Mid-depth oxygen drawdown during Heinrich events: evidence from benthic foraminiferal community structure, trace-fossil tiering, and benthic $\delta^{13}C$ at the Portuguese Margin

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Abstract

The distribution of trace fossils and benthic foraminiferal assemblages in two sediment cores from 2160 m water depth at the northern and 1100 m at the southern Portuguese continental margin was used to reconstruct the bottom-water oxygenation during the last 40 ka. Emphasis was given to the Heinrich events, during which enhanced meltwater flux associated with the iceberg surges reduced or even halted deep water formation in the North Atlantic. Condensed trace-fossil tiering structures and high proportions of low-oxygen-tolerant benthic foraminifera suggest a major drawdown of bottom-water oxygenation during Heinrich events. Using the benthic foraminiferal oxygenation index (BFOI) of Kaiho (1991, 1994) that links benthic foraminiferal communities to ambient bottom-water oxygenation, we extracted apparent oxygen concentrations from benthic assemblages. BFOI values suggest low-oxic conditions during Heinrich events 1 and 4 with mean oxygen levels of 2.6 to 2.8 ml l$^{-1}$ and high-oxic conditions with 4.1 ml l$^{-1}$ during Heinrich event 2 at the shallower site. High proportions of low-oxygen-tolerant foraminiferal species and BFOI minima are recorded a few centimetres below the maximum concentrations of ice-rafted debris, indicating that the original microhabitat depth of dysoxic species is preserved beneath the Heinrich layers even though bioturbation continued during the events. Trace-fossil tiering calibrated with the redox boundary in low-oxic environments and dysoxic ichnotaxa commonly associated with black shales indicate oxygen levels lower than those implied by the BFOI. Oxygenation estimates derived from trace-fossil tiering denote low-oxic conditions during H1 (13.3 ka) with oxygen concentrations slightly above 1 ml l$^{-1}$, and dysoxic conditions during H2 (20.6 ka), H3 (27 ka) and H4 (33.5 ka) with oxygen concentrations between 0.1 and 1 ml l$^{-1}$. During the Younger Dryas, bottom waters likely were low oxic. Negative excursions of benthic carbon isotope values provide independent control on the oxygen drawdown during Heinrich events. Considering a bottom-water oxygenation of 6.1 to 6.5 ml l$^{-1}$ during the last glacial, the benthic $\delta^{13}C$ minima reveal an oxygen depletion to values between 3.4 and 5.0 ml l$^{-1}$ during H1 through H4 at the shallower core site. Differences between estimates from benthic $\delta^{13}C$, BFOI and trace-fossil tiering suggest that benthic foraminiferal communities are rather robust to oxygen depletion if the level does not fall below 3 ml l$^{-1}$, whereas burrowing organisms react sensitively to depth variations of the redox boundary in near-surface sediments due to even small changes of bottom-water oxygenation. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The North Atlantic region episodically experienced sudden changes in climate and thermohaline circulation on time scales of 7–10 ka during the last glacial period. As a result, distinctive layers of ice-rafted debris (IRD) were deposited between 40°N and 60°N (Ruddiman, 1977; Heinrich, 1988; Bond et al., 1992, 1993). The IRD layers were generated by major breakdowns of the North American Laurentide ice sheet, releasing large amounts of meltwater and icebergs into the North Atlantic, known as Heinrich events (Bond et al., 1992; Broecker et al., 1992; Alley and MacAyeal, 1994; Andrews et al., 1994; Broecker, 1994). The cause for these events is still under debate. Iceberg release may follow quasi-periodic, geothermally controlled surging of the Laurentide ice sheet (MacAyeal, 1993; Alley and MacAyeal, 1994). Alternatively, climate change has been proposed as the cause for the breakdown of the Laurentide ice sheet (Bond et al., 1993; Bond and Lotti, 1995).

Heinrich events are associated with major palaeoceanographic changes in the North Atlantic. Decreased concentrations of foraminifera and a dominance of the left-coiling planktonic foraminifer *Neogloboquadrina pachyderma* in the remaining fauna (Heinrich, 1988; Broecker et al., 1992; Bond et al., 1992) indicate a decrease in marine surface productivity at polar water temperatures. Depletion of planktonic $\delta^{18}O$ denotes salinity drops due to the introduction of large volumes of meltwater (Heinrich, 1988; Broecker et al., 1992; Bond et al., 1993; Andrews et al., 1993). Dramatic decreases in benthic $\delta^{13}C$ values (Keigwin and Lehman, 1994; Zahn et al., 1997) are evidence for a reduction in deep-water formation during Heinrich events, possibly to such a degree that the North Atlantic conveyor belt was shut off entirely and a stratified water mass covered the North Atlantic (Bond et al., 1992; Duplessy et al., 1992; Sarnthein et al., 1994; Broecker, 1994). Model calculations suggest that the North Atlantic conveyor belt was switched off and on rapidly at the beginning and the end of Heinrich events within periods of about 100 years (Paillard and Labeyrie, 1994; Manabe and Stouffer, 1995).

Reduced thermohaline overturn in the North Atlantic during Heinrich events resulted in a significant nutrient enrichment in intermediate to deep waters, displayed by high Cd/Ca values in benthic foraminiferal shells (Boyle and Keigwin, 1987; Willamowski et al., 1996; E.A. Boyle, pers. commun., 1996). This invokes a drastic reduction in dissolved oxygen of the North Atlantic Deep Water (Zahn et al., 1997), which should have major implications for the composition of benthic communities. Assemblages dominated by species that are able to withstand low oxygen concentrations in bottom water are to be expected for Heinrich layer intervals.

We describe the distribution of benthic foraminifera and trace fossils in sediment cores from the Portuguese continental margin: (1) to reconstruct relative changes in the degree of bottom-water oxygenation during the last 40 ka, with special emphasis on Heinrich events, and (2) to constrain oxygen concentrations of bottom waters during Heinrich events by applying oxygenation models for benthic foraminifera (Kaiho, 1991, 1994) and trace fossils (Savrda and Bottjer, 1986) and by comparison with estimates of apparent oxygen utilisation from benthic $\delta^{13}C$ records.

2. Study area and hydrography

Debris-laden icebergs reached the Portuguese continental margin after crossing the North Atlantic during Heinrich events (Schönfeld, 1993; Mienert, 1994; Lebreiro et al., 1996; Baas et al., 1997). Although the flux of IRD was lower than in the open North Atlantic (Baas et al., 1997), the impact of the Heinrich events on surface-water hydrography and deep-water convection is well recorded at the southern Portuguese Margin (Zahn et al., 1997). At present, the hydrography of the North Atlantic adjacent to the western Iberian continental margin is determined by North Atlantic Central Water (NACW) from the thermocline down to 600 m, Mediterranean Outflow Water (MOW) between 600 to 1500 m, and North Atlantic Deep Water (NADW) from 1500 m down to the seafloor (Wüst, 1936; Meincke et al., 1975; Zenk and Armi, 1990). NADW formation was reduced during the last glacial maximum (Sarnthein et al., 1994) and may have been shut down entirely during Heinrich events. The advection of MOW was likely reduced during the last glacial due to a lowered sea level. Glacially increased salinity and lower
temperature of MOW probably also resulted in a deepening of the MOW core layer (Zahn et al., 1987; Schönfeld, 1993). Advection of nutrient-rich Antarctic Bottom Water (AABW) took place at depths between 2500 and 3500 m below the glacial NADW (Duplessy et al., 1988; Boyle and Weaver, 1994; Sarnthein et al., 1994). In this study we use assemblages of benthic foraminifera and trace fossils as indicators for ambient bottom-water oxygen levels. This strategy is based on the observation that different benthic foraminiferal species and different types of trace fossils are closely tied to different levels of bottom- and pore-water oxygenation (Savrda and Bottjer, 1986; Koutsoukos et al., 1990; Hermelin, 1992; Alve, 1995).

Besides changes in water-mass oxygen levels, the benthic foraminiferal and trace-fossil assemblages may have been influenced by other environmental parameters such as flux of carbon to the seafloor and sediment redep osition. Carbon flux fuelling the deep-sea benthic communities also has a strong impact on bentic environmental factors such as ecosystem stability, predation and competition among benthic species (Lipps, 1983; De Stigter, 1996). Today, limited coastal upwelling occurs along the Portuguese Margin (Fiúza, 1983; Abrantes, 1988) but productivity levels remain well below those known from other upwelling areas (60 to 90 g C m$^{-2}$ yr$^{-1}$ compared, e.g., to 345 g C m$^{-2}$ a$^{-1}$ off Peru; Berger et al., 1987). Coastal upwelling may have been stronger during the last glaciation as inferred from systematic changes of diatom assemblages (Abrantes, 1991). Increased flux of organic carbon to the seafloor potentially alters the chemical structure of the benthic boundary layer and may impart low-oxygen conditions in pore waters thus affecting the benthic biota.

Sediment gravity flows, which occur predominantly in east–west-trending submarine canyons along the Portuguese Margin, may transfer shelf sediments to greater depths (Vanney and Mougenot, 1990) and change the benthic environment there. This process was likely enhanced during periods of sea level lowstands, i.e. during the last glacial (Baas et al., 1997).

The influence of biotic environmental factors such as ecosystem stability and competition is difficult to assess (De Stigter, 1996). Yet, we need to separate the various environmental factors that may have contributed to glacial–interglacial changes of the benthic environment at the Portuguese Margin in order to estimate ambient oxygen levels from benthic foraminiferal and trace-fossil assemblages. As a first approximation, this will be done by using C$_{org}$-based records of palaeoproductivity and benthic foraminiferal $\delta^{13}$C as independent evidence for productivity and deep-water circulation-related changes of ambient bottom-water conditions.

