2009). Lower left: photographs showing characteristic 'coral graveyards' in the southern GoC, Moroccan margin (position is indicated on the map as p1, p2) (images ©MARUM, Bremen).

margin where they have been found in a water depth between 400 and 960 m (Foubert et al., 2008; Hebbeln et al., 2008; Wienberg et al., 2009). The coral mounds are mainly arranged as clusters and are situated amidst mud volcanoes and on top of diapiric ridges. Detailed knowledge about their origin, composition, and temporal development is to date still lacking.

Present-day oceanographic circulation in the GoC is dominated by the exchange of water masses between the Atlantic Ocean and the Mediterranean Sea (Ochoa and Bray, 1991). The relatively cold Atlantic Inflow Water flows eastward along the Iberian margin partly entering the Mediterranean Sea. It is composed of North Atlantic Surficial Water and North Atlantic Central Water (NACW). The upper-thermocline NACW deepens from about 300 m water depth close to the Strait of Gibraltar to about 600 m in the outer and southern parts of the gulf (Ochoa and Bray, 1991; Mauritzen et al., 2001). Below this level occurs Mediterranean Outflow Water (MOW). Flowing westwards through the Strait of Gibraltar, the MOW prevails in the northern gulf where it flows between ~500 and 1400 m water depth above the North Atlantic Deep Water (NADW) (Ambar et al., 1999; Baringer and Price, 1999) and acts as a strong contour current (García et al., 2009). It is characterised by a permanent salinity maximum of ~36–37 and temperatures of 10.5 to 12 °C (Fusco et al., 2008). For the southern GoC along the Moroccan Atlantic margin information about its hydrography is basically lacking (Machín et al., 2006). However, Pelegrí et al. (2005) suggests the presence of MOW at 800 m. This assumption is supported by the presence of an anticyclone or meddy close to the Moroccan shelf which implies at least some temporary southward transport of MOW along the Moroccan margin (Carton et al., 2002).

Today, the GoC constitutes an oligotrophic system with diminished primary production in the surface waters (Behrenfeld et al., 2005). Cold and productive upwelling is restricted to a narrow band along the Portuguese coast (García-Lafuente and Ruiz, 2007), and to the NW African margin south of 31°N (Cape Ghir) (Mittelstaedt, 1991; Pelegrí et al., 2005). Due to a prevailing anticyclonic circulation (Pelegrí et al., 2005), the basin of the GoC separates the Iberian upwelling from the upwelling off NW Africa (García-Lafuente and Ruiz, 2007).

3. Materials and methods

3.1. Core locations

During three expeditions between 2003 and 2006, a set of ten coral-bearing sediment cores was collected from various sites in the GoC (Table 1). The coring sites comprise two mud volcanoes (Hespérides and Faro) along the Spanish margin and coral mounds along the Moroccan margin which are situated on top of the

prominent Renard Ridge and its easternmost extension, the Pen Duick Escarpment. Finally, the southernmost core was collected north of Meknes mud volcano (Fig. 1).

The sediment cores have a length between 2.2 m and 8.6 m and are made up of abundant cold-water coral fragments embedded in a hemipelagic sediment matrix (Table 1). The sediment cores collected from mud volcanoes along the Spanish margin only contain cold-water corals in their upper parts, whereas the cores retrieved from coral mounds along the Moroccan margin are characterised by the occurrence of coral fragments throughout the sedimentary record.

To reconstruct oceanographic and environmental changes in the GoC during the last glacial–interglacial cycle and to compare this with the temporal distribution pattern of cold-water corals, sediment core GeoB 9064 (35°24.91'N, 06°50.72'W, 702 m water depth) was selected for a multiproxy study (Fig. 1). Core GeoB 9064 was collected along the Moroccan margin (RV *Sonne* cruise SO175) and has a total length of 5.4 m. Samples for the various analyses were taken in 5-cm-intervals.

3.2. U/Th age determination on coral fragments

Forty fragments of the reef-forming scleractinian coral species *Madrepora oculata* and *Lophelia pertusa* were sampled at different core depths from the sediment cores listed in Table 1. Uranium-series measurements were performed using multi-collector ICP and thermionization mass spectrometry at IFM-GEOMAR (Kiel, Germany; Fietzke et al., 2005) and at LSCE (Gif-sur-Yvette, France; Frank et al., 2004; Douville et al., 2010). Prior to analyses, samples were carefully cleaned to remove contaminants from the fossil skeleton surfaces according to procedures described by Fietzke et al. (2005) and Frank et al. (2004). Isotope concentrations and ratios as well as the absolute dates on the cold-water corals are provided in Table 2. Whole procedure blank values of this sample set were measured to be around 2 pg for thorium (Th) and between 4 and 8 pg for uranium (U). Both values are negligible compared to U- and Th-concentrations of the studied corals. The reproducibility of mass spectrometric measurements was tested using international U standard materials such as HU1 and NBL112, which provided identical values as the ones published by Fietzke et al. (2005) and Frank et al. (2004).

3.3. Analyses on core GeoB 9064

3.3.1. AMS radiocarbon dating

Accelerator mass spectrometry (AMS) dating was performed at the Leibniz Laboratory for Age Determinations and Isotope Research (University of Kiel, Germany; Nadeau et al., 1997) and at the Poznań Radiocarbon Laboratory (Poznań, Poland). AMS ¹⁴C dates were

Table 1

Metadata of coral-bearing sediment cores collected from various sites in the Gulf of Cádiz (indicated in Fig. 1 as A, B, C, D). Abbreviations: Lat, latitude; Lon, longitude; Wd, water depth; Rec, recovery; Mv, mud volcano; Cm, coral mound; SM, Spanish margin; MM, Moroccan margin; PDE, Pen Duick Escarpment; Mo, *Madrepora oculata*; Lp, *Lophelia pertusa*. Cruises: 1, RV *Sonne* cruise SO175; 2, RV *Maria S. Merian* MSM01-3; 3, RV *Pelagia* cruise 64PE229.

	Cruise	Location	Core-ID	Lat (°N)	Lon (°W)	Wd (m)	Rec (cm)	Coral content
A	Mv SM 1	Hespérides Mv	GeoB 9018	36°10.98'	07°18.37'	702	347	0–5 cm: dendrophylliids, 5–347 cm: solely Mo; strongly altered fragments.
B	Mv SM 1	Faro Mv (lower flank)	GeoB 9031	36°05.75'	07°23.28'	897	484	0–160 cm: Mo-dominated; strongly altered fragments.
	Mv SM 1	Faro Mv (top)	GeoB 9032	36°05.55'	07°23.57'	843	220	0–60 cm: Mo-dominated, 60–220 cm: mud breccia.
C	Cm MM 1	Western Renard Ridge	GeoB 9070	35°22.00'	06°51.90'	594	560 ^a	0–560 cm: Mo and Lp.
	Cm MM 2	Western Renard Ridge	GeoB 12104	35°21.99'	06°51.90'	590	523	0–523 cm: Mo and Lp
	Cm MM 2	Renard Ridge	GeoB 12102	35°21.11'	06°50.96'	585	518	0–518 cm: Mo, Lp, and dendrophylliids.
	Cm MM 2	Renard Ridge	GeoB 12103	35°21.18'	06°50.90'	591	568	0–568 cm: Mo and Lp.
	Cm MM 2	PDE	GeoB 12101	35°18.88'	06°48.08'	545	468	0–468 cm: Mo, Lp, and dendrophylliids.
	Cm MM 3	PDE	M2004-02	35°17.68'	06°47.25'	523	861	0–861 cm: Mo, Lp, and dendrophylliids.
D	Cm MM 2	North of Meknes Mv	GeoB 12106	34°59.49'	07°04.56'	758	303	30–303 cm: Mo and Lp.

