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Marine Micropaleontology 40 (2000) 277–294

MARINE MICROPALEONTOLOGY

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Aplanktonic zones in the Red Sea

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Received 30 December 1998; accepted 17 March 2000

Abstract

We use micropalaeontological and stable isotope results for a series of cores from north to south through the Red Sea, to assess temporal and spatial patterns of change in planktonic foraminiferal faunas leading up to the remarkable full-glacial Red Sea aplanktonic zones. Aplanktonic zones reflect salinities in the Red Sea in excess of the lethal 49 p.s.u. limit, caused by reduced exchange transport through the Strait of Bab el Mandab due to glacial sea-level lowering. Concerning the last glacial cycle, aplanktonic conditions began at 39 ka BP in the north, where salinities eventually reached 55–57 p.s.u. Paradoxically, planktonic faunas are reported to have survived the last glacial maximum in the northern Gulf of Aqaba, suggesting a poorly understood freshwater dilution at that time. Aplanktonic conditions ($S \geq 49$ p.s.u.) reached the south-central Red Sea by 22 ka BP, while planktonic foraminiferal faunas continued, albeit in very low abundances and limited diversity ($S \leq 45$ p.s.u.), in the southernmost Red Sea. During marine isotope stage (MIS) 6, the 49 p.s.u. isohaline appears to have resided in the central Red Sea, between cores KL11 and MD921017. We observe a systematic sequence of species disappearances before all glacial maxima of the last 500 kyr. Absence of a logical relationship with sea levels suggests that the disappearance sequences are not related to a general salinity increase. Instead, we argue that the sequences were driven by complex reorganisations in hydrography (stratification), productivity (food availability) and subsurface oxygenation (reproduction-habitats). The onset is marked by dramatic basin-wide expansion of conditions that today are restricted to only the southern Red Sea, suggesting an expansion of the dominance of NE monsoonal circulation over the entire Red Sea. This expansion occurred 15 or more kyr before the aplanktonic zones of MIS-12, 6 and 2, and also before MIS-10 and 8, which never reach the aplanktonic stage. Regarding the last glacial cycle, this event occurred as early as 75 ka BP (MIS-4/5 boundary). After this major climatic reorganisation, we reconstruct progressive intensification of the new conditions, especially marked by northward expansion and intensification of the subsurface oxygen minimum zone (OMZ). During the last glacial cycle, a shallow and very distinct OMZ affected the central Red Sea as early as 68 ka BP, and the north as late as 55 ka BP. The OMZ expansion/intensification appears to have been interrupted by episodes of increased ventilation. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: planktonic foraminifera; aplanktonic zones; oxygen minimum zone

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1. Introduction

This study concerns the nature of planktonic foraminiferal disappearance sequences during the development of glacial aplanktonic zones in the Red Sea. During glacial times, as today, Red Sea circulation is thought to have been anti-estuarine, with surface

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PII: S0377-8398(00)00042-6

Table 1
Basic habitat characteristics of the main Red Sea planktonic foraminiferal species (among others, Anderson, 1983; Hemleben and Spindler, 1983; Reiss and Hottinger, 1984; Spindler et al., 1984; Hemleben et al., 1989; Bijma et al., 1990b; Erez et al., 1991; Bijma and Hemleben, 1994; Reiss et al., 1999)

	Globigerinoides sacculifer	*Globigerinella siphonifera*	*Globigerinoides ruber*	*Globigerinita glutinata*
Temperature tolerance (°C)	14–31/32	11–30	13/14–32	Wide range
Salinity tolerance (p.s.u.)	24–47/49	27–45	22–49	Wide range
Dietary preferences	Voracious carnivore. Prefers (calenoid) copepods. Consumes algae in juvenile stages	Omnivore	Omnivore though cannot handle strong prey. Consequently feeds mostly on phytoplankton	Herbivore, specialised in diatoms
Depth habitat	Epi- to shallow mesopelagic mixed-layer species. Highest numbers in upper 100 m, significant numbers down to 200–300 m	Widely distributed in upper 100 m, but can live deeper; main calcification depth 50–75 m in N. Atlantic	Shallow epipelagic. Present in upper 100 m, but especially in upper 50 m	Epi- to mesopelagic. Cosmopolitan with enhanced abundances in fertile waters

inflow from the adjacent ocean compensated by subsurface outflow of high-salinity Red Sea water (among others Locke and Thunell, 1988; Thunell et al., 1988; Almogi-Labin, 1991; Rohling, 1994; Hemleben et al., 1996). Sea-level-induced reduction of exchange transport over the very shallow sill in the Strait of Bab el Mandab is generally held responsible for a salinity crisis in the Red Sea throughout the last glacial maximum (LGM). Estimates based on micropalaeontological and oxygen isotope data range around 50 p.s.u. or more. Such high salinities, corroborated by chemical precipitates and benthic foraminiferal species indicative of hypersaline conditions, are beyond the salinity tolerance of planktonic foraminifera, and hence resulted in the development of an aplanktonic zone (e.g. Ku et al., 1969; Milliman et al., 1969; Deuser et al., 1976; Schoell and Risch, 1976; Ivanova, 1985; Halicz and Reiss, 1981; Winter et al., 1983; Reiss and Hottinger, 1984; Locke, 1986; Locke and Thunell, 1988; Thunell et al., 1988; Almogi-Labin et al., 1991; Rohling, 1994; Hemleben et al., 1996; Rohling et al., 1998; Fenton, 1998; Geiselhart, 1998).

Because the only natural connection of the Red Sea with the open ocean is in the south, the ultimate disappearance related to the surpassing of a critical salinity threshold would be expected first in the northernmost Red Sea. We add two new high-resolution central Red Sea records to the records of Geiselhart (1998) from the northern and southern Red Sea, to evaluate whether such a trend is visible.