3. Material and methods

Two cores from the southern and northern Iberian Margin were chosen for the present study (Fig. 1). Core SO75-26KL is located off Cape Sines, southern Portugal (37°49.3′N, 09°30.2′W, 1099 m water depth). ENAM-core PO200-10-28-2 was collected in greater water depth at the northern Portuguese Margin (41°29.30′N, 9°43.26′W, 2155 m water depth)

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Fig. 1. Bathymetric map with coring sites at the Portuguese continental margin.
(Mienert, 1994). Both cores were sampled at 10 cm intervals, sample spacing was reduced to 2 cm at levels of particular interest, e.g. Heinrich layers. The samples were washed through a 63 μm mesh and size fractions >355 μm (core SO75-26KL) and 250–500 μm (core PO200-10-28-2) were examined for IRD content (Baas et al., 1997; Zahn et al., 1997). Benthic foraminiferal census counts were performed on the >250 μm size fraction.

Oxygen isotope stratigraphies were established for both sediment cores using 20–25 specimens per sample of the planktonic foraminiferal species Globigerina bulloides (Fig. 2; Baas et al., 1997; Zahn et al., 1997). The age model for core SO75-26KL is primarily based on 15 AMS 14C datings on 600 to 1100 specimens of G. bulloides (Fig. 2). Most of these datings are concentrated around Heinrich events H1 and H2, but additional age-control points were obtained by correlating the structure of the planktonic δ18O record with that of a continuously AMS 14C-dated isotopic curve from nearby core SU81-18 (Bard et al., 1987, 1989; Zahn et al., 1997). The chronostratigraphy of core PO200-10-28-2 is based on 6 AMS 14C datings on about 2000 specimens of G. bulloides (Fig. 2; Baas et al., 1997). A reservoir correction of 400 years was applied to all ages.

To monitor the evolution of the benthic foraminiferal community, benthic foraminifera were counted from the grain-size fraction >250 μm. This size fraction was used to obtain an autochthonous faunal record, as smaller tests from shelf and upper slope species are often displaced by downslope transport and may result in considerable bias of the benthic signal (Lohmann, 1978; Lutze and Coulbourn, 1984).

Trace fossils were studied on X-ray photographs from 5 mm thick slabs which were cut from split core sections. Anode voltage was 35 kV; exposure time was 11–15 s. Because core SO75-26KL was sampled immediately after retrieval onboard RV SONNE, shore-based preparation of X-ray slabs was not possible. We therefore studied the trace-fossil assemblage of nearby ENAM core PO200-10-6-2, which is located only 400 m to the northwest of SO75-26KL. Box core PO200-10-6-1 from the same location was used to examine the recent tier structure and depth distribution of trace fossils and foraminifera. Chronostratigraphic control on core PO200-10-6-2 is based on 4 AMS 14C datings. These data, as well as δ18O records, were used to correlate the cores.

To discern the influence of productivity variations and changes in bottom-water oxygenation on the benthic foraminiferal assemblages, palaeoproductivity was estimated by applying the equation of Stein (1986), which is based on total organic content (TOC) and sediment accumulation rates. The TOC from a second sample series of cores PO200-10-28-2 and SO75-26KL was determined with a CS-125 Leco furnace at GEOMAR (Kiel, Germany) and BGR (Hannover, Germany), respectively. Accumulation rates were calculated from sedimentation rates and dry bulk density data that were derived from weights (wet and dry) of discrete sample volumes (Van Andel et al., 1975; Boyce, 1976). To obtain consistent palaeoproductivity estimates that are comparable to present-day primary productivity, sedimentation rates were calculated between stratigraphic fixpoints on a calendar year time scale. This time scale deviates from the conventional radiocarbon time scale in that 14C ages are increasingly younger with increasing time into the last glacial due to changes in radiocarbon production in response to varying dipole strength of the earth’s magnetic field (Edwards et al., 1993). We have converted the AMS 14C ages using the empirical equations of Bard et al. (1992).

Apparent oxygen utilisation was estimated from benthic δ13C values in order to obtain independent support for trends in bottom-water oxygenation as inferred from benthic foraminiferal census counts and trace-fossil analysis. The δ13C measurements in core SO75-26KL were done with 1–8 specimens of Cibicidoides spp., mainly Cibicoides wuellerstorfi (Zahn et al., 1997).

4. Benthic communities and dissolved oxygen levels

4.1. Benthic foraminifera

Benthic foraminifera respond sensitively to changes in bottom-water oxygen concentration (Koutsoukos et al., 1990; Hermelin, 1992; Alve, 1995; De Smit, 1996). In case of oxygen depletion, foraminiferal species that are adapted to low-oxygen environments
Fig. 2. Planktonic oxygen isotope and IRD records of the cores studied. Age-control points are shown along the horizontal axis. AMS $^{14}$C datings are marked by asterisks. H = Heinrich layer.
become more abundant (Alve, 1990; Sen Gupta and Machain-Castillo, 1993; Kaiho, 1994). Deep-endo-
benthic species like *Chilostomella ovoidea* and *Glo-
obbulimina affinis* and *Chilostomella ovoidea* common
BFOI: 39 to 100

**Table 1**

Dissolved oxygen conditions, oxygen levels, benthic foraminiferal community structure and ichnocoenoses (after Rhoads and Morse, 1971; Kaiho, 1994)

<table>
<thead>
<tr>
<th>benthic foraminifera</th>
<th>trace fossils</th>
</tr>
</thead>
<tbody>
<tr>
<td>high oxic (3 ml L⁻¹ O₂)</td>
<td>high ratios of oxic indicators, <em>Globobulimina affinis</em> and <em>Chilostomella owoidea</em> common, BFOI: 39 to 100</td>
</tr>
<tr>
<td>low oxic (1.5 - 3 ml L⁻¹ O₂)</td>
<td>low ratios of oxic indicators, <em>Globobulimina affinis</em> and <em>Chilostomella owoidea</em> common, BFOI: -6 to 39</td>
</tr>
<tr>
<td>suboxic (0.3 - 1.5 ml L⁻¹ O₂)</td>
<td>no oxic indicators, high ratios of suboxic indicators, <em>Globobulimina affinis</em> and <em>Chilostomella owoidea</em> dominant, BFOI: -6 to -6</td>
</tr>
<tr>
<td>dysoxic (0.1 - 0.3 ml L⁻¹ O₂)</td>
<td>high ratios of dysoxic indicators, BFOI: -48 to -42</td>
</tr>
<tr>
<td>anoxic (&lt;0.1 ml L⁻¹ O₂)</td>
<td>barren or only few dysoxic indicators, BFOI: &lt;-48</td>
</tr>
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</table>

Applying benthic foraminiferal census counts, Kaiho (1994) demonstrated the potential of using benthic foraminiferal assemblages to monitor ambient bottom-water oxygen conditions. From a database comprised of samples from the Atlantic and Pacific oceans, the Sea of Japan, Gulf of Mexico and California, and the Mediterranean Sea, an empirical relation was derived between bottom-water dissolved oxygen levels and the benthic foraminiferal commu-
nity structure (Table 1). A benthic foraminiferal oxygen index (BFOI) was developed that allows to trace dysoxic, oxic, and suboxic environments based on the variation of the benthic foraminiferal assemblage (Kaiho, 1991, 1994):

$$BFOI = 100 \cdot \frac{O}{O + D} \quad (1)$$

where *O* and *D* are specimen numbers of oxic and dysoxic species, respectively. Dysoxic foraminifera comprise thin-walled, elongated, flattened infaunal species >63 μm, whereas oxic indicators are thick-walled, epibenthic species >355 μm (Kaiho, 1994). Large specimens of oxic species are often not recorded in the samples analysed. This would lead to erroneous estimates, designating even late Holocene samples to a low-oxygen environment. Furthermore, the fauna from the grain-size fraction <355 μm contains up to 67% of redeposited shelf Bolivinids and *Rectuvigerina* sp., suggesting that specimens from other species may have been
brought in from shallower depths as well. Therefore, the classification scheme of oxygen-related affinities of individual species and genera was modified to enable the application of Kaiho’s model to foraminiferal assemblages from the Portuguese Margin. Small specimens (<355 μm) of oxic species were classified as oxic rather than suboxic indicators because they are common in surface samples below well-oxygenated bottom waters (Schönfeld, 1997). Only dysoxic and oxic specimens from the grain-size fraction >250 μm were put into the model to exclude redeposited foraminifera from shallower water depths (Lutze and Coulbourn, 1984). Species of unknown affinity were discarded. By applying this restriction, autochthonous dysoxic species <250 μm, e.g. Stainforthia complanata, are also excluded. Hence, the BFOI values as defined by Kaiho (1994) may be lower. Nevertheless, Holocene BFOI values of both cores are well within the range of Kaiho’s (1994) data set. They correspond to even higher oxygen levels of the recent bottom water than those values suggested by the empirical relation between dissolved oxygen and BFOI.

In surface sediments underlying the NW African coastal upwelling zone between 15°N and 20°N, G. affinis and C. ovoidea are frequent in water depths between 2000 and 3000 m (Timm, 1989), where the bottom water is highly oxygenated (Lutze, 1980). Lutze et al. (1986) assigned both species to the ‘HPR-Group’ that is indicative of high carbon flux to the seafloor in response to enhanced productivity in overlying surface waters. Therefore, independent control on productivity and associated food supply to the benthic communities is needed to discern if increased abundances of G. affinis and C. ovoidea in the Late Pleistocene successions have been caused by low-oxygen bottom waters as a result of decreased deep ventilation or by an enhanced flux of organic carbon that led to a depletion of oxygen in ambient bottom waters and/or subsurface pore waters (Van der Zwaan and Jorissen, 1991; Sen Gupta and Machain-Castillo, 1993; Loubere, 1994).