^a The uppermost 40 cm of core GeoB 9070 were disturbed due to coring operation, thus the undisturbed core depth ranges from 40 to 600 cm.

Table 2

Ages, isotope concentrations and ratios (n.a., not available; n.d. not dateable).

N°	Sample ID	Depth (cm)	Coral	Labcode	Age (ka)	± (ka)	²³⁸ U (ppm)	± (ppm)	²³² Th (ppb)	± (ppb)	$\delta^{234}\text{U}(\text{M})$ (‰)	± (‰)	$\delta^{234}\text{U}(0)$ (‰)	± (‰)
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
01	GeoB 9018	3	Mo	n.a.	14.65	0.09	4.020	0.004	21.019	0.052	149.8	1.9	156.1	2.0
02	GeoB 9018	123	Mo	n.a.	294.00	7.00	4.329	0.004	3.021	0.006	73.1	1.4	167.7	3.3
03	GeoB 9018	272	Mo	n.a.	283.80	8.50	4.005	0.004	23.536	0.064	61.9	1.5	138.0	3.3
04	GeoB 9031	10	Mo	n.a.	20.92	0.12	4.956	0.005	21.400	0.055	139.9	1.8	148.5	1.9
05	GeoB 9031	93	Mo	n.a.	37.25	0.23	5.263	0.007	4.796	0.009	132.8	2.3	147.5	2.5
06	GeoB 9031	150	Mo	n.a.	45.94	0.33	4.338	0.004	8.875	0.016	120.6	1.4	137.4	1.6
07	GeoB 9032	20	Mo	n.a.	17.15	0.15	4.447	0.005	62.092	0.192	140.6	1.6	147.6	1.7
08	GeoB 9032	47	Mo	n.a.	41.17	0.25	4.512	0.005	25.841	0.070	130.3	1.8	146.4	2.0
09	GeoB 9070	47	Lp	n.a.	23.50	0.12	4.622	0.003	4.428	0.010	137.9	1.1	147.3	1.2
10	GeoB 9070	298	Mo	n.a.	43.68	0.28	3.552	0.003	51.216	0.079	129.6	1.8	146.6	2.0
11	GeoB 9070	520	Mo	n.a.	166.00	2.40	3.968	0.004	15.089	0.033	78.7	1.7	125.9	2.7
12	GeoB 12101	57	Mo	Gif-1525	n.d.		3.085	0.004	0.351	0.002	59.5	3.2	/	/
13	GeoB 12101	146	Lp	Gif-1389	n.d.		3.214	0.004	0.920	0.003	47.4	3.0	/	/
14	GeoB 12101	451	Mo	Gif-1527	430.76	56.55	2.589	0.002	8.092	0.026	48.9	3.3	165.2	3.3
15	GeoB 12102	28	Mo	Gif-1529	57.96	0.74	4.390	0.005	0.316	0.001	119.5	2.7	140.8	2.7
16	GeoB 12102	166	Lp	Gif-1528	118.16	1.10	4.220	0.003	1.075	0.003	103.0	1.9	143.8	1.9
17	GeoB 12102	238	Lp	Gif-1390	152.27	5.12	3.035	0.003	0.306	0.003	112.1	2.9	172.4	2.9
18	GeoB 12102	376	Mo	Gif-1388	151.56	3.37	3.614	0.003	0.491	0.002	90.7	3.0	139.2	3.0
19	GeoB 12102	493	Mo	Gif-1386	164.02	2.01	3.194	0.003	0.495	0.002	99.5	1.8	158.3	1.8
20	GeoB 12103	34	Lp	Gif-1530	22.88	0.38	3.881	0.004	0.636	0.003	131.0	2.0	139.8	2.0
21	GeoB 12103	88	Lp	Gif-1392	25.72	0.39	4.462	0.006	3.873	0.010	128.7	2.9	138.4	2.9
22	GeoB 12103	200	Mo	Gif-1531	29.98	1.26	3.610	0.004	2.644	0.011	129.4	3.3	140.9	3.3
23	GeoB 12103	317	Mo	Gif-1532	30.43	0.96	3.828	0.004	0.192	0.003	126.9	2.2	138.3	2.2
24	GeoB 12103	444	Mo	Gif-1533	49.85	0.80	3.693	0.005	19.205	0.071	121.1	2.4	139.4	2.4
25	GeoB 12104	8	Lp	Gif-1387	23.57	0.18	4.435	0.003	7.778	0.016	126.3	1.7	135.0	1.7
26	GeoB 12104	373	Lp	Gif-1534	311.20	15.74	3.658	0.003	2.161	0.012	69.8	2.2	168.3	2.2
27	GeoB 12104	491	Mo	Gif-1535	342.29	25.38	3.492	0.004	2.003	0.008	71.1	2.6	187.1	2.6
28	GeoB 12106	117	Mo	Gif-1391	295.86	23.27	3.421	0.004	3.421	0.004	65.9	2.8	152.0	2.8
29	M2004-02	49	Mo	Gif-1631	9.15	0.71	3.512	0.011	0.103	0.014	149.3	3.0	153.2	3.0
30	M2004-02	85	Lp	Gif-1632	19.36	0.54	3.943	0.007	0.625	0.008	138.8	2.5	146.6	2.5
31	M2004-02	105	Lp	Gif-1633	19.87	0.52	3.284	0.010	0.695	0.006	136.0	3.9	143.9	3.9
32	M2004-02	141	Lp	Gif-1634	21.37	0.42	3.862	0.007	4.666	0.013	136.5	2.3	145.0	2.3
33	M2004-02	147	Lp	Gif-1635	22.75	0.26	4.016	0.006	2.209	0.006	133.0	2.9	141.8	2.9
34	M2004-02	176	Lp	Gif-1636	24.03	0.26	3.921	0.008	11.534	0.031	131.4	3.3	140.6	3.3
35	M2004-02	247	Lp	Gif-1637	34.90	0.43	3.099	0.004	0.310	0.001	130.3	2.5	143.8	2.5
36	M2004-02	273	Mo	Gif-1638	36.27	0.43	3.804	0.008	3.049	0.008	124.5	1.6	138.0	1.6
37	M2004-02	313	Lp	Gif-1639	142.08	1.92	4.068	0.010	2.908	0.009	96.6	2.3	144.4	2.4
38	M2004-02	343	Lp	Gif-1640	175.01	2.79	3.846	0.005	14.820	0.026	85.3	2.5	139.9	2.5
39	M2004-02	363	Mo	Gif-1641	242.07	8.35	3.174	0.008	0.506	0.003	85.4	2.7	169.3	2.7
40	M2004-02	403	Lp	Gif-1642	262.80	7.46	3.126	0.007	3.116	0.007	74.2	2.9	155.9	2.9