Winter et al. (1983) propose that the disappearance sequence of planktonic foraminiferal species preceding the LGM aplanktonic zone was related to increasing salinities and the successive surpassing of salinity thresholds for the various taxa. Their data from the southern Gulf of Aqaba, however, do not support such a straightforward interpretation: continuation is reported of *Emiliania huxleyi* after the disappearance of the main planktonic foraminiferal taxa, whereas a maximum salinity tolerance of 41–45 p.s.u. was acknowledged for *E. huxleyi* (after Mjaaland, 1956), compared with limits for *Globigerinoides sacculifer* and *Globigerinoides ruber* around 47 and 49 p.s.u., respectively (Hemleben et al., 1989; Table 1). Reiss et al. (1980) and Reiss and Hottinger (1984) suggest that the disappearance of *G. sacculifer* in the Gulf of Aqaba was instead due to a drop in winter-temperatures, and hence in temperatures at the depth of reproduction (estimated around 100–150 m), to values below 17°C. *G. ruber* would have continued because of a lower temperature tolerance, to 14°C. However, it seems likely that a wider range of critical habitat characteristics should be considered, since *G. sacculifer* is less abundant than *G. ruber* in the southern Red Sea, whereas present-day temperatures are consistently above 17°C (see below). Additional controls on relative species abundances include food-quantity and quality, and reproductive strategies.

Halicz and Reiss (1981) argue that presence–absence patterns of planktonic foraminifera in the northernmost Red Sea and Gulf of Aqaba strongly reflect productivity changes in the photic layer, and *Globigerinoides sacculifer* would be indicative of more eutrophic conditions than *Globigerinoides ruber*. Hemleben et al. (1989) argue that the widespread occurrence of *G. ruber* in the southern Red Sea may be attributed to its capacity to establish a significant advantage in competing for energy resources in regions of limited food-supply. Simple arguments of food-quantity, however, do not suffice: productivity in the present-day southern Red Sea is higher than towards the north, but *G. ruber* is more abundant in the south and *G. sacculifer* dominates the north (see below). Hemleben et al. (1989), however, also suggest that food-quality (dietary preference) plays an important role, as *G. sacculifer* is a specialised predator of zooplankton and *G. ruber* is adapted to a more herbivorous diet (see also Table 1). This would fit their distributions in the Red Sea, where the north is generally more oligotrophic than the south. Auras-Schudnagies et al. (1989) suggest that besides feeding preferences and food-supply, potentially adverse conditions at (reproduction-) depth may also be important, since *G. ruber* is a shallow epipelagic species, while *G. sacculifer* reproduces at around 80 m depth (Bijma and Hemleben, 1994) or deeper (Reiss et al., 1980, 1999; Reiss and Hottinger, 1984).

It is apparent that potential changes in a broad spectrum of ecological controls should be considered when assessing the causes of disappearance sequences. These controls would be superimposed

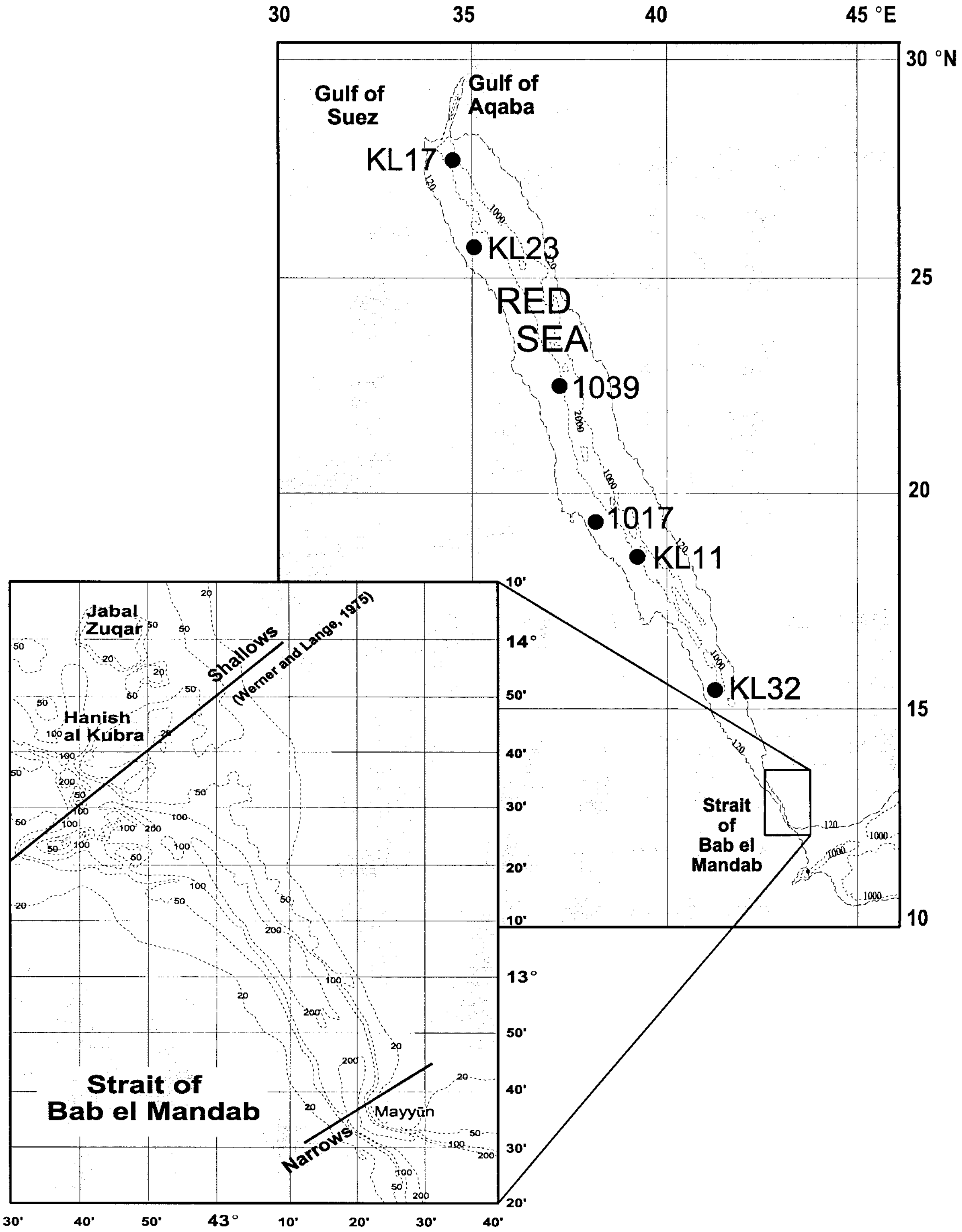

Fig. 1. Map of the Red Sea, with locations of the cores discussed in this paper. Contours in metres.

on an underlying sea-level-related trend towards hypersalinity that eventually terminates even the most hardy species. As yet, nature and interplay of the additional ecological controls remain elusive.