4.2. Trace fossils

Changes in distribution and character of trace fossils monitor changes in ecological factors that determine the distribution of organisms and the traces they leave in sediments (Bromley, 1990). Trace fossils are particularly well suited for reconstructing palaeoenvironmental conditions, because they are usually not transported from their original place of formation. As such, they constitute an in situ tracer for palaeoenvironmental studies. Among the environmental factors delimiting different types of ichnofacies are pore-water and bottom-water chemistry (salinity, temperature, oxygen concentration, etc.), substrate character (substrate consistency, sediment grain size, etc.), sedimentation rate, availability of food, and wave and bottom-current energy (Ekdale, 1988). Oxygen concentration appears to be especially critical as has been inferred from an oxygen-related depth zonation (tiering) of trace fossils (Bromley and Ekdale, 1984; Savrda and Bottjer, 1986, 1991, 1994; Ekdale and Mason, 1988; Wheatcroft, 1989; Savrda and Ozalas, 1993). Savrda and Bottjer (1991) defined a biofacies scheme based on depth zones with varying degree of oxygenation. The following zones, listed after decreasing depth in the sediment, are important for the present study (Table 1): (1) anaerobic zone (oxygen concentration <0.1 ml l⁻¹; Rhoads and Morse, 1971), consisting of well-laminated strata lacking macro- and microbenthic body fossils and microburbation; (2) quasi-anaerobic zone (oxygen concentration close to, but greater than 0.1 ml l⁻¹) consisting of laminated strata with microbenthic body fossils and microburbation; (3) dysaerobic zone (oxygen concentration 0.1–1.0 ml l⁻¹; Rhoads and Morse, 1971) consisting of bioturbated strata with low-diversity macrobenthic body fossils and systematically decreasing diversity, size and depth of penetration of burrows with declining oxygenation; (4) aerobic zone (oxygen concentration >1.0 ml l⁻¹; Rhoads and Morse, 1971) characterised by thorough mixing by bioturbation and the presence of diverse assemblages of benthic body fossils. This biofacies scheme defines three bioturbation levels with increasing depth in the sediment (Savrda and Bottjer, 1991): a surface mixed layer with thorough biogenic homogenisation, a transition layer of heterogeneous mixing, and a historical layer without active burrowing. Environmental conditions change from aerobic through dysaerobic to anaerobic with increasing depth in the transition layer. Bromley and Ekdale (1984) proposed the following oxygen-controlled tier levels with increasing depth in the sediment:
Planolites, Thalassinoides, large Zoophycos, small Zoophycos, large Chondrites, and small Chondrites. Some studies, however, indicate that Zoophycos may occur at a deeper tier level than Chondrites. (Wetzel, 1984; Kotake, 1993; Tyszka, 1994). Transition-layer trace fossils may form piped zones, extensions of burrows into older sediment with contrasting texture.

The depth range of the three layers depends on the concentration of oxygen within the overlying bottom water. With decreasing oxygen content the bases of mixed and transition layers move upward in the sediment column and tier levels in the transition layer are progressively removed (Bromley and Ekdale, 1984; Savrda and Bottjer, 1986). Hence, the dysaerobic trace fossil Chondrites may form a deep tier well below the sediment surface under well-oxygenated bottom-water conditions, or a single, shallow tier under oxygen-deficient bottom-water conditions. Trace-fossil assemblages (ichnocoenoses) are preserved when the redox boundary, and thus tier levels, migrate upward through the sediment column under continuous sedimentation. Usually, deep tier, transition-layer trace fossils are preserved best because they comprise the last class of burrowing organisms present before burrowing ends in the historical layer (Savrda and Ozalas, 1993). Cross-cutting relationships within ichnocoenoses allow original tiering structures to be reconstructed, which in turn provide a qualitative measure for oxygen concentration in the dysaerobic realm during the time of formation.

The above concept will be applied for establishing relationships between ichnocoenoses and bottom-water oxygenation together with the vertical distribution of oxygen-related benthic foraminifera in an attempt to reconstruct relative degrees of palaeo-oxygenation of ambient bottom waters at the Portuguese continental margin across Heinrich layers H1 through H4.

4.3. Benthic δ¹³C

To decipher potential oxygenation levels in ambient mid-depth waters at the upper Portuguese Margin, we use benthic δ¹³C as a third independent tool. Benthic δ¹⁸O and δ¹³C records of core SO75-26KL have been used to infer a glacial reduction of MOW advection to the upper Portuguese Margin by more than 50% and a glacially enhanced mid-depth ventilation by intermediate waters that formed at open North Atlantic sources (Zahn, 1997; Zahn et al., 1997). Marked minima in the benthic δ¹³C record of core SO75-26KL are indicative of distinct reductions of mid-depth ventilation during Heinrich events (Fig. 3).

Benthic δ¹³C does not trace absolute O₂ concentrations but is a function of O₂ consumption during the oxidation of organic matter (Kroopnick, 1985). This contention is based on the observation that δ¹³C of total dissolved inorganic carbon (δ¹³CΣCO₂) in ambient seawater is closely correlated to biologically cycled nutrients and dissolved oxygen concentrations (Kroopnick, 1985). In addition to this ‘Redfield’ fractionation, δ¹³CΣCO₂ is a function of thermodynamically controlled isotope fractionation during air–sea gas exchange (Mook et al., 1974; Broecker and Maier-Reimer, 1992; Zahn and Keir, 1994). Thus, benthic δ¹³C variations do not trace absolute O₂ concentrations but are a function of O₂ consumption during the oxidation of organic matter (Kroopnick, 1985) and temperature-dependent carbon isotope fractionation during gas exchange between the surface ocean and overlying atmosphere.

To estimate absolute O₂ concentrations from benthic δ¹³C requires information on ‘preformed’ O₂ and δ¹³CΣCO₂ (i.e. O₂ concentrations and δ¹³CΣCO₂ prior to O₂ consumption by organic matter decomposition), and temperature during carbon isotope fractionation of dissolved CO₂ in surface waters with the overlying atmosphere. The ‘preformed’ O₂ level is best described by the O₂ saturation concentration which is a function of water-mass temperature and salinity (T, S) (Weiss, 1970). Using O₂ saturation as a starting point, ambient bottom-water O₂ concentrations at a given coring site can be derived by subtracting the Apparent Oxygen Utilisation (AOU) estimate that has been derived from benthic δ¹³C from the saturation O₂ value. The empirical relation between δ¹³CΣCO₂ and AOU is given by:

\[
\delta^{13}C_{ΣCO₂} = a - 0.0075 \times AOU
\]

\(n = 1107, \ r = 0.95\)  

where AOU is in μmol kg⁻¹ and variable a describes the ‘preformed’ δ¹³CΣCO₂, i.e. the zero AOU δ¹³CΣCO₂ intercept. Typical modern values for a as seen in the global GEOSECS database (Ostlund et al., 1987) are +1.5‰ PDB for the deep ocean and
Fig. 3. Benthic $\delta^{13}C$ and BFOI values for the past 22 ka in core SO75-26KL. Also indicated are IRD maxima of Heinrich events H1 and H2. Benthic $\delta^{13}C$ and BFOI show minima that are associated with both events. The subtle offset between the $\delta^{13}C$ and BFOI minima during H1 are best explained by increased burial depth of benthic foraminifera during enhanced IRD flux. Both records coherently indicate a reduction of water-mass O$_2$ concentrations during Heinrich events. See text for discussion.

$C_{1.2-1.6}$ PDB for the shallow ocean above 1.5 km water depth (Kroopnick, 1985; Zahn and Keir, 1994).

Using glacial benthic $\delta^{13}C$ for $\delta^{13}C_{S\ CO_2}$ in Eq. 2 requires correction by 0.32$\%$ of the benthic $\delta^{13}C$ values to account for changes of the marine carbon reservoir and associated shifts in mean-ocean $\delta^{13}C_{S\ CO_2}$ that went along with glacial–interglacial climate change (Duplessy et al., 1988). The correction value of +0.32$\%$ has been estimated for glacial-maximum conditions, and not necessarily represents mean-ocean $\delta^{13}C_{S\ CO_2}$ levels for pre-LGM conditions when benthic $\delta^{13}C$ at deep-ocean sites was less depleted than during the LGM. Also, from marked decreases in benthic $\delta^{13}C$ during Heinrich events that are seen at numerous core sites throughout the northern North Atlantic (Jung, 1996; Zahn, 1997), it appears conceivable that changes in the global carbon cycle occurred during these events that would have also affected the mean-ocean $\delta^{13}C_{S\ CO_2}$ composition. However, these changes have not yet been evaluated in detail and thus, the glacial-maximum correction value of +0.32 is applied also for pre-LGM and Heinrich event periods.

5. Results

5.1. Chronostratigraphy and Heinrich events

The age model for core SO75-26KL was developed from different sources (Fig. 2). Age control
for the last glacial–interglacial transition is based on AMS 14C datings and the correlation of the planktonic δ18O record with a continuously AMS 14C-dated planktonic δ18O curve from nearby core SU81-18 (Bard et al., 1989). Below the Last Glacial Maximum, oxygen isotope event 3.13 was identified in the benthic δ18O record and used as chronostatigraphic fixpoint (Martinson et al., 1987). Three horizons with abundant ice-rafted debris were recognised in core SO75-26KL that have been shown to be coeval with Heinrich events 1, 2, and 4 in the open North Atlantic (Zahn et al., 1997) dated to 14 ka, 20.7 ka, and 35.5 ka, respectively (Bond et al., 1992, 1993). In this paper, we use 14C ages of 13.32 ka, 20.6 ka and 33.5 ka for H1, H2 and H4 which are based on continuous AMS 14C datings in core SO75-26KL (H1 and H2) and PO200-10-28-2 (H4) (Fig. 2; Baas et al., 1997; Zahn et al., 1997). The age for H4 lies within the range of 35.1 to 33.2 ka given by Cortijo (1995). The present age model for core SO75-26KL differs from a more detailed one given by Cortijo (1995). The present age model for core PO200-10-28-2 from the southern Portuguese Margin. The IRD layers are asymmetric in shape with rapidly increasing IRD content in the lower part and slowly decreasing IRD content in the upper part. Maximum concentrations of IRD in the Heinrich layers off southern Portugal are 3.9, 2.3 and 13.5 grains >355 μm per gram sediment, respectively. Maximum IRD concentrations in the 250–500 μm fraction in core PO200-10-6-2 from the same area are 43.9 grains for H1 and 16.7 grains for H2, which is less than half the concentrations on the northern Portuguese Margin.

The age model for core PO200-10-28-2 from northern Portugal is based on 6 AMS 14C datings down to 33.85 ka (Fig. 2). Linear sedimentation rates are about half of those in core SO75-26KL. Three IRD horizons are recorded corresponding to H1, H2, and H4. Maximum concentrations of IRD for H1 and H2 are 53.7 and 43.1 grains 250–500 μm per gram sediment, respectively. H4 shows two separate maxima in detrital sand content (56.2 and 110.4 grains per gram sediment) which may signify two distinct periods of ice-rafting related to the glaciological processes in the source area (cf. Alley and MacAyeal, 1994). Twinning of this Heinrich layer was not observed in cores PO200-10-6-2 and SO75-26KL from the southern Portuguese Margin.