Note: Column 1: Sample label. Column 2: Depth in core. Column 3: Reef-forming scleractinian cold-water coral species, Lp *Lophelia pertusa*, Mo *Madrepora oculata*. Column 4: Labcode (not available for datings conducted at IFM-GEOMAR, N° 1–11). Column 5: Calculated coral ages. Column 6: ²³⁸U concentration. Column 7: ²³²Th concentration. Column 8: Measured ²³⁴U/²³⁸U activity ratios ($\delta^{234}\text{U}(\text{M})$) are presented as deviation permil (‰) from the equilibrium value. Column 9: Decay corrected ²³⁴U/²³⁸U activity ratios ($\delta^{234}\text{U}(0)$) are calculated from the given ages and with $\lambda_{234\text{U}}: 2.8263 \times 10^{-6} \text{ yr}^{-1}$. Note that ages are strictly reliable having values between 146.6‰ and 149.6‰ (modern seawater), reliable with values of $149 \pm 10\%$, unreliable with values $> 149 \pm 10\%$ (see also Stirling et al., 1998; Robinson et al., 2004; Esat and Yokoyama, 2006).

determined on ~8 mg calcium carbonate of mixed planktonic foraminifera. All ages were corrected for ¹³C and a mean ocean reservoir age of 400 years (Bard, 1988). AMS ¹⁴C ages were converted to calendar years using the CALPAL 2007 Hulu software (Joeris and Weninger, 1998) and are reported as calendar years before present (ka; Table 3).

3.3.2. Stable oxygen isotopes

The stable oxygen isotope ($\delta^{18}\text{O}$) composition of the planktonic foraminifera *Neogloboquadrina pachyderma* (dex.) was measured with a Finnigan MAT 251 mass spectrometer (Isotope Laboratory of the Department of Geosciences, University of Bremen, Germany). The isotopic composition was measured on the CO₂ gas evolved by treatment with phosphoric acid at a constant temperature of 75 °C. A working standard (Burgbrohl CO₂ gas) was applied, which has been calibrated against PDB by using the NBS18, 19 and 20 standards. Consequently, all $\delta^{18}\text{O}$ data presented here are given relative to the PDB standard. Analytical standard deviation was about $\pm 0.07\%$.

3.3.3. Grain-size analysis and end-member modelling

Grain sizes were measured on bulk and terrigenous material using a Malvern Instruments Mastersizer 2000 (Hydraulic Research Laboratory, Borgerhout, Belgium), which determines particle grain sizes between 0.26 μm and 2 046 μm grouped into 66 size classes. The terrigenous sediment fraction was obtained by treating bulk sediment with H₂O₂ (30% at 85 °C) and HCl (10% at 100 °C) to remove organic carbon and calcium carbonate, respectively. The sediments contained negligible amounts of biogenic opal, and microscopic analyses revealed that the applied method successfully removed all biogenic constituents. Finally, the samples were suspended in demineralised water by stirring and ultrasonic dispersion before analysis.

The terrigenous fraction of deep-sea sediments in the ocean is considered a mixture of ice-rafted, aeolian, and fluvial transported sediments. End-member modelling allows the distinction between possible lithic subpopulations of the grain-size spectrum (Weltje, 1997) that can be assigned to different sediment transport mechanisms (e.g., Stuut et al., 2002; Holz et al., 2007). To estimate the minimum number of end-members (EM) required for a satisfactory approximation of the data, the coefficients of determination were

Table 3

AMS ^{14}C dates determined on multi-species samples of planktonic foraminifera from sediment core GeoB 9064. The AMS ^{14}C ages were corrected for ^{13}C and a mean ocean reservoir age of 400 years, and were converted to calendar years using the CALPAL 2007 Hulu software. Estimated sedimentation rates for core GeoB 9064 are supplemented.

Core depth (cm)	Labcode	Conventional age		CALPAL age		Sedimentation rate (cm kyr $^{-1}$)
		^{14}C age (years)	\pm error	1 σ (68%) (calendar years B.P., P. = AD 1950)	\pm error	
4	Poz-20282	2095	30	1630	50	–
74	KIA-10065	9665	60	10430	100	7.95
169	KIA-13060	12660	80	14370	240	24.11
289	KIA-23840	23440	180	27860	190	8.90
399	KIA-29420	29020	320	33090	420	21.03
524	KIA-35660	35260	630	39960	960	18.20

calculated. These coefficients represent the proportion of the variance of each grain-size class that can be reproduced by the approximated data. This proportion is equal to the squared correlation coefficient (r^2) of input variables and their approximated values (Weltje, 1997; Prins and Weltje, 1999). As the terrigenous sediment fraction from the southern GoC is relatively fine-grained (<170 μm), the number of input variables for the end-member model of core GeoB 9064 was reduced from 66 to 47 classes in the range of 0.29–170 μm .

3.3.4. Planktonic foraminiferal assemblage

The analysis for planktonic foraminiferal relative abundance counts is based on the >150 μm fraction. For each sample a minimum of ~200 specimens were identified following the taxonomy of planktonic foraminifera proposed by Hemleben et al. (1989). For *N. pachyderma* the relative abundances of right (dex.) and left (sin.) coiling individuals were determined, and the two forms were treated as individual species. The data are represented as percentages of total planktonic foraminiferal number.

4. Results

4.1. U-series dating

All selected coral fragments indicated minor to moderate physico-chemical alteration or dissolution which may disturb U-series ages. Initial $\delta^{234}\text{U}_0$ values are variable and range between $125.9 \pm 2.7\%$ and $187.1 \pm 2.6\%$ (Table 2, Fig. 2). Measured ^{232}Th concentrations are small (<10 ng g^{-1}) for 75% of all samples (Fig. 2) but clearly specimens of *M. oculata* reveal more residual Th than *L. pertusa* (Table 2). This is a consequence of the cleaning procedure as the thinner polyps and more fragile skeleton of *M. oculata* is by far more difficult to clean. However, Th contamination is negligible since in general the $^{230}\text{Th}/^{232}\text{Th}$ activity ratios are >1000.