To date, most palaeoceanographic studies have focussed on the youngest, LGM, aplanktonic zone. To investigate which processes drive the disappearance sequences, however, it is worthwhile to first establish whether this LGM sequence and the timescales involved are typical, or not. Here, we present new data from the youngest and several previous aplanktonic zones in two central Red Sea pistoncores, which we combine with the data of Geiselhart (1998), to re-evaluate the nature of the disappearance sequences.

2. Background

2.1. Oceanography

The only natural connection of the Red Sea to the open ocean (Gulf of Aden) is over the Hanish Sill at the Strait of Bab el Mandab (Fig. 1), which is about 105 km wide and up to 137 m deep (Werner and Lange, 1975). River inflow and precipitation are negligible with respect to evaporation over the Red Sea (evaporation rate $\approx 2\ \mathrm{yr}^{-1}$; Privett, 1959; Morcos, 1970; Pedgley, 1974; Maillard and Soliman, 1986). The consequent net buoyancy loss causes anti-estuarine circulation, with surface water inflow compensated by subsurface outflow through the Strait (e.g. Neumann and McGill, 1962; Siedler, 1969; Morcos, 1970; Wyrtki, 1971; Maillard and Soliman, 1986; Cember, 1988; Eshel et al., 1994; Woelk and Quadfasel, 1996; Tragou and Garrett, 1997). In the southern Red Sea, including the Strait of Bab el Mandab, this pattern is complicated by seasonal reversal of surface water flow due to monsoonal wind reversal.

During the summer SW monsoon, northwesterly winds over the entire basin drive a south flowing surface current, and inflow into the basin is constrained to a weak shallow-subsurface current. This subsurface inflow of cold nutrient-rich water from the Gulf of Aden extends up to 17–18°N (Jones and Browning, 1971; Patzert, 1972; Murray and Johns, 1997; Smeed, 1997). The winter inflow of surface waters and especially the July to September subsurface inflow from the Gulf of Aden supply nutrient-enriched waters to the southernmost Red Sea, boosting biological productivity (Weikert, 1987; Souvermezoglou et al., 1989).

During the winter NE monsoon, northwesterly winds to the north of 20°N drive a weak southward surface water flow, while southeasterly winds to the south of that latitude drive strong northward surface flow. The result is a zone of surface water convergence at 20–25°N, which migrates north as the intensity of the NE monsoon increases (Patzert, 1972, 1974). North of the convergence, sea surface temperatures are low (22–26°C) and surface water salinity is high (>40 p.s.u.), relative to the south (24 to >30°C and <37.0 to 38.5 p.s.u., respectively) (e.g. Neumann and McGill, 1962; Siedler, 1969; Morcos, 1970; Wyrtki, 1971; Patzert, 1972, 1974; Woelk and Quadfasel, 1996).

Intense buoyancy loss due to high salinity and winter cooling in the northernmost sector and the Gulf of Suez drives the formation of deep water ($T = 21.5$–22.0°C; $S = 40.5$–41.0 p.s.u.) that ventilates the entire deep Red Sea (e.g. Neumann and McGill, 1962; Grasshoff, 1969; Siedler, 1969; Morcos, 1970; Wyrtki, 1971; Maillard and Soliman, 1986; Cember, 1988; Eshel et al., 1994; Woelk and Quadfasel, 1996; Tragou and Garrett, 1997). Isopycnals in the surface 400 m show a general downward slope from north to south (Patzert, 1972, 1974; Quadfasel and Baudner, 1993; Van Couwelaar, 1997; Tragou and Garrett, 1997), while the vertical density gradient is generally weak in the north and strong in the south (see also Morcos, 1970). In summer, the above-mentioned studies place the top of the main pycnocline around an average 50 m depth in the south, and at a similar level in the north. In between, a transect during the NE–SW monsoon transition showed a deep pycnocline (top at 200 m) around 21–23°N, caused by an anti-cyclonic eddy (Quadfasel and Baudner, 1993). Data in Tragou and Garrett (1997) also suggest a deeper pycnocline in the central area (>50 m in station 6, ~22.5°N). In winter, the various studies find the top of the pycnocline around 70–80 m in the south, while the north is characterised by a very weak to non-existent gradient (if recognisable, top around 50–80 m). The main water-column stability maxima appear to be typically 40–50 m below the top of the pycnocline.

Dissolved oxygen in the Red Sea has been discussed by Neumann and McGill (1962), Morcos (1970), Wyrtki (1971), Grasshoff (1975), Weikert (1982, 1987), Quadfasel and Baudner (1993) and Woelk and Quadfasel (1996). In summary, Red Sea surface waters are rich in dissolved oxygen (>4 ml $O_2\,l^{-1}$), with maximum concentrations in winter in the north (>5 ml $O_2\,l^{-1}$). Oxygen concentrations decrease rapidly with depth, reaching a distinct minimum ("core") around 300–400, 350–450, and 400–500 m in the southern, central and northern Red Sea, respectively. The top of the oxycline lies close to 100 m in the south, and towards 200 m in the north, while the oxygen minimum zone (OMZ) is more pronounced in the south than in the north. In summer, very low concentrations in the core of the OMZ (0.3–0.5 ml $O_2\,l^{-1}$) extend from the Strait up to 20°N. Minimum oxygen concentrations are higher in winter (≤1.0 ml $O_2\,l^{-1}$) because of the active formation of subsurface water in the cooler season. Below the OMZ, dissolved oxygen concentrations increase to values >2.0 ml $O_2\,l^{-1}$. Note that saturation values for Red Sea deep water would be around 4.4 ml $O_2\,l^{-1}$ (Weiss, 1970). For comparison: active ventilation in the Gulf of Aqaba causes the absence of a distinct OMZ in that basin, where concentrations are always >3.7 ml $O_2\,l^{-1}$ (Weikert, 1987).

The 1% light penetration level is found around 60 m in the southern Red Sea, 80–100 m in the central basin, and 100 m or more in the northern regions (Weikert, 1982, 1987; Wiebinga et al., 1997). In the Gulf of Aqaba, this level is at 80 m or more (Reiss and Hottinger, 1984; Weikert, 1987).