5.2. Benthic foraminiferal assemblages

Fifty-eight different benthic foraminiferal species were counted in samples from core PO200-10-28-2 on the northern Portuguese Margin. The benthic foraminiferal assemblage displays bathyal characteristics (Fig. 4; Table 2). Frequent species show strong fluctuations which allow to separate core intervals with different assemblage compositions. The Holocene part of the succession (core top to 40 cm) is characterised by high abundances of Uvigerina peregrina that makes up to 58% of the benthic foraminiferal fauna. Hoeglundina elegans, Sigmolopsis schlumbergeri, Pyrgo murrhyna and Pyrgo lucernula were also more frequent in the Holocene than in the glacial and deglacial periods. The Holocene assemblage composition is in good agreement with modern faunas from the Portuguese continental margin even though the proportion of Uvigerina peregrina is higher than in adjacent surface samples from the same water depth (Seiler, 1975; Schönfeld, 1997). The deglacial section (40 to 100 cm) displays high, but variable proportions of Cibicidoides wuellerstorfi and Bulimina striata mexicana. Eggerella bradyi, Melonis pompilioides, Pyrgo oblonga and Spaeriodina bulloides are occasionally frequent. Co-occurring high abundances of C. wuellerstorfi and B. striata mexicana are recorded in recent surface samples only from the northern Rockall Trough (J. Schönfeld, unpubl.), an area characterised by higher primary productivity and much stronger seasonality than off northern Portugal (Sathyendranath et al., 1995). The low-oxygen-tolerant species Globobulimina affinis and Chilostomella ovoidea show distinct maxima immediately below and within Heinrich layer H1, where Uvigerina peregrina parva is frequent as well. Bulimina aculeata, Cassidulina laevigata, Globobulimina turgida, Melonis barleeanaum, and Pyrgo murrhina are frequent in the glacial part of the succession (100 to 248 cm). C. ovoidea and G. affinis show distinct maxima immediately above and below Heinrich layer H2. G. affinis

Fig. 4. Distribution of selected benthic foraminifera versus core depth. Values are percentages of the benthic foraminiferal fauna >250 μm. H = Heinrich layer.
Table 2
Foraminiferal census data and BFOI values from core PO200-10-28-2

<table>
<thead>
<tr>
<th>sample (cm)</th>
<th>age (ka B.P.)</th>
<th>counted species</th>
<th>specimen number</th>
<th>BFOI</th>
</tr>
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<tbody>
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<td></td>
<td></td>
<td>1</td>
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<tr>
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<td>68</td>
<td>11,862</td>
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<tr>
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<td>12,591</td>
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<td></td>
<td>19</td>
</tr>
<tr>
<td>85</td>
<td>13,101</td>
<td></td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>83</td>
<td>13,320</td>
<td></td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>93</td>
<td>14,073</td>
<td></td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>98</td>
<td>14,827</td>
<td></td>
<td></td>
<td>20</td>
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<td>108</td>
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<td></td>
<td>20</td>
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<td>138</td>
<td>23,671</td>
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</tr>
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</tr>
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<td></td>
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</tr>
<tr>
<td>248</td>
<td>57,457</td>
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<td></td>
<td>20</td>
</tr>
</tbody>
</table>

Classification: o = oxic, s = suboxic, d = dysoxic, u = unknown affinity (after Kaiho, 1994).
*aOnly the 20 ranked species and those used for BFOI calculations are included.*
also displays maxima within the twinned Heinrich layer 4 as well as below it. *C. ovoidea* is frequent below Heinrich layer H4. During full glacial times, *Cassidulina laevigata* and *Melonis barleeanum* were most frequent. *C. laevigata* and *M. barleeanum* are opportunistic species adapted to high food concentrations, where *Cassidulina* requires more stable conditions and *Melonis* also tolerates variable flux rates of organic detritus (Mackensen et al., 1985; Caralp, 1989; Altenbach, 1992). The peak abundance of *C. laevigata* in core PO200-10-28-2 is synchronous to a short period of enhanced palaeoproductivity during the last glacial as inferred from diatom abundances in other cores off northern Portugal (Abrantes, 1991). However, the *M. barleeanum* maximum shows a slight offset with peak values after the *Cassidulina* maximum.

In core SO75-26KL from the southern Portuguese Margin, the faunal diversity, with 99 different species, is higher than in core PO200-10-28-2. The benthic foraminiferal assemblage displays bathyal characteristics. Frequent species show strong fluctuations which allow a distinction of three faunal units to be made, which are similar to core PO200-10-28-2. The Holocene section (0–110 cm) is characterised by high proportions of *Bulimina striata striata*, *Planulina ariminensis* and *Uvigerina mediterranea* (Fig. 4; Table 3). Peak abundances of *Planulina ariminensis* and *Valvulina penmatula* in the late deglacial indicate an intensive bottom-current activity, stronger than the Mediterranean Outflow Water (MOW) at this depth today (Schönfeld, 1997). The early deglacial section (110 to 190 cm) contains high abundances of *Cibicidoides pseudoungeri*anus, *Globobulimina affinis* and *Uvigerina peregrina parva*. *Cibicidoides wuellerstorfi*, *Melonis barleeanum* and *Sigmolopis schlumbergeri* are also frequent. In the glacial section (190 to 300 cm), these species show even higher proportions. *Uvigerina mediterranea* and *Cibicidoides pseudoungeri*anus were also more frequent and displayed maxima between 350 and 450 cm. The scarcity of *Planulina ariminensis* and *Valvulina penmatula* indicates that the MOW current did not flow at this water depth during glacial times. Irregular, short-term fluctuations of *Melonis barleeanum* at low values in combination with long-term variations of *U. mediterranea* and *C. pseudoungeri*anus at high values imply that stable conditions, similar to those today, prevailed off southern Portugal during the last glacial. Neither a strong seasonality nor high-productivity events were recognised.

The striking feature of glacial and deglacial benthic foraminiferal assemblages in core SO75-26KL is the distribution of low-oxygen-tolerant species. Though *Chilostomella ovoidea* occurs only sporadically with low percentages, *Globobulimina affinis* is frequent and shows a broad maximum throughout the deglacial part of the core. It culminates in peak values of up to 38% immediately below H1. A second, distinct maximum of *G. affinis* is located just below H4. Smaller maxima are developed at the beginning of Termination 1a and shortly after H2. *Uvigerina peregrina parva* is apparently also related to this phenomenon because it shows distinct maxima within the Heinrich layers H1 and H4, slightly above those of *G. affinis*. In core PO200-10-28-2, *U. p. parva* is much rarer than in core SO75-26KL and its maxima are at the same levels as the peaks of *G. affinis*. This pattern implies that an underlying controlling factor drives the distribution of both species and that this parameter is largely related to Heinrich events.

### 5.3. Trace-fossil assemblages

Four main trace fossils were observed on the X-ray photographs from core PO200-10-28-2 off northern Portugal: *Thalassinoides*, *Planolites*, *Chondrites*, and *Zoophycos*. The tiering structure was reconstructed from the vertical distribution of these traces below the core top, which is believed to represent the present-day sediment surface (Fig. 5). Above the redox boundary in the upper 12 cm of the core, only *Planolites* and *Thalassinoides* are present. Both trace fossils are lumped as one tiering level, because it proved difficult to separate them without a three-dimensional view of the traces (cf. Bromley, 1990). *Chondrites* trace fossils first appear at 12 cm. Their frequency increases down to 28 cm. *Chondrites* traces cross-cut *Planolites*/*Thalassinoides* traces in this interval. The deepest tier is formed by *Zoophycos*, which first appears at 28 cm depth. It cross-cuts all other traces. Two distinct trace-fossil assemblages, referred to as ichnocoenoses A and B, were recognised in this core. Ichnocoenosis A contains all three tier levels. The
Table 3
Foraminiferal census data and BFOI values from core SO75-26KL.a

<table>
<thead>
<tr>
<th>Sample</th>
<th>Age</th>
<th>Temperature (°C)</th>
<th>Bathymetry (m)</th>
<th>BFOI</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>3.39</td>
<td>-36.9</td>
<td>1.0</td>
<td>1.2</td>
</tr>
<tr>
<td>58</td>
<td>5.87</td>
<td>8.3</td>
<td>0.02</td>
<td>0.1</td>
</tr>
<tr>
<td>87</td>
<td>9.36</td>
<td>18.2</td>
<td>1.6</td>
<td>0.2</td>
</tr>
<tr>
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<td>0.7</td>
</tr>
<tr>
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<td>2.1</td>
<td>0.9</td>
</tr>
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<td>0.1</td>
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<td>0.7</td>
<td>0.6</td>
</tr>
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<td>1.3</td>
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<tr>
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<td>2.5</td>
<td>0.6</td>
<td>1.3</td>
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<tr>
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<td>0.5</td>
<td>0.9</td>
<td>0.6</td>
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<td>1.3</td>
</tr>
<tr>
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<td>1.3</td>
<td>0.6</td>
<td>0.4</td>
</tr>
<tr>
<td>279</td>
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<td>0.5</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
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<td>0.7</td>
<td>1.3</td>
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<tr>
<td>372</td>
<td>41.82</td>
<td>0.3</td>
<td>0.5</td>
<td>0.6</td>
</tr>
<tr>
<td>385</td>
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<td>1.6</td>
<td>7.0</td>
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</tr>
<tr>
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</tr>
<tr>
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<td>0.7</td>
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</tr>
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<td>1.1</td>
<td>3.8</td>
</tr>
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<td>1.2</td>
<td>0.6</td>
</tr>
<tr>
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<td>3.1</td>
<td>1.1</td>
<td>3.8</td>
</tr>
<tr>
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<td>0.9</td>
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<td>3.8</td>
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</tr>
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<td>0.7</td>
<td>0.9</td>
<td>0.7</td>
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<tr>
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<td>65.77</td>
<td>1.1</td>
<td>1.3</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Classification: o = oxic, s = suboxic, d = dysoxic, u = unknown affinity (after Kaiho, 1994).