Calculated U-series ages from all investigated coral sites in the GoC range from 9.2 ka to more than 400 ka (Fig. 3). Two samples from core GeoB 12101 could not be dated due to above equilibrium radioactive isotopic composition indicating U-series open system behaviour. More than 90% of all obtained ages correspond to glacial periods (Marine Isotope Stage (MIS) 2 back to MIS12), and 70% of these glacial coral ages cluster within the last glacial (MIS2-4) (Fig. 3). With regard to the initial $\delta^{234}\text{U}_0$, it is evident that the scatter increases largely beyond a coral age of 150 ka which is clearly indicative of increasing U-series system opening (Thompson et al., 2003; Scholz et al., 2004; Frank et al., 2006; Robinson et al., 2006). Consequently, those ages are less precise than the measured uncertainty would suggest which has to be taken in consideration for our data interpretation. Coral ages between 14 and 60 ka yield a mean initial $\delta^{234}\text{U}_0$ of $143.2 \pm 2.3\%$ ($n = 22$, 2σ standard deviation), which is slightly lower than measured in modern corals and seawater (146.6–149.6%; Delanghe et al., 2002; Robinson et al., 2004). Thus either corals suffer from minor U-series system opening, and thus, preferential loss of ^{234}U , or the glacial mean value of seawater was slightly lower than compared to today as suggested by Esat et al. (1999). Overall we consider that within a range of $149 \pm 10\%$ calculated ages are representing the chronological ages of the corals within the uncertainty of measurement (see also Stirling et al., 1998; Robinson et al., 2004; Esat and Yokoyama, 2006). However, we are aware that a more detailed analysis of the U-series data and uncertainties considering potential seawater U-isotopic variations, diagenetic alteration and U-series system opening is needed to improve in particular the quality of coral ages beyond 150 ka.

4.2. Age model core GeoB 9064

The age model of core GeoB 9064 for the last ~40 kyr is based on six AMS ^{14}C age control points and linear interpolation between these dates (Table 3, Fig. 4). The age model is supported by the correlation of the $\delta^{18}\text{O}$ measurements of the record (showing heavy $\delta^{18}\text{O}$ values of

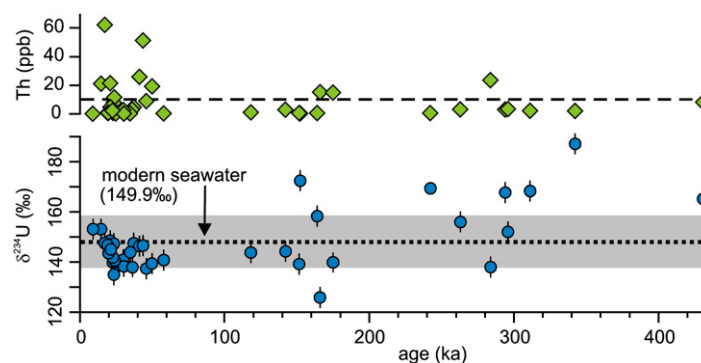


Fig. 2. Initial U-isotopic ratios of cold-water corals (lower graph) and ^{232}Th concentration (upper graph). $\delta^{234}\text{U}$ is in almost all cases very close to present-day seawater (149.9‰; black dotted line; range of $149.9 \pm 10\%$; light grey bar), except for the deepest sample in core GeoB 12104 (+38‰). ^{232}Th concentrations for 75% of all samples are below 10 ng g^{-1} (black dashed line).

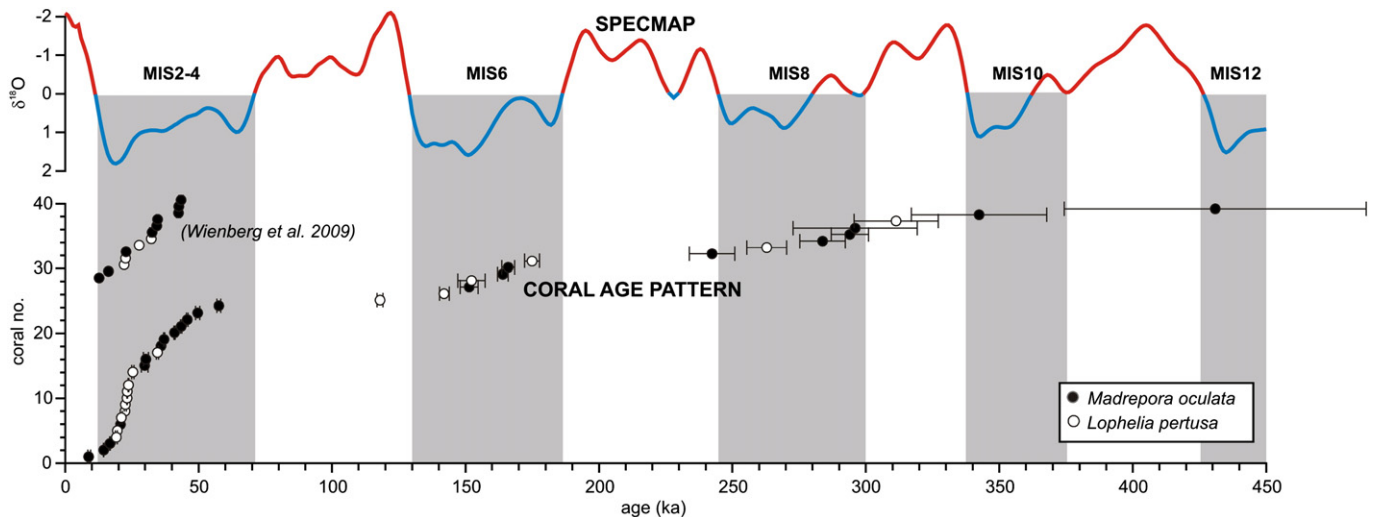


Fig. 3. $^{230}\text{Th}/\text{U}$ datings conducted on cold-water coral fragments collected in the GoC. AMS ^{14}C ages presented by Wienberg et al. (2009) are implemented. Note that solely reef-forming species such as *M. oculata* and *L. pertusa* are considered showing that >90% of all coral ages coincide with glacial periods. Marine Isotope Stages (MIS) are indicated by grey bars based on SPECMAP $\delta^{18}\text{O}$ stack (Imbrie et al. 1989).

1.5–2.5‰ for the last glacial and light values of <1.0‰ for the Holocene; Fig. 4) with the $\delta^{18}\text{O}$ record of the GRIP ice core (GRIP Members, 1993). The estimated average sedimentation rate is $\sim 16 \text{ cm ka}^{-1}$ (Table 3). Highest sedimentation rates of $18\text{--}24 \text{ cm ka}^{-1}$ occur during MIS3 and the last deglaciation. Lowest sedimentation rates of $8\text{--}9 \text{ cm ka}^{-1}$ are obtained for MIS2 and the Holocene (Fig. 4).