2.2. General phytoplankton and zooplankton distributions

In general, low to moderate annual production occurs in the Red Sea (Halim, 1984; Weikert, 1987). Halim (1984) describes an overall northward decrease of primary production through the Red Sea. This is corroborated by Weikert (1987), who in addition cites an overall decrease in zooplankton diversity towards the north.

In the southernmost Red Sea, imported phytoplankton and zooplankton add significantly to the overall plankton biomass and diversity, because of inflow through the Strait of Bab el Mandab. Most of these displaced specimens from the Gulf of Aden do not reproduce and hence do not extend their influence further north than 16–18°N (Weikert, 1982, 1987; Halim, 1984). However, in situ primary production is also increased in the southern sector due to local phytoplankton blooms in response to nutrient entrainment from the thermocline in winter (Wiebinga et al., 1997; van Couwelaar, 1997). Winter is the normal productive season in the Red Sea between 18 and 27°N, but summer blooms are important in the coastal regions and in the southernmost and northernmost sectors of the basin (Weikert, 1987). The overall S–N production decrease through the basin is masked by a summer/autumn production event in the central Red Sea, which consists of patchy blooms of blue–green algae that can overcome nitrogen depletion by absorption of dissolved atmospheric nitrogen (Weikert, 1987). These blue–green algae can resist high light intensities, and their blooms break the normal pattern of subsurface production maxima in the Red Sea, which typically range from 50 to 80 m in summer, and 20 to 50 + m in winter. North of the convergence zone, annual primary production is low, with a maximum in winter due to convective upmixing of nutrients from deeper waters (Halim, 1984; Weikert, 1987).

In a survey of the central Red Sea (21.0–21.5°N), between 30 October and 14 November 1977, copepods were found to make up the bulk of mesozooplankton in surface and deep water habitats, while foraminifera were found in significant numbers in the upper 100 m (Weikert, 1982). Calanoid copepods were the dominant copepod group, and likely serve as food-source for planktonic foraminifera such as *Globigerinoides sacculifer.* Two mesozooplankton abundance maxima were distinguished: a distinct maximum in the upper 100 m epipelagic zone, and a secondary peak in the core of the OMZ (250–300 m). Zooplankton abundances are exceptionally low in deep mesopelagic and deeper levels of the Red Sea (Weikert, 1982).

2.3. Planktonic foraminifera

Today, the Red Sea planktonic foraminiferal fauna predominantly consists of spinose species (*Globigerinoides ruber*, *Globigerinoides sacculifer*, *Globigerinella siphonifera*, *Globoturborotalita rubescens*, *Globoturborotalita tenella* and *Orbulina universa*). Non-spinose species like *Globorotalia menardii*, *Neogloboquadrina pachyderma* and *dutertrei*, and *Pulleniatina obliquiloculata* are present only in low abundances in the southern sector of the basin, during the time of winter inflow from the Gulf of Aden (Kleijne et al., 1988; Auras-Schudnagies et al., 1989; Ganssen and Kroon, 1991).

Globigerinoides sacculifer dominates extant planktonic foraminiferal faunas of the northern Red Sea, while *Globigerinoides ruber* and *Globigerinella siphonifera* are more important south of 20°N, where *G. sacculifer* abundances are reduced (Auras-Schudnagies et al., 1988; Hemleben et al., 1989; Kroon, 1991). *G. sacculifer* not only dominates in the northern Red Sea, but also in the Gulf of Aqaba (Almogi-Labin, 1984; Reiss and Hottinger, 1984). There, *G. ruber* is relatively frequent throughout the year, while stong annual abundance variations are found in *G. siphonifera* (rare during summer) and, especially, *G. sacculifer* (high in October to January, and high in April). Mean annual standing crops of *G. sacculifer* were found to be over four times higher than those for *G. ruber* and *G. siphonifera* (Almogi-Labin, 1984; Reiss and Hottinger, 1984). For the northernmost Red Sea, Almogi-Labin (1984) and Reiss and Hottinger (1984) report high abundances for *G. sacculifer* down to 200 m, while substantial numbers of *G. ruber* were restricted to much shallower water (50–100 m). Within the Red Sea, Auras-Schudnagies et al. (1988, 1989) and Kroon (1991) report a gradient from: (a) strong dominance of *G. sacculifer* to the north of 22°N, via (b) roughly equal proportions of *G. sacculifer* and *G. ruber* between 22 and 19°N, to (c) dominance of *G. ruber* with substantial numbers of *G. siphonifera* and *G. sacculifer* between 19 and 16°N, and (d) mixed faunas of *G. ruber*, *G. siphonifera*, *G. glutinata*, *Neogloboquadrina dutertrei*, *G. bulloides*, and *Globorotalia menardii* towards the Strait of Bab el Mandab.

Concerning core-top samples, a lot depends on the size-fractions investigated. In general, Almogi-Labin (personal communication, 1999) found *Globigerinoides ruber* and *Globigerinoides sacculifer* in equal proportions (30–40%) between 19 and 28°N, while Auras-Schudnagies et al. (1988, 1989) show that in the size-class 125–250 μm *G. ruber* with *Globigerinita glutinata* are numerically dominant throughout the Red Sea. In the size-class >250 μm, Auras-Schudnagies et al. (1988, 1989) report a trend from dominance of *G. sacculifer* north of 22°N, via roughly equal proportions of *G. sacculifer* and *G. ruber* between 22 and 17°N, to dominance of *G. ruber* between 17 and 16°N. Further south and to the Strait of Bab el Mandab, *Globigerinella siphonifera* and *G. bulloides* dominate core-top sediments in this size-fraction (Auras-Schudnagies et al., 1989). Note that dominance of *G. sacculifer* in core-top sediments with respect to *G. ruber* is a strong indication of its dominance in the water-column, since the test-flux per unit standing stock would be greater for *G. ruber* with its twice-monthly reproduction cycle than for *G. sacculifer* with its monthly cycle (e.g. Reiss and Hottinger, 1984; Hemleben et al., 1989).

In summary, there is a southward decrease in *Globigerinoides sacculifer* with greatest numbers of this species to the north of the convergence zone. The southward decrease in *G. sacculifer* (see also Bijma and Hemleben, 1994) gives way to an increase in *Globigerinoides ruber*. *Globigerinella siphonifera* is found throughout the Red Sea, but is most abundant to the south of 16°N, where *Globigerina bulloides* also appears in core-top sediments. *G. glutinata* shows a general presence in water and core-top samples of the Red Sea, with highest abundances in the Strait of Bab el Mandab, northward decreasing numbers through the southern and central Red Sea, and low abundances in the northern Red Sea (Auras-Schudnagies et al., 1988, 1989; Kroon, 1991).