*a Only the 20 ranked species and those used for BFOI calculations are included.

Fig. 5. Distribution of ichnofossils observed on X-ray photographs and interpreted oxygenation curves for core PO200-10-28-2 (left) and core PO200-10-6-2 (right). The grey colours denote the degree of X-ray absorption by the sediment slabs which is a qualitative measure for grain size. Dark grey is coarse, sand-rich sediment, light grey is silty mud and white is hemipelagic mud. Note the condensed piped zones below Heinrich layers filled with coarse sediment from above. H = Heinrich layer; YD = Younger Dryas.
Fig. 6. Vertical distribution of Globobulimina affinis and trace-fossil tiering sequence below the recent sediment surface in box core PO200-10-6-1 from the southern Portuguese Margin. MnO₂ = black, manganese-oxide-stained horizon; FeOOH = brown, iron-oxide-stained horizon. The shallowest occurrence of Chondrites matches a marked colour change from light brownish to dark olive grey. See Fig. 4 for explanation of ichnogenera symbols.

Thalassinoides/Planolites tier level is missing from ichnocoenosis B. An ichnocoenosis with only the Zoophycos tier level was not observed.

The Holocene section of the sedimentary sequence contains ichnocoenosis A (Fig. 5). Ichnocoenosis A is condensed during deglaciation according to the piped zone at 50 cm. Piped zones dominate the period from about 35 ka to 13 ka, when H1, H2 and H4 were formed. Piped zones below Heinrich layers have active fills of sand- and silt-sized sediment from above. Within Heinrich layers, trace fossils are filled with younger mud which clearly contrasts with the coarse-grained in situ sediment. The piped zone below H1 consists of ichnocoenosis A, which is condensed compared to the present-day tiering sequence. Below H2, a highly condensed interval with Chondrites was observed and interpreted as ichnocoenosis B. The piped zone below H4 also contains Chondrites-dominated ichnocoenosis B. However, the condensation is less than below H2. An additional piped zone with ichnocoenosis B was observed below a silty layer between H2 and H4 at 134–142 cm. All trace-fossil assemblages within Heinrich layers consist of an ichnocoenosis A. At 191–196 cm, a silty interval contains ichnocoenosis B. Below it, ichnocoenosis A prevails.

Trace-fossil tiers in core PO200-10-6-2 from the southern Portuguese Margin are confined to Thalassinoides/Planolites and Chondrites (Fig. 5). Box core PO200-10-6-1 from the same location was used to reconstruct the present-day tiering structure (Fig. 6). Thalassinoides/Planolites form the only tier level in the upper 15 cm of the core. Below that level, the Chondrites tier sets in and clearly crosscuts Thalassinoides/Planolites traces. Two ichnocoenoses were recognised in this core. Ichnocoenosis A comprises both Thalassinoides/Planolites and Chondrites traces, while ichnocoenosis B only contains Chondrites.

Core PO200-10-6-2 is dominated by ichnocoenosis A (Fig. 5). Ichnocoenosis A is slightly condensed during deglaciation. Ichnocoenosis B was observed above Heinrich layer 2. The piped zone below H1 consists of ichnocoenosis A with a condensed Thalassinoides/Planolites tier level.

5.4. Palaeoproduction

Palaeoproduction values vary between 78 and 117 g C m⁻² yr⁻¹ in core SO75-26KL and 70 and 153 g C m⁻² yr⁻¹ in core PO200-10-28-2. The fluctuations are mainly due to variations of Corg values and not to changes in sedimentation rates (Fig. 7; Abrantes, 1991). In the glacial sections of both cores, palaeoproduction estimates show similar fluctuations up to the onset of Termination I. Values are generally higher in core PO200-10-28-2 during times of high productivity whereas values are more similar during times of lower productivity. A distinct productivity maximum is absent between 21
Fig. 7. Palaeoproductivity estimates and age distribution of *Globobulimina affinis* in core PO200-10-28-2 (left) and core SO75-26KL (right). $H$ = Heinrich layer.

and 19 ka, during which the benthic foraminiferal assemblage indicates enhanced palaeoproductivity. A productivity minimum roughly coincides with H2. A similar minimum is present around H4. In contrast, productivity levels remain constant across H3 at 27.0 ka. As palaeoproductivity fluctuations are largely related to $C_{org}$ variations in core PO200-10-28-2, the above pattern may result from short time increases
in terrigenous sediment flux during Heinrich events, leading to a significant dilution of organic matter and thus inferring palaeoproductivity minima (Thomson et al., 1995; Zahn et al., 1997). A strong minimum at the beginning of Termination Ia precedes H1 by about 700 years, however, and may be affected by enhanced sediment supply during the early deglacial transgression (Baas et al., 1997). The productivity records of both cores show an increase across H1, but the trend diverges at 13 ka. In the north, core PO200-10-28-2 shows a further increase towards a distinct maximum at 11 ka from whereon productivity steadily declines. Core SO75-26KL, on the other hand, displays a productivity minimum at 12 ka and increasing values thereafter. The youngest productivity estimates at 3.4 and 3.8 ka are 78 and 81 g C m\(^{-2}\) yr\(^{-1}\) and are similar in both cores. The values are in good agreement with the present-day primary production ranging from 60 to 90 g C m\(^{-2}\) yr\(^{-1}\) in this area (Berger et al., 1987).

6. Discussion

6.1. Reconstruction of dissolved oxygen levels from benthic foraminifera

We use the modified benthic foraminiferal oxygen index (BFOI) to reconstruct dissolved oxygen levels of ancient bottom waters. Oxic and dysoxic species constitute on average 46% and 40% of the total assemblage, ranging between 22% and 82%, and between 5% and 63%, in cores PO200-10-28-2 and SO75-26KL, respectively. The BFOI values vary between 8 and 99 (Tables 2 and 3). Three BFOI minima, indicating low oxygen levels, are recognised in core SO75-26KL immediately below Heinrich event H1, slightly above Heinrich event H2 and in a level tentatively assigned to Heinrich event 3 (Fig. 8; Zahn et al., 1997). They mainly result from high percentages of \textit{Globobulimina affinis} (H1 and H2; Fig. 7) or from the scarcity of oxic species (H3; Table 3). Around H4, however, BFOI values are well in the high-oxic realm, even though \textit{G. affinis} shows an abundance maximum below the Heinrich layer. Palaeoproductivity remains on average levels, which indicates that the \textit{Globobulimina} maxima and inferred oxygenation minima were not caused by higher carbon fluxes. The BFOI values imply a drawdown to low-oxic conditions for H1, the minimum above H2 and for H3. The present-day values from this water depth are in the high-oxic realm (4.4 to 4.8 ml l\(^{-1}\); Zenk and Armi, 1990). In the glacial section of core PO200-10-28-2 from greater water depth, the BFOI values are generally lower than in core SO75-26KL. They show distinct minima immediately below H1, above and below H2, and at the two IRD maxima in H4 (Fig. 8). A smaller minimum also occurs immediately below H3 which has no counterpart in the IRD record, however. With the exception of the minimum above H2, all BFOI minima are due to high percentages of \textit{Globobulimina affinis} (Fig. 7) and \textit{Chilostomella ovoidea}. The minimum above H2 corresponds to low proportions of specimens of oxic species and to high percentages of \textit{Cassidulina laevigata} as mentioned above. As inferred by \(C_{\text{org}}\) values, the minimum below H2 matches a small palaeoproductivity maximum, which is present in core SO75-26KL as well (Fig. 8). This may indicate a higher flux of organic matter to the seafloor, although species adapted to high food concentrations as \textit{Cassidulina laevigata} and \textit{Melonis barleeanum} are rare at this level. The BFOI values suggest low-oxic conditions for H1 and H4. The minimum below H2 indicates even lower oxygen levels which may have been close to the suboxic realm. The present-day bottom water is highly oxygenated at this water depth (>5.6 ml l\(^{-1}\); Zenk and Armi, 1990). The BFOI minima for H1 in cores PO200-10-28-2 and SO75-26KL.

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Fig. 8. Correlation of trace-fossil oxygen index, benthic foraminiferal oxygen index (BFOI) and palaeoproductivity in core PO200-10-28-2 and cores PO200-10-6-2 (trace fossils) and SO75-26KL (BFOI, palaeoproductivity). Please note offset of oxygen indices for trace fossils and benthic foraminifera due to differences in methodology. Trace-fossil tiering allows the original depth below the sediment surface for each depth in core to be reconstructed through piped zones. The trace-fossil oxygen index diagram therefore gives oxygen levels corrected for habitat depth of trace fossils (cf. Fig. 4). Such a correction was not possible for BFOI. Hence, oxygenation trends for trace fossils correlate with oxygenation trends for benthic foraminifera at a slightly deeper level, despite the fact that low-oxygen-tolerant types occur at similar depths in core. \(H = \) Heinrich layer; \(YD = \) Younger Dryas.
suggest similar oxygen levels. The BFOI minimum above H2 is slightly lower in core PO200-10-28-2, while the minimum below H2 is only recorded in core PO200-10-28-2. Thus, the lower values above and below H2 are probably a combined feature of enhanced productivity and higher deoxygenation at the northern site. The BFOI minima in levels corresponding to H3 indicate again similar oxygen values for both locations. BFOI values show two minima corresponding to the double IRD maximum of H4 in core PO200-10-28-2 from which the lower minimum suggests low-oxic conditions. Despite the fact that only a single IRD maximum is recognised at H4, the twofold structure, even with a similar offset of both minima, is displayed in core SO75-26KL. The inferred oxygen levels are still in the high-oxic realm, however. This pattern implies, that the same force drives the dynamics of the BFOI but the impact is stronger at the northern site leading to a higher deoxygenation there. The congruence of this pattern with the detailed structure of the H4 $^{13}$C excursion in core SO75-26KL (fig. 7 in Zahn et al., 1997) points to a sluggish thermohaline circulation as cause for reduced deep-water ventilation during Heinrich events.