4.3. Grain size distribution and source

The median grain size of the terrigenous (bulk) fraction of sediment core GeoB 9064 varies between $5.71 \mu\text{m}$ ($5.93 \mu\text{m}$) and $12.03 \mu\text{m}$ ($17.88 \mu\text{m}$). The last glacial period and the Younger Dryas (YD) cold event are characterised by relatively coarse sediment deposition. In contrast, during the Holocene a distinct and continuous decrease of grain sizes is clearly visible ($6\text{--}9 \mu\text{m}$) (Fig. 4). A three-end-member model was created (with $r^2 = 0.77$) to describe the grain size data set of core GeoB 9064. The grain size distributions of the three end members are all unimodal, well-sorted and have relatively fine modal grain sizes with $25 \mu\text{m}$ for EM1, $16 \mu\text{m}$ for EM2, and $5 \mu\text{m}$ for EM3. Several sedimentological studies confirmed that aeolian sediments deposited in the deep-sea close to the continent are coarser grained than hemipelagic sediments with terrigenous sediments with mean grain sizes $>6 \mu\text{m}$ being generally attributed to aeolian transport, and sediments $<6 \mu\text{m}$ to hemipelagic transport (Ratmeyer et al., 1999; Prins et al., 2000). In addition, the mean modal sizes of present-day aeolian dust, collected along a transect of the NW African coast (33°N to 12°S) vary between $8 \mu\text{m}$ and $42 \mu\text{m}$ (Stuut et al., 2005). Hence, for core GeoB 9064, the two coarsest end members of the three-end-member model are considered to be of aeolian origin with EM1 interpreted as ‘coarse’ aeolian dust and EM2 as ‘fine’ aeolian dust. In contrast, EM3 is interpreted to result predominantly from fluvial input (Koopmann, 1981; Holz et al., 2007). During the last glacial, the aeolian content varies considerably between 30% and 60% and shows in particular during MIS3 rapid fluctuations. Close to the end of the last glacial ($\sim 17 \text{ ka}$), the aeolian content decreases before it increases again up to 60% during the YD. With the end of the YD ($\sim 11.5 \text{ ka}$), the proportion of the aeolian content on the total terrigenous fraction decreases continuously down to 25% (Fig. 4).

The EM1/EM2-ratio is considered as a measure for the relative wind intensity (Stuut et al., 2002). For core GeoB 9064, relatively high wind strength is indicated for the last glacial showing millennial-scale fluctuations. At $\sim 22 \text{ ka}$, the wind conditions changed dramatically. Within a time period of 1.5 kyr, wind intensity decreased remarkably

by 50% and stayed low during the entire Holocene (Fig. 4). This is deduced from a reduction of the content of ‘coarse’ aeolian dust (EM1) to almost zero, whereas the ‘fine’ aeolian dust (EM2) slightly increased towards the present.

4.4. Planktonic foraminiferal assemblage and abundance

The most abundant species in core GeoB 9064 is *N. pachyderma* dex. (27.1%), followed by *Globigerinita glutinata* (21.1%), *Globigerina bulloides* (15.8%), and *Globorotalia inflata* (12.2%). Together with *Globigerinoides ruber* (5.2%), *Globorotalia scitula* (4.5%), and *N. pachyderma* sin. (4.5%), these species account on average for >90% of the total planktonic foraminifera.

Maximum relative abundances of *N. pachyderma* dex. are recorded during the last glacial, contributing up to 60% of the total planktonic foraminifera fauna. At the end of the last glacial (15.5–14.5 ka), its relative abundances decreased remarkably down to 10%, followed by an increase up to 40% during the YD. At the end of the YD ($\sim 11.5 \text{ ka}$), relative abundances of *N. pachyderma* dex. significantly decreased down to <5% (Fig. 5). A similar trend is indicated for *N. pachyderma* sin., although it shows comparably lower abundances below 18%. Another abundant species during the last glacial was *G. glutinata* with relative abundances of 10–40%. During the course of the Holocene, its contribution was rather low with minimum rates of <10% except for the period between 10 and 8.5 ka, with relative abundances of up to 28%. An opposite trend to the above mentioned species is observed for *G. bulloides*. Relatively low abundance occurred during the last glacial (<20%), whereas during the Holocene, its relative contribution to the total fauna increased to >20%. In particular between 8.5 and 2 ka, *G. bulloides* was the most common species within the planktonic foraminiferal fauna with relative abundance of 30–48%. Between 40 and 18 ka, abundances of *G. inflata* were below 20%, and increased up to 38% until the onset of the YD. During the Holocene, its abundances varied between 8% and 20%. One distinct minimum (<10%) of *G. inflata* abundance is indicated between 10 and 8.5 ka that mirrors the concomitant maxima of *G. glutinata*. Contributions of *G. scitula* to the total fauna was rather moderate for most of the last glacial, and decreased remarkably around 18 ka to <5%, and remained low thereafter (Fig. 5). During the last glacial and until the end of the YD ($\sim 11.5 \text{ ka}$), *G. ruber* shows a low abundance of 0–10% that increased to 10–25% during the Holocene. *Globigerinoides sacculifer* was even absent during the last glacial. This species is exclusively found during the Holocene with relative abundances of up to 7.5% (Fig. 5).