Table 1 summarises general habitat characteristics of the main Red Sea planktonic foraminiferal species. In this paragraph, we summarise key-points from a recent ecological review (Reiss et al., 1999 and references therein). *Globigerinoides ruber* is an exclusively epipelagic species, whereas *Globigerinoides sacculifer* migrates to deeper water for reproduction (Bijma et al., 1990a). In the central Red Sea, reproduction is concentrated around 60–80 m (Bijma and Hemleben, 1994). Reiss et al. (1999) infer that *G. sacculifer* thrives only in areas where the pycnocline is shallow, near the base of the photic layer. Although Reiss et al. (1999) argue that the presence of a deep

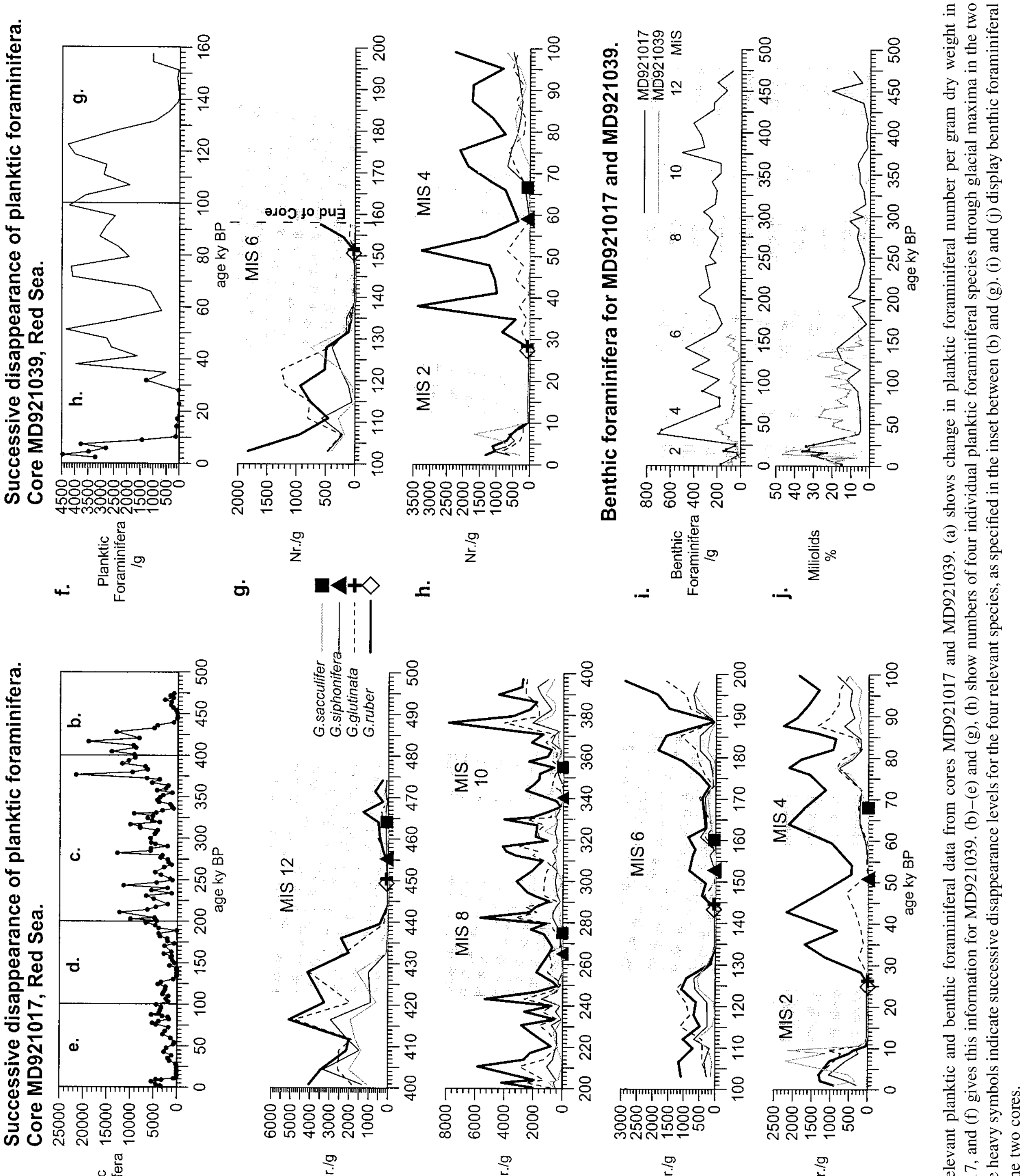

Fig. 2. Relevant planktic and benthic foraminiferal data from cores MD921017 and MD921039. (a) shows change in planktic foraminiferal number per gram dry weight in MD921017, and (f) gives this information for MD921039. (b)–(e) and (g), (h) show numbers of four individual planktic foraminiferal species through glacial maxima in the two cores. The heavy symbols indicate successive disappearance levels for the four relevant species, as specified in the inset between (b) and (g). (i) and (j) display benthic foraminiferal data for the two cores.

chlorophyll maximum is not essential, the observations of Bijma and Hemleben (1994) demonstrate that it does coincide with the preferred level of reproduction. Reiss et al. (1999) suggest that a shallow pycnocline may also be crucial in enabling juveniles to migrate back to the surface for feeding. Changes in light intensity, possibly the light–dark transition, may be the actual trigger for gametogenesis (e.g. Erez et al., 1991). In areas where the pycnocline is deep relative to light penetration, and/or where adverse conditions (e.g. low oxygen) occur in the shallow mesopelagic zone, therefore, *G. sacculifer* seems to be at a competitive disadvantage compared to shallow epipelagic species, e.g. *G. ruber.*

In addition to the different dietary requirements between carnivorous *Globigerinoides sacculifer* and largely herbivorous *Globigerinoides ruber* (Table 1; Hemleben et al., 1989), we propose that the shallow and intense OMZ in the southern Red Sea may be a key to the spatial gradient in *G. sacculifer* versus *G. ruber* abundances. This would imply that temporal changes in the depth and intensity of the OMZ through the basin would cause important shifts in the relative abundances of *G. sacculifer* versus *G. ruber.* In the present paper, we integrate this working hypothesis with independent data regarding intensification and/or lateral expansion of the OMZ.