Low-oxygen-tolerant foraminifera and other deeper-dwelling species are considered to be under-represented in the dead assemblage with reference to the living fauna because they have much lower test-production rates than shallow-dwelling species in near-surface oxic environments. To create an abundance maximum, low-oxygen-tolerant species have to achieve a strong competition advantage against the more reproductive oxic foraminifers in that the bottom-water oxygen concentration falls below a level tolerable by shallow-dwelling species (De Stigter, 1996). In both cores studied, low-oxygen-tolerant foraminifers show abundance maxima below Heinrich layers (Fig. 7). At H1, the maximum was found exactly 10 cm below the IRD maximum in both cores. An abundance maximum of dysoxic species is recorded 2 cm below H2 in core PO200-10-28-2. No corresponding maximum was observed in core SO75-26KL. Yet, Globobulimina affinis shows slightly higher proportions 4 cm below the IRD maximum and 4 cm below the onset of deposition of IRD. Two Globobulimina peaks are recorded at H4 in core SO75-26KL. The upper maximum occurs exactly 8 cm below the peak IRD abundance and the lower one is recorded 5 to 1 cm below the onset of IRD deposition. At H4 in core PO200-10-28-2, Globobulimina maxima occur exactly at the level of both IRD peaks. Chilostomella ovoidea shows maximum abundances 10 cm below H4, however.

If a close relationship is considered between the abundance of dysoxic foraminiferal species and deep-water ventilation, the offset between abundance maxima of low-oxygen-tolerant foraminifera and Heinrich events would imply that a short period of bottom-water deoxygenation occurred immediately before the events. Although meltwater discharge significantly increased before the iceberg surges (Andrews et al., 1994), its impact on deep-water formation may have been low if a certain threshold value was not exceeded (Paillard and Labeyrie, 1994; Rahmstorf, 1995). The excess of the threshold meltwater flux happened contemporaneously with the Heinrich events, however, and nearly brought the thermohaline overturn to a halt (Labeyrie et al., 1995; Maslin et al., 1995). Hence, a significant nutrient enrichment and a drastic reduction in dissolved oxygen of intermediate to deep waters has to be expected during the main phase of the Heinrich events (Zahn et al., 1997). The corresponding levels rather show decreasing abundances of G. affinis than distinct maxima (Fig. 7). We infer that the observed patterns of abundance maxima of low-oxygen-tolerant foraminifera below the IRD layers reflect the original microhabitat depth of suboxic species in the sediment rather than short periods of low-oxygen conditions preceding the input of IRD.

In box core PO200-10-6-1, the abundance maximum of G. affinis was found 6 cm below the sediment surface (Fig. 6). The maximum is located between 3.5 and 6 cm if the absolute abundance of specimens per 10 cm$^3$ is regarded. In both cases, the maximum is just below a manganese-oxide-stained horizon which lower boundary indicates the transition between oxic and anoxic pore waters. During the RV Meteor cruise M39/1 in May 1997, we revisited the location of box core PO200-10-6-1 and recorded the redox boundary with an oxygen needle probe between 3.8 and 4.2 cm below the sediment surface. Despite difficulties of core correlations on a centimetre scale, the relation of Globobulimina depth–habitat and redox boundary as revealed from box core PO200-10-6-1 is
in good agreement with data from Corliss and Emerson (1990), who found an abundance maximum of living *Globobulimina* 4.5 cm below the sediment surface, approximately 2 cm below the redox boundary (station KN104/10-4-2: northwestern Atlantic, 1075 m water depth). In core SO75-26KL, a situation similar to the present only occurred during H2, in that the difference in depth between the IRD- and *Globobulimina*-maxima is 4 cm and the BFOI values remain high (Fig. 8). In core PO200-10-28-2, the difference in depth is smaller for H2 and H4, which may have been caused by an upward migration of *Globobulimina affinis* during IRD deposition following a shallowing of the redox boundary in the near-surface sediments (Bernhard, 1992). For H2, this may have been caused by a higher C*org* flux (Reimers et al., 1992) as discussed above and for H4, by a stronger oxygen depletion (Loubere et al., 1993) as inferred from the benthic δ¹³C excursion in core SO75-26KL (Zahn et al., 1997).

In both cores, the difference in depth between the *Globobulimina* maximum and maximum IRD occurrence for H1 is larger than the present microhabitat depth of this species at the upper Portuguese Margin. *Globobulimina* maxima were previously observed about 10 cm below the sediment surface in 2200 and 3000 m water depths at sites where carbon flux is low and ambient bottom waters are well oxygenated (Corliss, 1985; Corliss and Emerson, 1990). The palaeoproductivity records from our cores show a marked minimum 10 cm below H1 with values slightly lower than those at other minima (Fig. 7). Sedimentation rates around H1 were approximately one third higher than around H2 in core SO75-26KL (Zahn et al., 1997). A possible explanation for the larger difference in depth between the *Globobulimina* maximum and H1 is that the higher sediment supply caused a dilution of fresh organic material, different equilibrium conditions between the decay of organic matter, and oxygen advection in the ambient pore water (Berner, 1980), and thus a deepening of the redox boundary in near-surface sediments. This would guide low-oxygen-tolerant species to dig deeper into the subsurface sediments in order to occupy their familiar microhabitat. Their greater abundance at these depths is again most likely due to a competition advantage against other species at lower bottom-water oxygenation.

The benthic foraminiferal assemblages imply significant deoxygenation during Heinrich events (Fig. 8). The benthic foraminiferal oxygen index (BFOI) has been calibrated to in situ O2 levels of ambient bottom waters (Kaiho, 1994) and may thus be used to estimate palaeo-oxygenation levels. The samples used for the calibration originate from various regions of the world oceans and cover a range of O2 concentrations between 0.1 and 6.0 ml l⁻¹, i.e. from dysoxic to high oxic (Fig. 9). The linear regression of these data is:

\[ y = 1.686 + 0.033337x \quad n = 71; \quad r = 0.895 \quad (3) \]

where \( y \) is the oxygen concentration in ml l⁻¹ and \( x \) is the BFOI value. The coefficients differ from those given by Kaiho (1994) who considered only data with BFOI values below 50. As the Holocene BFOI values from the Portuguese Margin fall in the high-oxic field, we use the whole data set as modern control and estimate absolute O2 levels from our benthic foraminiferal census counts along cores SO75-26KL and PO200-10-28-2 by applying Eq. 2. The accuracy of this estimate is ±0.75 ml l⁻¹ as expressed by the residual standard deviation. It may even be less in the high-oxic realm where the BFOI values show a much greater variance of associated O2 levels (Fig. 9). Trace-fossil tiering relationships allow determination of critical oxygen levels (i.e. 0.1 and 1 ml l⁻¹). Between these levels, relative changes in oxygenation can be inferred from the degree of condensation of piped zones.

According to BFOI minima associated with H1, O2 levels were reduced to mean values of 2.6 ± 0.08 ml l⁻¹ in core SO75-26KL (\( n = 3 \)), and 2.7 ± 0.04 ml l⁻¹ in core PO200-10-28-2 (\( n = 2 \)). H2 shows oxygen concentrations close to present-day values in core SO75-26KL (4.1 ± 0.26 ml l⁻¹, \( n = 5 \)), whereas significant O2 reduction is present in core PO200-10-28-2 (2.8 ± 1.16 ml l⁻¹, \( n = 2 \)). O2 levels during H4 were 2.8 ± 0.06 ml l⁻¹ (\( n = 2 \)) at the northern site and only a slight reduction is recorded in core SO75-26KL (3.7 ± 0.36 ml l⁻¹, \( n = 6 \)).

### 6.2. Reconstruction of dissolved oxygen levels from trace fossils

To extract information on palaeo-oxygenation of ambient bottom waters from vertical zonation of
trace-fossil tiers, we assume that bottom-water oxygenation exerts primary control on pore-water oxygenation and bioturbation. If so, trace fossils are indicative of changes in thermohaline circulation and water-mass stratification. Again, palaeoproductivity records serve as an independent control to check for secondary effects such as organic carbon supply and decomposition affecting pore-water oxygen levels and the rate of bacterial metabolism (Savrda and Bottjer, 1994).

Today, bottom waters at the Portuguese Margin are well-oxygenated. As a result, a well-developed three-level tiering zonation is observed in core PO200-10-28-2 (Fig. 5). The *Thalassinoides*/Planolites* tier level occurs in aerobic sediments above the redox boundary. In box core PO200-10-6-1, the *Chondrites* tier level starts at the transition in sediment colour from light brownish to dark olive grey at 14 cm (Fig. 6). The darker colours most likely result from disseminated iron sulphides in the sulphate reduction zone below, which is characterised by nearly anoxic pore waters (Hesse, 1986). Thus, the *Chondrites* tier level lies in dysaerobic sediments below the redox boundary. In present-day sediments, the deep *Zoophycos* tier level marks the lowest dissolved oxygen concentrations. A similar interpretation is possible for the two-level tiering structure on the southern margin. *Thalassinoides*/Planolites* forms the shallower tier level in well-oxygenated sediment. The *Chondrites* tier level occurs in oxygen-depleted sediment below it (Fig. 6).

The present-day aerobic trace-fossil tiering structure can be used as the basis for the analysis of concentrations of dissolved oxygen from ichnocoenoses in the Late Pleistocene and Holocene. Piped zones record ichnocoenoses during deposition of sediment from which they extend downward. Therefore, they are well suited for the reconstruction of palaeo-oxygenation levels during Heinrich events and other periods during the last 40 ka.