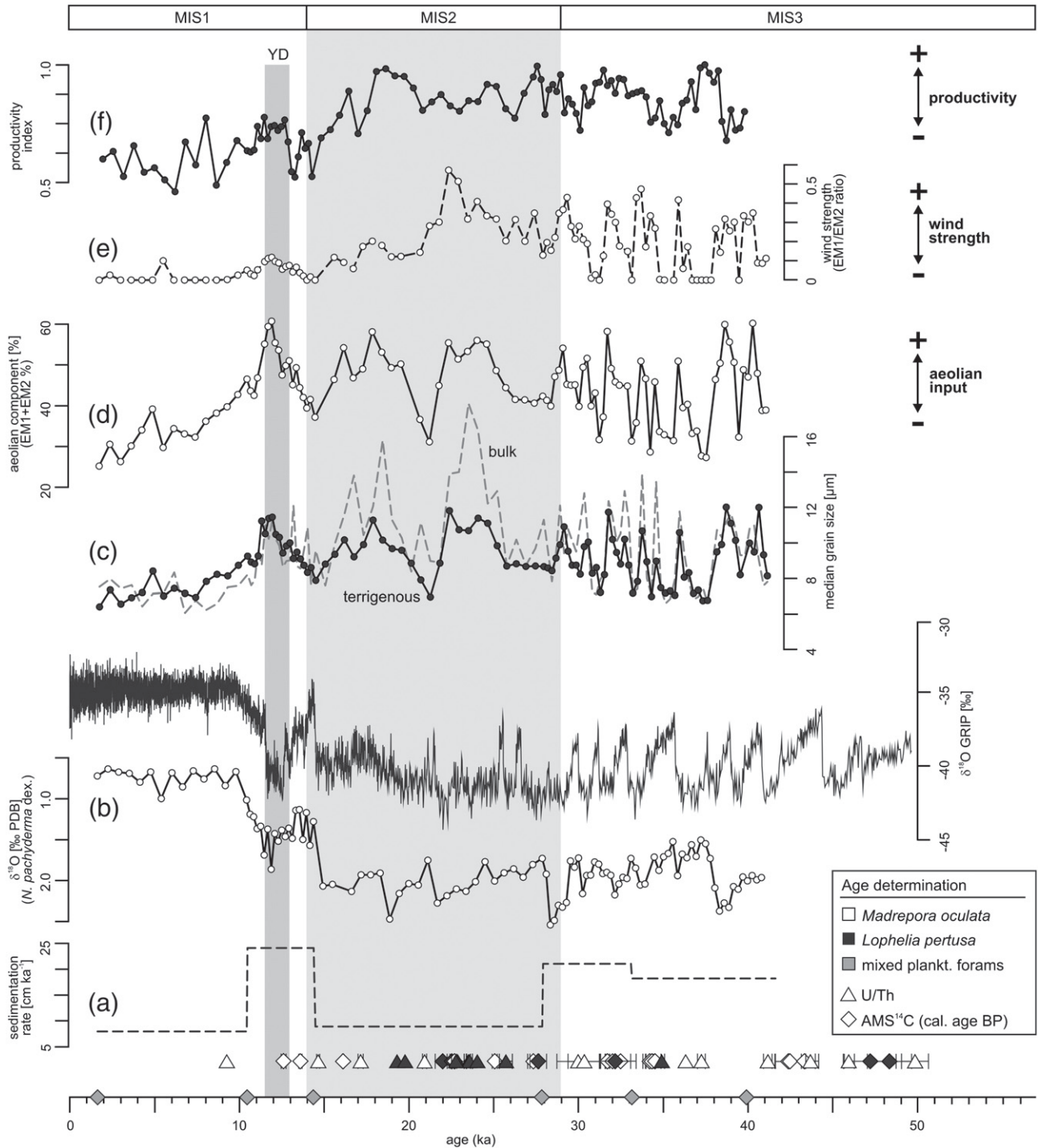


Fig. 4. Multi-proxy data of sediment core GeOB 9064. (a) Estimated sedimentation rate, (b) stable oxygen isotopes record (lower curve) compared with the GRIP ice core record (upper curve) (c) median grain size (terrigenous and bulk sediment), (d) relative aeolian input, (e) relative wind strength, and (f) productivity index based on the ratio of high- to low-productivity planktonic foraminiferal assemblages. AMS ^{14}C dates obtained for core GeOB 9064 are marked by grey diamonds. For comparison, U/Th (squares; this study) and AMS ^{14}C coral dates (triangles; Wienberg et al., 2009) obtained for the past 50 kyr are implemented. Note that solely reef-forming species such as *Madrepora oculata* and *Lophelia pertusa* are considered.

5. Discussion

5.1. Glacial coral growth phases in the Gulf of Cádiz

During the past years, much effort has been invested into dating cold-water corals from various sites along the NE Atlantic margin. The most comprehensive data set of coral ages exists for the Irish margin and reveals that coral growth in this area is restricted to the Holocene and prior interglacial periods (Frank et al., 2005; Rüggeberg et al., 2007; de Haas et

al., 2009; Frank et al., 2009). In contrast, for coral sites south of 50°N the data set of coral ages is rather scattered. However, the available dates suggest that the major phase of coral growth along the French, Iberian and Moroccan margins coincide with the last glacial period (Taviani et al., 1991; Schröder-Ritzrau et al., 2005; Wienberg et al., 2009).

For the GoC, it was shown that the reef-forming coral species *L. pertusa* and *M. oculata* have been restricted to a period between 12 and 45 ka (Wienberg et al., 2009). This preliminary result is confirmed by our data. In addition, the U/Th dates presented here show that

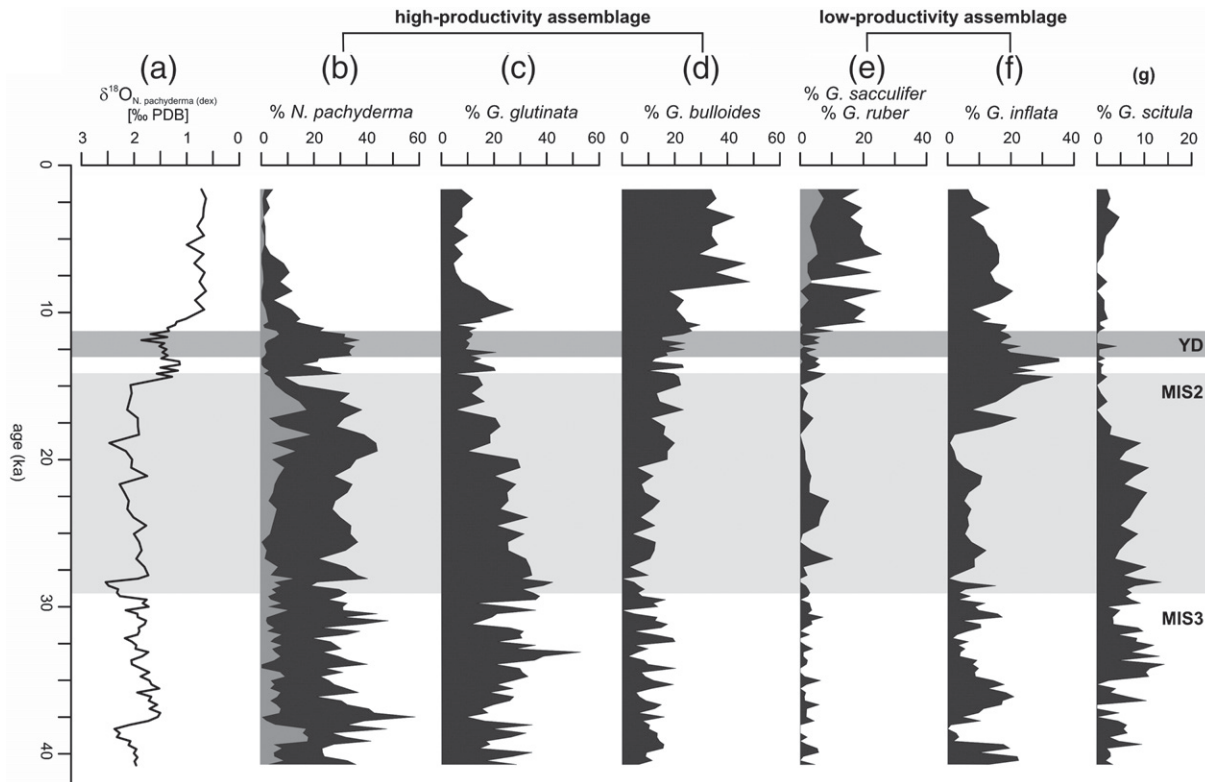


Fig. 5. The $\delta^{18}\text{O}$ record and planktonic foraminiferal abundance for sediment core GeoB 9064. (a) $\delta^{18}\text{O}_{N. pachyderma}$ (dex.), (b) *Neogloboquadrina pachyderma* (black: dex., grey: sin.), (c) *Globigerinita glutinata*, (d) *Globigerina bulloides*, (e) *Globigerinoides ruber* (black) and *Globigerinoides sacculifer* (grey), (f) *Globorotalia inflata*, (g) *Globorotalia scitula*. Younger Dryas (YD) and Marine Isotope Stages (MIS) 2 and 3 are indicated.

major phases of coral growth in the GoC are not solely restricted to the last glacial but also to prior glacial periods (back to MIS12), whereas during interglacials coral growth seems to be reduced or even absent (Fig. 2).

Most conspicuous is that the widespread decline of the coral ecosystems in the GoC during the YD cold reversal (12.9–11.5 ka) corresponds to the re-start of coral mound formation on Rockall Bank and the re-establishment of coral mound growth along the slopes of the Porcupine Seabight at around 11 ka (Frank et al., 2009). Regarding this pattern, we suggest that at the transition of the last glacial–interglacial, a latitudinal shift of areas with optimum cold-water coral growth conditions towards the northern NE Atlantic occurred that was most probably related to dramatic changes of the oceanographic and environmental conditions caused by climate change. Moreover, this northward shift happened rapidly over just a few hundreds of years and over a distance of 2000–2500 km (GoC to Irish margin).