3. Material and methods

Central Red Sea cores MD921017 (19°23.24′N, 38°40.84′E, 570 m) and MD921039 (22°26.24′N, 37°13.15′E, 1050 m) were collected by R.V. *Marion Dufresne*, Leg 73, in September 1992 (Fig. 1). Stratigraphic frameworks for cores KL32, 17, 13, and 11 (Fig. 1), collected during R.V. *Meteor*, Leg 31-2 in spring 1995, are elaborated in Geiselhart (1998). The time-stratigraphic frameworks for the MD-cores were obtained from correlation of the *Globigerinoides ruber* (250–350 μm) based oxygen isotope records to the SPECMAP record with assigned ages for discrete isotope events (Imbrie et al., 1984), including several AMS^{14}C datings for the younger sections based on clean planktonic foraminiferal carbonate and calibrated using program Calib 3.03 (Stuiver and Reimer, 1993; cf. Rohling et al., 1998; Fenton, 1998). The micropalaeontological results concern quantitative studies of planktonic foraminiferal abundances based on aliquots containing at least 200 specimens, and include a pilot inventory of the total benthic foraminiferal content of selected samples (150–600 μm fraction) (results are listed in an online **Background dataset**[1]).

4. Results

First, we emphasise that an occasional presence of planktonic foraminifera in extremely low numbers is sometimes observed within the "aplanktonic" intervals, i.e. after what we describe as the species' "disappearance". These occasional specimens could be: (1) extremely rare survivors, suggesting that salinities cannot have been much above the lethal thresholds; (2) expatriates, transported into the aplanktonic basin but not calcifying/reproducing there; (3) reworked; or (4) a result of the previous three options combined. We favour option (4), since reasonable isotope values were occasionally obtained from trace-specimens, whereas others yielded more erratic/poorly organised results.

Cores MD921017 and MD921039 show aplanktonic zones associated with glacial marine isotope stages (MIS) 2, 6, and 12. Planktonic foraminiferal faunas continue in low numbers through MIS-8 and 10 (Fig. 2a and f), and also in very low numbers through stage 6 in KL11. Core KL23 shows aplanktonic zones associated with MIS-6 and 2 (Geiselhart, 1998). We observe a systematic sequence of species disappearances approaching aplanktonic zones (Fig. 2b–e, g and h; Table 2). Each sequence begins with the disappearance of *Globigerinoides sacculifer* about 15 kyr or more before the onset of aplanktonic conditions. Next follow the disappearances of *Globigerinella siphonifera*, *Globoturborotalita rubescens* and *Globoturborotalita tenella*. Ultimately, *Globigerinoides ruber* and *G. glutinata* become extinct as well, marking the onset of the aplanktonic zone. Only the earlier stages of the disappearance sequence are developed in the approaches to glacial MIS-8 and

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[1] http://www.elsevier.nl/locate/marmicro; Mirror site: http://www.elsevier.com/locate/marmicro.

Table 2

Ages (ka BP) of last occurrence of notable trace-abundances preceding aplanktonic zones in MD921017, MD921039, and KL23 (n/r, not recorded)

		Globigerinoides sacculifer	*Globigerinella siphonifera*	*Globoturborotalita tenella* and *Globoturborotalita rubescens*	*Globigerinita glutinata*	*Globigerinoides ruber*
Core MD921017						
MIS-2	Aplanktonic 25.5–12.0 ka BP	68[a]	58[a]	35	26	25.5
MIS-6	Aplanktonic 143.8–134.0 ka BP	158	152	148	144	143.8
MIS-8	No aplanktonic zone	275	265	[b]	[b]	[b]
MIS-10	No aplanktonic zone	355	340	[b]	[b]	[b]
MIS-12	Aplanktonic 450.5–444.0 ka BP	464	454.8	454	451	450.5
Core MD921039						
MIS-2	Aplanktonic 27.7–16.0 ka BP	67.5[a]	58.8[a]	28	27.8	27.7
MIS-6	Aplanktonic 150.5–139.0 ka BP	>157.5[c]	>157.5[c]	151.5	151.5	150.5
Core KL23 (Geiselhart, 1998)						
MIS-2	Aplanktonic 36–12 ka BP	60[a]	50[a]	n/r	n/r	36
MIS-6	Aplanktonic 140–133 ka BP	160	155	n/r	n/r	140

[a] No return of species following MIS-4.

[b] No disappearance of the species.

[c] Dates for *Globigerinoides sacculifer* and *Globigerinella siphonifera* in MD921039 preceding MIS-6 uncertain, as record stops at 157.5 ka BP.

10, which have no fully developed aplanktonic zone (Fig. 2; Table 2).

The aplanktonic zones in MD921017 and MD921039 are in addition characterised by absences of many benthic foraminiferal species, and consequent relative abundance peaks of miliolids. This is especially well represented in the high-resolution record of MD921039 (Fig. 2j). The most pronounced example is seen in MIS-2, corroborating similar observations by Halicz and Reiss (1981) and Locke and Thunell (1988).

Monospecific assemblages of pteropod-tests of the salinity tolerant epipelagic species *Creseis acicula* were noted throughout the aplanktonic zones in MD921017, MD921039, KL23, and KL17, in agreement with the results of Almogi-Labin et al. (1986, 1991, 1998). The pteropod-tests are found in a predominantly encrusted state of preservation.

5. Discussion

5.1. Aplanktonic zones

The aplanktonic zones in our cores show many features that have been observed in previous studies as well, and which confirm the commonly inferred hypersalinity in the basin at those times. First, we note the absence of planktonic foraminifera, which as a group have a maximum salinity tolerance around 49 p.s.u. Secondly, we note a loss of diversity in the benthic foraminiferal faunas with increased importance of miliolid taxa, several species of which are known from hypersaline marine environments around the Red Sea. Thirdly, we observe strong tendencies to heavily enriched oxygen isotope ratios in our (planktonic) *Globigerinoides ruber* records towards the aplanktonic zones, while Hemleben et al. (1996) note similar trends that continue into the aplanktonic zones using the benthic taxa, *Hanzawaia* sp. and *Cibicides mabahethi*, and using pteropods.