The high degree of bioturbation and the presence of ichnocoenosis A implies that ambient bottom waters at the Portuguese Margin remained well-oxygenated during the Holocene (Fig. 5). During the
last glacial–interglacial transition, ichnocoenosis A is condensed and points to slightly decreased oxygen concentrations. Sediments above the deglacial piped zones correlate with the Younger Dryas period (Fig. 2). The condensed ichnocoenosis A thus suggests that bottom waters may well have been low aerobic during this period. The higher degree of condensation of the piped zone in core PO200-10-28-2 implies that the decrease in oxygen content was largest on the northern Portuguese Margin. Heinrich events were likely associated with decreased water-column oxygenation due to reduced thermohaline overturn in the North Atlantic as is indicated by the presence of condensed ichnocoenoses A and ichnocoenoses B in piped zones. However, significant differences between Heinrich events exist (Fig. 5). Piped zones of H1 contain condensed ichnocoenosis A in both cores, suggesting that tier levels migrated upward and bottom-water oxygenation was reduced, but still in the aerobic realm. In core PO200-10-28-2, the piped zone below H2 is thin and only contains Chondrites burrows. This indicates dysoxic bottom waters during H2. Oxygen-depleted bottom waters are also inferred from ichnocoenosis B following H2 in core PO200-10-6-2. Heinrich event 4 on the northern margin lacks an aerobic tier level, but bottom-water oxygen depletion was less compared to H2, as inferred from the smaller degree of tier level condensation. The piped zone with ichnocoenosis B between H2 and H4 in the northern core likely marks dysoxic bottom-water conditions during H3. If so, the hydrographic signal of reduced water-mass convection in the open North Atlantic during Heinrich event 3 reached the Portuguese Margin, whereas only few icebergs approached, as implied by the scarcity of sand-sized IRD. The presence of ichnocoenosis A within and between Heinrich layers demonstrates that bottom water was well-oxygenated in between Heinrich events.

6.3. Estimation of mid-depth oxygen levels from benthic $\delta^{13}$C

Today, mid-depth $O_2$ concentrations at the upper Portuguese Margin are 4.2 ml l$^{-1}$ as measured in hydrocasts at TTO (Transient Tracers in the Ocean program; TTO, 1986) Station 113 off southern Portugal. The $O_2$ saturation value is 6.0 ml l$^{-1}$, according to mid-depth $T$–$S$ values of 11°C/36.1 at this depth. Hence, in situ $O_2$ concentrations of 4.2 ml l$^{-1}$ are 1.8 ml l$^{-1}$ below the saturation value. An AOU (Apparent Oxygen Utilisation, see above) of 1.8 ml l$^{-1}$ translates into a $\delta^{13}$C$_{\text{SCO}}$ shift of $-0.6\%$ as defined by the slope of Eq. 2, assuming that all $O_2$ has been consumed by oxidation of marine organic matter (Fig. 10). Mean Holocene benthic $\delta^{13}$C in core SO75-26KL is $+1.0 \pm 0.08\%$ PDB ($n = 10$, range = 0.8–1.1% PDB). Correcting the mean Holocene benthic $\delta^{13}$C for the AOU-induced $\delta^{13}$C decrease of 0.6% gives a ‘preformed’ $\delta^{13}$C$_{\text{SCO}}$ value of $+1.6\%$ PDB. This value agrees well with the ‘preformed’ $\delta^{13}$C$_{\text{SCO}}$ value of $+1.56\%$ PDB that has been determined for the mid-depth North Atlantic at potential densities of 26.8 < $\sigma_\theta$ < 27.7, equivalent to water depths between 0.8 and 1.5 km (Zahn and Keir, 1994).

Evaluation of benthic $\delta^{18}$O from upper Portuguese Margin cores in $T$–$S$ fields has been used to infer that the contribution of mid-depth water masses from the open North Atlantic to the upper Portuguese Margin was increased during the last glacial at the expense of Mediterranean Outflow Waters (MOW) (Zahn, 1997; Zahn et al., 1997). A potential $T$–$S$ shift from 11°/36.1 today to around 7°C/37.1 during the last glacial (due to a higher contribution of cold and saline North Atlantic Central Water) suggests an increase in $O_2$ saturation by 0.5 ml l$^{-1}$, from 6.0 ml l$^{-1}$ today to 6.5 ml l$^{-1}$ during the last glacial (Fig. 10). As temperature also determines the fractionation of carbon isotopes of dissolved carbon in surface waters during air–sea gas exchange (about 0.1% increase per 1°C decrease; Mook et al., 1974), a temperature decrease by 4°C of glacial waters would have induced an increase in $\delta^{13}$C$_{\text{SCO}}$ in the source region by about 0.4%, if isotope equilibrium has been achieved during air–sea gas exchange. Glacial ‘preformed’ $\delta^{13}$C$_{\text{SCO}}$ is thus +2.0% PDB for the last glacial (1.6% PDB for modern ‘preformed’ $\delta^{13}$C$_{\text{SCO}}$ plus 0.4% = 2.0% PDB; Fig. 10).

Mean glacial benthic $\delta^{13}$C is $+1.7 \pm 0.06\%$ PDB ($n = 11$, range = 1.5–1.7% PDB) in core SO75-26KL (Figs. 3 and 10). Correcting this value for the mean-ocean shift in $\delta^{13}$C$_{\text{SCO}}$, by adding 0.32%, one arrives at a glacial benthic $\delta^{13}$C value of $+2.0\%$ PDB for core SO75-26KL. Even if the global carbon isotope shift during periods prior to the LGM was half the LGM value, the corrected benthic $\delta^{13}$C value of $+1.86\%$ PDB (mean glacial benthic $\delta^{13}$C
Fig. 10. Relation between $\delta^{13}C$ decrease and oxygen consumption ($AOU =$ apparent oxygen utilisation). Slope and intercept of this relation are given by dashed line (see Eq. 2 in text). Also shown are benthic $\delta^{13}C$ scales (top) and scales of absolute $O_2$ concentration (right-hand scales). $O_2$ scales have been derived by estimating $O_2$ saturation as a function of glacial–interglacial changes of water-mass temperature and salinity. Benthic $\delta^{13}C$ scales have been plotted using ‘preformed’ $\delta^{13}C$ values of $C_{\text{PDB}}$ and $C_{\text{PDB}}$ for the Holocene and last glacial, respectively. Mean Holocene and glacial benthic $\delta^{13}C$, as well as mean benthic $\delta^{13}C$ for Heinrich events H1, H2, and H4 as recorded in core SO75-26KL, are indicated along the benthic scales. Range of benthic $\delta^{13}C$ during Heinrich events is indicated by horizontal bars along top scales. See text for discussion.

Assuming a glacial ‘preformed’ $\delta^{13}C_{\text{CO}_2}$ of +2.0‰ PDB (parameter $a$ in Eq. 2) and glacial $O_2$ saturation of 6.5 ml l$^{-1}$, $O_2$ concentrations during Heinrich events can be estimated from benthic $\delta^{13}C$ values — once the values are corrected for the mean-ocean $\delta^{13}C_{\text{CO}_2}$ shift — and resultant AOU.

In core SO75-26KL, the range of benthic $\delta^{13}C$ is 1.1–1.4‰ PDB with a mean value of +1.2 ± 0.11‰ PDB for H2 ($n = 6$), and 0.5–1.2‰ PDB with a mean value of +0.9 ± 0.19‰ PDB for H4 ($n = 17$) (Figs. 3 and 10). Corrected mean benthic $\delta^{13}C$ values are +1.5‰ and +1.2‰ PDB for H2 and H4, respectively. Using these values as input into Eq. 3, $O_2$ concentrations in ambient bottom waters at the upper Portuguese Margin were 4.7–5.6 ml l$^{-1}$ (mean = 5.0 ± 0.33 ml l$^{-1}$) for H2 and 3.0–5.1 ml l$^{-1}$ (mean = 4.2 ± 0.57 ml l$^{-1}$) for H4 (Fig. 10).

The range of benthic $\delta^{13}C$ during H1 is 0.5–0.8‰ PDB with a mean value of +0.71 ± 0.1‰ PDB ($n = 12$) (Figs. 3 and 10). H1 occurred during the last glacial–interglacial transition when disintegration of Northern Hemisphere ice sheets led to large-scale reorganisation of ocean circulation. Reliable $T–S$ conditions in the North Atlantic region cannot be
derived from foraminiferal $\delta^{18}O$ for this period because increased meltwater fluxes conceivably led to significant deviations in the $\delta_w : S$ relation that is an essential parameter in palaeotemperature equations. Therefore, both the glacial and mean Holocene parameterisation are used to estimate in situ $O_2$ levels. ‘True’ $O_2$ concentrations may have been somewhere around these estimates.

Correcting the benthic $\delta^{13}C$ value of 0.71‰ PDB for the glacial scenario by adding 0.32‰, one arrives at around +1.0‰ PDB in $\delta^{13}C$ for H1. Comparing this value with the glacial ‘preformed’ $\delta^{13}C_{ECO}$, of +2.0‰ PDB and an $O_2$ saturation of 6.5 ml l$^{-1}$ suggests an AOU of 3.0 ml l$^{-1}$, arriving at ambient $O_2$ concentrations between 3.0 and 3.9 ml l$^{-1}$ (mean = 3.6 ± 0.30 ml l$^{-1}$, ‘$H1_{gl}$’ in Fig. 10). For the alternative interpretation in a Holocene scenario, benthic $\delta^{13}C$ of +0.71 ± 0.1‰ is left unchanged. Using a Holocene ‘preformed’ $\delta^{13}C_{ECO}$, of +1.6‰ PDB and $O_2$ saturation of 6.0 ml l$^{-1}$, AOU is estimated to 2.7 ml l$^{-1}$ and absolute $O_2$ concentrations to 2.8–3.7 ml l$^{-1}$ (mean = 3.4 ± 0.30 ml l$^{-1}$) for this event (‘$H1_{mod}$’ in Fig. 10).