Unfortunately, we still lack detailed understanding of the reproductive ecology and larval dispersal mode of scleractinian cold-water corals. Histological studies show that the cosmopolitan species *L. pertusa* exhibits an annual gametogenic cycle with spawning around January/February (Waller and Tyler, 2005). The widespread occurrence of *L. pertusa* and the rapid colonisation of man-made structures such as oil rigs (25 mm year⁻¹; Bell and Smith, 1999), point to a dispersive planula larva being capable to remain in the water column for several weeks.

5.2. Driving factors for coral growth

A combination of environmental and oceanographic conditions is required to promote a sustained development of cold-water coral ecosystems. Cold-water corals require (1) hard substrate to settle on, (2) protection against burial to grow, and (3) sufficient food supply. Therefore, they predominate in areas where strong currents prevail that reduce deposition of fine-grained sediments and supply large

quantities of food (Roberts et al., 2006). Today, thriving coral ecosystems occur in high concentrations in areas that are characterised by enhanced primary production in the surface waters of eutrophic systems, allowing a considerable part of the new production to be transported to the seafloor. In addition, tidal currents and internal waves have been identified (1) to enhance concentrations of organic matter at the shelf edge and (2) to transport fresh food particles to and through the cold-water coral reefs (Frederiksen et al., 1992; White et al., 2005, 2007). Recently, Dullo et al. (2008) indicated for the Celtic and Nordic margins that living cold-water corals occur within the density envelope of sigma-theta (σ_{θ}) = 27.35–27.65 kg m⁻³ emphasising the importance of physical boundary conditions. Finally, the world's most common cold-water coral species *L. pertusa* tend to be associated with oceanic water masses with a temperature of 4–12 °C (Roberts et al., 2006), and even up to 14 °C in the Mediterranean Sea (Taviani et al., 2005; Freiwald et al., 2009), salinities between 31.7 and 38.78 (Freiwald et al., 2004; Davies et al., 2008), and oxygen concentrations of 4.3–7.2 ml l⁻¹ (for the NE Atlantic; Davies et al., 2008).

For the GoC, all these requirements must have been fulfilled during glacial periods as cold-water corals were widespread during these times. During interglacial periods, these optimal environmental and oceanographic conditions must have been changed dramatically resulting in a widespread (gulf-wide) demise of the formerly thriving corals. As our obtained coral ages mainly cluster within the last glacial (~70%), the environmental and oceanographic changes of the GoC, focussing on the last glacial–interglacial cycle, are discussed in detail to identify the main forcing factors for coral growth in the GoC.

5.2.1. Effects of increased palaeo-productivity on cold-water coral growth

Strong vertical fluxes of labile organic matter, as often found in eutrophic regions, result in rich benthic fauna (e.g., De Stigter et al.,

1998; Schmiedl et al., 2000; Fontanier et al., 2002). In the NE Atlantic, seasonal algae blooms that sink rapidly to the deep-sea floor can even have a positive effect on the reproductive biology of benthic invertebrates (Billett et al., 1983; Thiel et al., 1989; Tyler et al., 1992), a relationship which is also hypothesised for *L. pertusa* and *M. oculata* thriving along the Irish margin (Waller and Tyler, 2005). Thus, enhanced productivity is a pre-requisite for a sustained development of healthy cold-water coral ecosystems. Indeed, regions with enhanced primary production as deduced from satellite-based observations of the chlorophyll content in surface waters (Behrenfeld et al., 2005) seem to mirror the recent distribution of thriving coral sites in the NE Atlantic.

Certain species of planktonic foraminifera strongly depend on primary productivity in the modern ocean (Hemleben et al., 1989), and hence downcore variations of the abundance of planktonic foraminiferal species within sedimentary records can be applied to assess palaeo-productivity conditions (e.g., Ivanova et al., 2003). In this context, the environmental constraints of the most abundant foraminiferal species identified for the GoC are reviewed in detail.

G. bulloides mainly thrives in the surface mixed layer above the thermocline and prefers relatively cold and nutrient-rich waters (e.g., Ganssen and Kroon, 2000; Chapman, 2010). Moreover, this species preferably occurs in areas along the Iberian and NW African margins that are characterised by pronounced seasonal upwelling, and thus, by high phytoplankton density and prey abundance (Salgueiro et al., 2008; Wilke et al., 2009). The opportunistic and cosmopolitan species *G. glutinata* is also strongly associated with the increase in productivity during spring bloom events in the North Atlantic (Chapman, 2010). However, the distribution of this species is found to be even more significantly associated with productivity than that of *G. bulloides*, which can be explained by its diet that preferentially consists of diatoms (Bé and Tolderlund, 1971; Hemleben et al., 1989; Schiebel et al., 2001). The sub-polar species *N. pachyderma* dex. prefers colder waters than *G. bulloides* (Bé and Tolderlund, 1971). Off the northern Iberian margin, high percentages of this species have been related to increased productivity generated by high river runoff (Salgueiro et al., 2008). In the GoC, *G. glutinata* and *N. pachyderma* dex. clearly dominate the foraminiferal assemblage during the last glacial with relative abundances of 55 to 75% (Fig. 5), thus pointing to rather nutrient-rich and cold conditions compared to the following Holocene when both species account for only ~10%. However, although *G. bulloides* is regarded as an indicator for nutrient enriched conditions it shows an opposite trend compared to the other two species.

G. inflata is considered a non-upwelling species and high relative abundances of this species in the North Atlantic coincide with oligotrophic waters (Pflaumann et al., 2003; Salgueiro et al., 2008). The two surface-dwelling species *G. ruber* and *Globigerinoides sacculifer* show a preference towards oligotrophic conditions as well (e.g., Ivanova et al., 2003; Mohtadi et al., 2007). These species prefer warm and well stratified surface waters (Duplessy et al., 1981; Stoll et al., 2007; Chapman, 2010). For the NE Atlantic, a significant increase in the relative abundances of *G. sacculifer* is observed when surface stratification is at a maximum and high sea surface temperatures prevail (Chapman, 2010). The significant increase of *G. ruber* and *G. sacculifer* after the YD cold event as found in our record (Fig. 5) thus indicates such warm and well stratified conditions in the GoC during the Holocene.

Taking all these findings for the NE Atlantic into account, *G. sacculifer*, *G. ruber* and *G. inflata* are inferred to represent a low-productivity assemblage, whereas *G. glutinata*, *G. bulloides* and *N. pachyderma* dex. are grouped as indicators for enhanced productivity. Similar to the approach of Stoll et al. (2007), we calculated the ratio of both assemblages and interpreted this ratio as an indicator of productivity (Fig. 4f), regardless of their affinity to upwelling processes. This ratio clearly shows that during the last glacial palaeo-productivity was overall enhanced in the GoC, which is in

particular expressed by high relative abundances of *G. glutinata* (Fig. 5). Following the end of the last glacial, this ratio significantly changed towards more oligotrophic conditions (Fig. 4).