Further corroborating evidence of high salinity comes from the encrusted state of preservation of the aragonitic *Creseis acicula* tests. Almogi-Labin et al. (1986, 1991, 1998) attributed the aragonite encrustation on pteropod shells of glacial maxima in cores MD76-140, KL 13 and KL 11 to aragonite supersaturation of the bottom waters owing to elevated salinity and/or temperature (cf. Chen, 1969; Milliman et al., 1969). Besides pteropod encrustation, we observe increases in sediment coarseness in especially MIS-2 and to a lesser extent MIS-6 in cores MD921017 and MD921039, and in MIS-12 in core MD921017. This agrees with similar observations concerning the LGM interval in other Red Sea cores (including KL11), and has been attributed to lithification of particles, cemented by inorganically precipitated aragonite. This, again, suggests that bottom and pore waters were supersaturated with respect to aragonite (Milliman et al., 1969; Ivanova, 1985; Almogi-Labin et al., 1991). However, some cores paradoxically show no lithified sediments in glacial intervals (notably KL23).

Lowering of the global sea level would cause a reduction in strait dimensions at Bab el Mandab, resulting in reduced water exchange between the Red Sea and the open ocean. Even with a constant net evaporation rate, the pronounced sea-level drops of full-glacial periods would thus lead to a strong rise in salinity (among others, Locke and Thunell, 1988; Thunell et al., 1988; Rohling, 1994; Hemleben et al., 1996; Rohling et al., 1998). Note that the less abundant but typical planktonic foraminiferal fauna recorded in southern Red Sea core KL32 indicates that salinities in that area (15°33.4′N) remained below 45 p.s.u., implying that some communication with the Gulf of Aden persisted even during the LGM (Geiselhart, 1998).

Although compositional changes do occur in the benthic foraminiferal and pteropod faunas, the simple fact that such faunas persisted through glacial maxima confirms that some communication (perhaps a seasonal exchange) remained between the Red Sea and open ocean, preventing worse salinisation and consequent sterilisation of the basin. Hence, we support most previous reconstructions, estimating that salinities during the deposition of MIS-2 aplanktonic zone ranged up to 45 p.s.u. in the south and well over 50 p.s.u. in the central to northern Red Sea. The upper limits were estimated at 55–57 p.s.u., respectively, by conversion of oxygen isotope results (Thunell et al., 1988; Hemleben et al., 1996; Geiselhart, 1998). Within the MIS-6 (virtually) aplanktonic zone in central Red Sea core KL11, we observe occasional planktonic foraminiferal survivors whose exceptionally heavy isotope signatures argue against reworking. In core MD921017, 100 km further north, no such trace-abundances were present, suggesting that the lethal salinity boundary (49 p.s.u.) resided between the sites of KL11 and MD921017 during MIS-6.

The onset of the LGM aplanktonic zone can be traced through the Red Sea. We reinterpret the onset of MIS-2 in the Geiselhart (1998) δ^{18}O record of the northernmost Red Sea core KL17 (27°41.1′N), placing it at the strong enrichment she describes around 270 cm. This reinterpretation is supported by correlation of the strong abundance increase in *Creseis acicula*, and places the start of aplanktonic conditions *prior to* a brief δ^{18}O enrichment within MIS-3, at an estimated age of 39 ka BP. Further south, in KL23 (25°44.9′N), the same brief enrichment (also marked by the rapid decline of *Limacina trochiformis*) can be recognised around 215 cm, and aplanktonic conditions start *within* that enrichment event (Geiselhart, 1998), at an estimated age of 36 ka BP. In MD921039 (22°26.2′N; Table 2), aplanktonic conditions start much later, at 27.7 ka BP. Next, aplanktonic conditions appear at 25.5 ka BP in MD921017 (19°23.2′N; Table 2), and at 21–22 ka BP in core KL11 (18°46.3′N; Hemleben et al., 1996). The stratigraphy of KL32 (15°33.4′N) is more complicated, and no truly aplanktonic conditions are found. A strong decrease of planktonic foraminiferal abundances is found, however, to very low (if still countable) numbers, but this did not take place before 20 ka BP (Geiselhart, 1998). The onset dates of the aplanktonic conditions are plotted versus latitude in Fig. 3.

The end of the aplanktonic zone in all cores is placed at 11–12 ka BP, with the exception of MD921039, where an AMS^{14}C dating suggests 16 ka BP. We use the dating at face value, although it might reflect a slight dating problem for that sample (Fig. 3). There are no trace-abundances of any foraminifera in the MIS-2 aplanktonic zone of cores KL11, MD921017, KL23 and KL17. The occasional single specimens that are found, also in MD921039, have light isotope values suggesting a reworked origin. The isotope values reported by Geiselhart (1998) for MIS-2 and MIS-6 in KL23 and KL17 were spliced in, using calibrated results on the