The above estimates from benthic $\delta^{13}C$ suggest that oxygenation during the last glacial was significantly increased at the upper Portuguese Margin and that $O_2$ levels were close to the saturation value implying rapid ventilation with only little ‘ageing’ of mid-depth water masses. This is in agreement with conceptual models that use enhanced benthic $\delta^{13}C$ levels at shallow-ocean coring sites throughout the world oceans as evidence for increased upper ocean ventilation (Zahn et al., 1987; Duplessy et al., 1988; Mix et al., 1991; Zahn and Pedersen, 1991; Veum et al., 1992; Oppo and Lehmann, 1993; Sarnthein et al., 1994; Jung, 1996). Decreased benthic $\delta^{13}C$ values indicate reductions in $O_2$ concentrations during ‘Heinrich’ events. $O_2$ estimates for H4 and H2 of 4.2 and 5.0 ml l$^{-1}$ are lower than mean-glacial levels (6.1–6.5 ml l$^{-1}$) but remain at and above Holocene levels (4.2 ml l$^{-1}$) (using the glacial and Holocene scenarios) that oxygenation sunk below Holocene levels. H1 occurred early in the last glacial–interglacial transition when thermohaline overturn in the North Atlantic wound down and conceivably came to a complete halt in response to large-scale meltwater supply from the disintegra-

6.4. Oxygenation estimates from BFOI, trace-fossil tiering, and benthic $\delta^{13}C$: a comparison

Trace-fossil tiering indicates that deoxygenation was largest during H2 and H4, and smallest during H1 and H3 as well as during the Younger Dryas. However, absolute estimates of bottom-water oxygenation diverge. In general, $O_2$ levels inferred from BFOI values are higher than those inferred from trace-fossil assemblages. Trace-fossil tiering indicates dysoxic conditions during H2 and H4, and low-oxic conditions during H1, whereas BFOI values imply low-oxic conditions for most Heinrich events (Fig. 8). Even during H3, which has no significant IRD signature, the ichnocoenosis in core PO200-10-28-2 implies dysoxic bottom waters whereas the subtle minimum in BFOI values implies low-oxic bottom waters (2.8 and 3.1 ml l$^{-1}$) at core sites SO75-26KL and PO200-10-28-2. The Younger Dryas is characterised by low-oxic bottom water, based on the presence of condensed piped zones in both cores. No corresponding minima are visible in the BFOI records.

The observed discrepancies may be due in part to the limitation of the benthic census counts to the >250 μm size fraction. Although this approach to a large extent eliminates redeposited specimens, there is a chance that autochthonous dysoxic species that typically have a smaller size are also excluded. Hence, BFOI values may be too high compared to Kaiho’s calibration. They may therefore suggest higher $O_2$ levels than those extant during sediment deposition, at least in the low-oxic realm. Moreover, the BFOI model assumes that oxic species are absent from suboxic and dysoxic environments. However, bioturbation likely sustained a constant admixture of oxic species into sediments that were deposited during periods of reduced bottom-water oxygenation, thereby driving BFOI values up to higher $O_2$ equivalents. Environmental factors like availability of food, varying sedimentation rates, ecosystem stability, and competition among species may also account for the
Fig. 11. Comparison of oxygen level estimates for core SO75-26KL. The symbols and error bars of BFOI and δ¹³C indicate mean value and standard deviation. Boxes of trace-fossil tiering indicate total range. Holocene oxygen level after TTO (1986). See text for discussion.

differences in inferred oxygenation levels. For H1, O₂ depletion may have been higher than estimated due to the counteracting effect of enhanced terrigenous sedimentation and deeper dwelling of dysoxic species. For H2, deoxygenation may have been less, because high proportions of low-O₂-tolerant foraminifera at this level are most likely affected by increased primary productivity. Even though palaeoproductivity may have contributed to some extent to the observed variability of the benthic foraminiferal assemblage and trace-fossil zonation, it cannot explain the highly condensed trace-fossil tiers below H2 in core PO200-10-28-2 (Figs. 5 and 8).

BFOI-based O₂ concentrations diverge from those inferred from benthic δ¹³C in that within the range of error the O₂ concentrations from BFOI data are similar for mean glacial, H2 and the Holocene, whereas mean glacial O₂ concentrations from benthic δ¹³C are about 1 ml l⁻¹ higher than Holocene values, and O₂ concentrations during H2 are significantly reduced relative to glacial background (Fig. 11). O₂ concentrations for these periods remain in the high-oxic range. It thus appears that the benthic community is less sensitive to O₂ changes as long as oxygenation remains in the high-oxic range (above 3 ml l⁻¹). Only for H1 BFOI and benthic δ¹³C consistently document reduced O₂ concentrations. O₂ estimates from benthic δ¹³C still remain in the high-oxic range whereas the BFOI estimates are in the upper low-oxic range. Trace-fossil tiering indicates even lower O₂ concentrations at a suboxic (H2) to low oxic (H1) level.

H1 occurred during the last glacial–interglacial transition when thermohaline overturn in the North Atlantic wound down and conceivably came to a complete halt in response to large-scale meltwater supply from the disintegration of the Laurentide and Fennoscandian ice sheets. Apparently, the breakdown in ventilation was significant enough to cause a change in O₂ concentrations that was large enough for low-oxic species to become the dominant faunal constituents at the upper Portuguese Margin. This
ventilation crisis may have led to an even higher oxygen depletion in the near-surface sediment as indicated by the condensed ichnocoenosis A due to a shallowing of the redox boundary during the last deglaciation. This is supported by BFOI data from core PO200-10-28-2 that is situated in 2155 m water depth. During the last glacial, a strong contribution of low-oxic, nutrient-laden Southern Hemisphere waters at this depth level caused considerable reduction in ventilation (Sarnthein et al., 1994). The BFOI data in this core shift from low-oxic during the last glacial to high-oxic during the Holocene (Fig. 8). Hence, the O2 drawdown was significant enough to cause generally higher proportions of low-oxic species thus resulting in a systematic change of the benthic foraminiferal community.

Variable air–sea gas exchange and potential changes in the $\delta^{13}$C composition of oxidisable organic matter may modulate the benthic $\delta^{13}$C data and limit the reliability of benthic $\delta^{13}$C as a means to estimate changes in ventilation and O2 concentration. As the Heinrich events were associated with temperature decreases in the open North Atlantic, indicated by the dominance of polar planktonic foraminifera (Bond et al., 1993), ‘preformed’ $\delta^{13}$C$_{\text{CO}_2}$ could have been higher than during mean-glacial conditions (Mook et al., 1974). On the other hand, reduced air–sea gas exchange due to enhanced stratification of surface–subsurface waters brought about by meltwater-induced salinity reductions could have led to a decrease in ‘preformed’ $\delta^{13}$C$_{\text{CO}_2}$. Reduced surface water $P_{\text{CO}_2}$ in response to lower glacial atmospheric $P_{\text{CO}_2}$ in the absence of the upwelling of nutrient-enriched deep waters would result in reduced carbon isotope fractionation of the marine biota and cause the $\delta^{13}$C composition of marine organic matter to increase (Jasper and Hayes, 1994; Rau, 1994). Using modern marine $\delta^{13}$C$_{\text{org}}$ of $-25\%_e$ PDB would thus underestimate the magnitude of AOU and ultimately, overestimate absolute O2 concentrations.

Evidently, the database used for this intercomparison is too small to allow for a statistically robust evaluation of the BFOI, trace-fossil and benthic $\delta^{13}$C data in the light of oxygenation conditions. Whereas the use of benthic $\delta^{13}$C in palaeoceanographic reconstructions is reasonably well constrained, the BFOI approach is novel and needs to be tested by extending this method on other sediment cores from different oceanographic regimes. Trace-fossil tiering and the degree of condensation of piped zones provide a useful first-order constraint on oxygenation conditions. Independent proxies such as benthic Cd/Ca will add further constraints on water-mass ventilation and help to separate thermodynamic and $P_{\text{CO}_2}$ effects from ventilation effects on benthic $\delta^{13}$C.

7. Conclusions

Benthic foraminiferal associations and trace-fossil assemblages can be used to reconstruct O2 concentrations of ancient bottom waters, although accurate quantitative estimates strongly suffer from inaccuracies in the existing models and the scarcity of recent data from the study area for calibration. Trace fossils and benthic foraminifera in sediment cores from the Portuguese continental margin reveal drastic changes in the degree of bottom-water oxygenation during the last 40 ka. A qualitative assessment implies that O2 concentrations were in the low-oxic to dysoxic realm during the main phase of Heinrich events H1 to H4. Suboxic and dysoxic conditions prevailed during H2 and H4, whereas low-oxic bottom waters were present during H1. Even during H3, when significant amounts of sand-sized IRD were lacking, low-oxic to dysoxic bottom-water conditions could be inferred from the data. The Younger Dryas is characterised by slightly reduced O2 levels. Comparing the results from both proxies, trace-fossil tiering always suggests lower O2 levels than BFOI values. Benthic foraminifera rather yield maximum O2 concentrations because of methodological modifications.

Other factors than O2 content may affect the depth distribution of benthic organisms. Environmental factors like sedimentation rate, substrate character, ecosystem stability, competition and especially the availability of food resources may control the presence and distribution of benthic foraminifera and trace fossils in such a way that O2 level estimations are obscured. Palaeoproductivity calculations imply that enhanced productivity before and after H2 may partly account for the abundance maximum of *Globobulimina affinis*. Abundance maxima of low-O2-tolerant foraminifera were recognised up to 10 cm below Heinrich layers. This systematic offset most likely reflects the original microhabitat
depth of dysoxic species in the sediment rather than short periods of low-O$_2$ conditions preceding Heinrich events. Benthic $\delta^{13}$C records from mid-depth cores from the Portuguese Margin show short-term minima during the main phase of Heinrich events (Zahn et al., 1997). They suggest a drawdown of North Atlantic thermohaline circulation at the same stratigraphic levels where the trace fossils and benthic foraminifera indicate decreased O$_2$ levels. Using stratigraphic levels where the trace fossils and benthic foraminifera indicate decreased O$_2$ levels. Using the relation between $\delta^{13}$C of total dissolved carbon and AOU in the modern oceans (Kroopnick, 1985), the decline in benthic $\delta^{13}$C reveals a reduction of dissolved O$_2$ in the bottom water to mean values of 3.4 to 5.0 ml l$^{-1}$ during Heinrich events. These values are higher than estimates from BFOI for H1, H2 and H4. Taking into account that the glacial O$_2$ concentration were higher than today at mid water depth but the mean glacial BFOI matches the range of Holocene values, the differences between $\delta^{13}$C and BFOI estimates imply that benthic foraminiferal assemblages are rather robust to changes in bottom-water oxygenation if the values do not fall below 3 ml l$^{-1}$. Trace-fossil tiering structures indicate much lower oxygen levels than values obtained from the other proxies. The burrowing organisms appear to be much more sensitive than foraminifera, even to small reductions in bottom-water oxygenation which change the equilibrium between the influx and oxidation of organic matter in the near-surface sediment leading to a shallowing of the redox boundary and an upward movement of trace-fossil tiers.

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