5.2.2. Implications of frontal upwelling on glacial productivity in the GoC

This pattern of eutrophic conditions during the last glacial and oligotrophic conditions during the Holocene found for the GoC might be explained by a shift of the Azores Front (Rogerson et al., 2004). The Azores Front marks a zone of strong hydrographic transition associated with enhanced biological production caused by locally intense upwelling (Alves and DeVerdière, 1999). Today, the easternmost extension of the Azores Front is situated at 30°N off the Moroccan margin (Gould, 1985; Schiebel et al., 2002), and hence, does not penetrate into the GoC that extends from 37°N to 33°N (Fig. 1). But there is evidence that the Azores Front shifted northward and thus penetrated eastward into the GoC prior to 16 ka and during the YD (Rogerson et al., 2004). Rogerson et al. (2004) indicated this glacial shift of the Azores Front towards the GoC by high abundances of the planktonic foraminifer *G. scitula* in their records. This deep-dwelling species (100–700 m water depth) (Schiebel et al., 2002) is used as an indicator for cool surface waters and enhanced vertical mixing at temperate latitudes (e.g., Thunell and Reynolds, 1984; Perez-Folgado et al., 2003). Today *G. scitula* is found in high numbers in the Azores Front where upwelling causes high productivity (Schiebel et al., 2002), but it is almost absent in the GoC (Rogerson et al., 2004). The record of core GeoB 9064 shows that *G. scitula* is common prior to the Last Glacial Maximum (LGM), but is rare throughout the Holocene (Fig. 5) pointing to enhanced productivity during the last glacial caused by frontal upwelling.

5.2.3. Fertilisation effect of aeolian dust

Besides the effect of locally intensified upwelling that likely occurred in the GoC during the last glacial also the high input of aeolian dust might have significantly enhanced glacial productivity in the area. Grain size data from various sediment cores in the GoC, including our data (Fig. 4), show that during the last glacial mean grain sizes were rather coarse compared to the following Holocene (e.g., Rogerson et al., 2005; Voelker et al., 2006). Up to now, these grain size variations have been primarily attributed to changes in the strength of the prevailing bottom currents implying that bottom current strength was enhanced during the last glacial probably caused by a shift and intensification of the MOW's flow pathway (Schönfeld and Zahn, 2000; Rogerson et al., 2005; Voelker et al., 2006). Another common finding for the GoC is a rather low Holocene sedimentation rate (e.g., Rogerson et al., 2005; Voelker et al., 2006). Rogerson et al. (2005) estimated a Holocene accumulation rate that is only one fifth of that of the last glacial, and thus is in agreement with our estimated rates (Fig. 4). They assumed that this tremendous change in sedimentation rate was caused by a higher sediment supply prior to the last deglaciation but without indicating the major source of sediments supplied to the GoC.

However, this study shows that the variations in grain size and sedimentation rate as found for the GoC are rather the result of changes in the source of the terrigenous sediments and the amount of sediment input. Our grain size data clearly reveal that during the last glacial the deposition of aeolian transported sediments prevailed in the GoC (Fig. 4). During this time rather arid and cold conditions prevailed over the NW African continent (Gasse, 2000), and the intensity of the northern trade winds, which transport the aeolian dust, was enhanced especially from about 36°N to 24°N (Sarnthein et al., 1981; Hooghiemstra et al., 1987; Moreno et al., 2002). This is supported by our record showing that wind strength off Morocco (35°N) was significantly enhanced during the last glacial (Fig. 4). With the end of the YD, the proportion of the aeolian content on the total terrigenous fraction decreased continuously from 60 to 25% (Fig. 4), corresponding to the African humid period, which is known to be

characterised by a relatively humid and green Sahara with significantly lower amounts of aeolian dust being produced (e.g., deMenocal et al., 2000; Gasse, 2000). The African humid period terminated at 5.5 ka and the area of the Saharan desert returned to a state of hyperarid conditions (deMenocal et al., 2000). However, wind strength remained relatively low compared to the strong glacial trade winds (Hooghiemstra et al., 1987) and dust fluxes have been estimated to be today 2–4 times lower compared to the LGM (Grousset et al., 1998). Also our data show no significant increase of the input of aeolian dust in the GoC after 5.5 ka until today (Fig. 4).

The large input of aeolian dust during the last glacial coincides with a prosperous cold-water coral community in the GoC (Fig. 4). The link between dust input and coral prosperity was probably established by a simple fertilisation effect. During periods of enhanced Saharan dust input over the NE Atlantic, the supply of iron and manganese to the surface ocean is enhanced as well (de Jong et al., 2007) which promotes primary production in the surface waters (e.g., Boyd et al., 2000), and as a consequence, also might increase food availability for the bathyal cold-water corals.

5.2.4. Limitation of water temperatures on the prosperity of cold-water corals

The planktonic foraminiferal abundance data of core GeoB 9064 is consistent with the thermal history of the LGM and deglaciation. The general warming of the North Atlantic at the transition from the last glacial to the Holocene is reflected by a considerable increase in the abundance of *G. ruber* and *G. sacculifer* and a concurrent decrease in abundance of *N. pachyderma* dex., which is even more pronounced after the YD cold reversal (Fig. 5). This pattern is in agreement with other foraminiferal fauna records from the GoC (Sierro et al., 1999; Rogerson et al., 2004). The change from rather cool towards warm surface waters after the end of the YD was most likely accompanied by a change in subsurface temperatures in intermediate water depths, thus having an impact on the bathyal cold-water corals. Regarding the average temperatures of the intermediate water masses prevailing in the GoC (NACW: ~12 °C, Ait-Ameur and Goyet, 2006; MOW: 10.5–12 °C, Fusco et al., 2008), it becomes obvious that at least today water temperatures are at the very upper tolerance for reef-forming scleractinian cold-water corals such as *L. pertusa* (12 °C; Roberts et al., 2006). Moreover, dendrophylliid coral species that prefer rather warm conditions compared to *L. pertusa* seem to have been more common during the late Holocene (Wienberg et al., 2009).

6. Conclusion

This study clearly shows that the occurrence of cold-water corals in the GoC is dominant within the last glacial and prior glacial periods and that hardly any cold-water corals exist in this region during interglacials. Moreover, it could be identified that at the end of the YD cold event a shift from eutrophic to oligotrophic and warm conditions have been responsible for the demise of the formerly thriving coral ecosystems. The enhanced productivity conditions during the last glacial have been most probably caused by (1) an enhanced input of aeolian dust and (2) a shift of the Azores Fronts towards the GoC causing locally intense upwelling. Both factors supported enhanced primary productivity in the GoC, and thus resulted in enhanced food availability for the corals. By comparing our data set for the GoC with coral ages from the Norwegian and Irish margins that reveal a sustained prosperity of coral ecosystems right after the YD, it appears that a northward shift of areas with optimum cold-water coral growth conditions took place during the transition from the last glacial to the recent interglacial. The cold-water corals responded very rapidly to climate change over just a few hundreds of years, and it is most likely that in the course of global warming going along with dramatic changes in the environmental setting this northward trend will further continue.

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