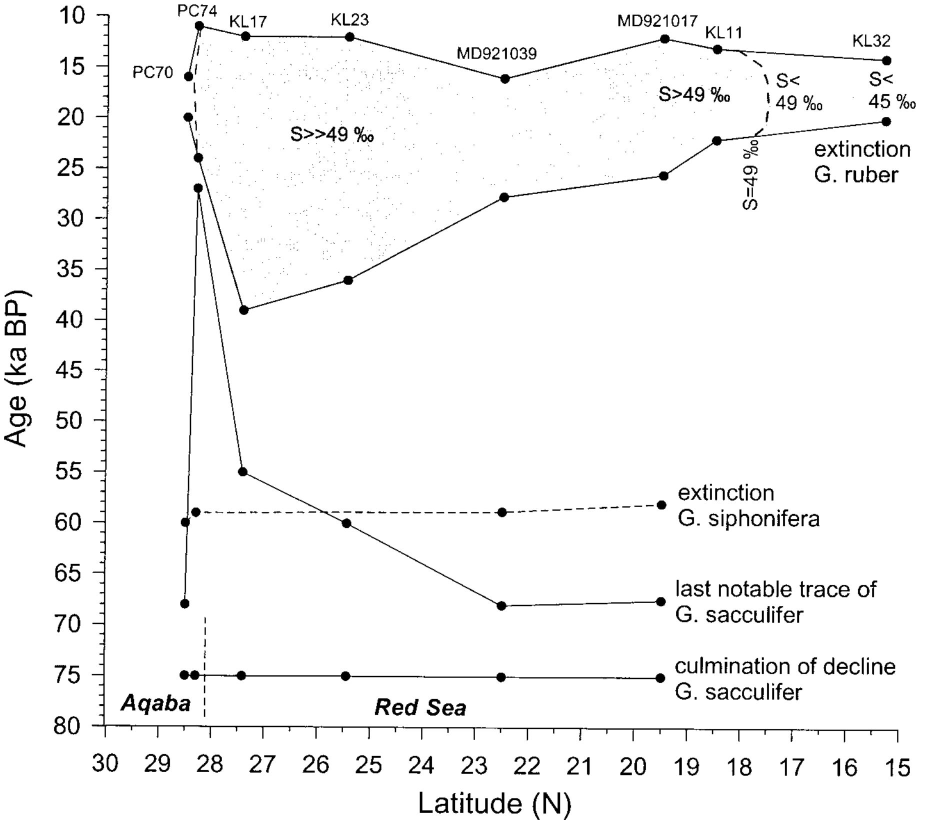

Fig. 3. Time–latitude plot for the various main faunal changes leading up to, and through the aplanktonic zone of MIS-2, as elaborated in the discussion.

pteropod *Creseis acicula*. The very heavy values in those intervals suggest harshest (highest salinity) conditions in the north. Fluctuating MIS-2 isotopic values in KL32 (Geiselhart, 1998) are suggestive of influx fluctuations from the Gulf of Aden, while the (limited) continuation of faunas in KL32 also suggests that MIS-2 salinities remained at or below 45 p.s.u. It appears that conditions in the south were considerably less hostile than further basin-inward (Fig. 3).

In summary, we infer that the onsets of the aplanktonic zones, marked by the final disappearances of *Globigerinoides ruber* and *G. glutinata*, were due to the spatially diachronous crossing of a salinity threshold around 49 p.s.u. Harshest conditions are reflected in the northern Red Sea, which is consistent with the present-day S–N salinity increase. Paradoxically, there appears to have been a late (~24 ka BP) onset of aplanktonic conditions in the southern Gulf of Aqaba (PC74), and continuation of planktonic foraminifera through the LGM in the N-central and northern Gulf of Aqaba (weak in PC70, stronger in PC71, 72, and 73) (e.g. Reiss et al., 1980; Halicz and Reiss, 1981). Glacial (salinity) conditions in the Gulf of Aqaba may have been milder than in the Red Sea, which is completely opposite to the present trend. This apparent anomaly needs validation from further studies, especially because of poor recovery of MIS-2 in the Gulf of Aqaba cores. If true, however, the explanation may have to be sought in intensified Mediterranean climate influences. LGM evaporation is thought to have been intensified over the easternmost Levantine basin (Myers et al., 1998; Rohling and De Rijk, 1999), which may have caused enhanced rainfall over the drainage basin to the Gulf of Aqaba. Our inference of glacial humidity in this region is corroborated by high lake levels in Lake Lisan (Dead Sea rift) between 27 and 21 ka BP, followed by a pronounced drop around 19 ka BP (M. Stein, personal communication, Trins, Austria, February 2000).

5.2. Species disappearance sequences

We note that *Globigerinoides sacculifer* abundances went into severe decline around 80 ka BP, a trend that culminated around the MIS-5/4 boundary (70–75 ka BP), and that notable trace-abundances ended at 68 ka BP in central Red Sea cores MD921017 and MD1039. After that, only occasional specimens were found until about 40 ka BP, after which time the species remained completely absent until the end of the MIS-2 aplanktonic zone. Further north, *G. sacculifer* went through the same decline, but notable trace-abundances continued until ~60 and 55 ka BP in northern Red Sea cores KL17 and KL23, respectively (Geiselhart, 1998; stratigraphy reassessed as above). After those dates, occasional specimens are present until 40 ka BP. The severe decline in *G. sacculifer* also culminated around 75–70 ka BP throughout the Gulf of Aqaba, but in southernmost Gulf of Aqaba core PC74, traces of *G. sacculifer* remain present up to ~27 ka BP, compared with ~68 ka BP in core PC70 from the S-central Gulf (Reiss et al., 1980; Halicz and Reiss, 1981) (Fig. 3).

The severe decline of *Globigerinoides sacculifer* around the MIS-5/4 boundary left a fauna dominated almost exclusively by *Globigerinoides ruber*, with some *Globigerinita glutinata* and only traces of *G. sacculifer*, similar to faunas found today in the southern Red Sea between 17 and 16°N (cf. Fenton, 1998; Geiselhart, 1998). Schematically, therefore, this suggests that the conditions typical for the modern southern Red Sea had rapidly expanded northward by 75–70 ka BP. Next, specific conditions developed that "eliminated" the still notable traces of *G. sacculifer*, starting in the south and slowly expanding northward. This development reached the south-central Red Sea by 68 ka BP and the northernmost Red Sea by ~55 ka BP (Fig. 3). At times, conditions became sufficiently favourable to allow occasional survival of *G. sacculifer* until ~40 ka BP, but after that time the species remained totally absent throughout the central and northern Red Sea.

The complex temporal and spatial distributions of the faunal changes precludes their explanation by means of a simple basin-wide forcing, such as salinity increase and stagnation of the water-column. Physical constraints due to stratification and its influences on productivity also need to be considered. Global sea level throughout MIS-4, 3, and 2 consistently stood 60 m or more below the present-day mark (e.g. Shackleton, 1987; Bard et al., 1996; Rohling et al., 1998). In a similar marginal basin, the Mediterranean, such low sea-level positions cause increased surface to intermediate water density gradients and basin-wide shallowing of the pycnocline, because of restricted exchange transport through the shallow and narrow connection with the open ocean (Rohling, 1991; Rohling and Bryden, 1994; Myers et al., 1998). A comparable response is envisaged for the Red Sea, which has an even smaller strait. A shallower and intensified pycnocline allows shallowing of the oxy-/nutricline, fuelling increased productivity in the lower euphotic zone, while erosion of a shallower nutricline during winter overturn would also intensify winter-time production throughout the mixed layer. The resultant respiratory oxygen utilisation, combined with poorer ventilation at times of increased density gradients, would intensify and expand the OMZ, which today is most distinct in the southern Red Sea.

Expansion/intensification of the OMZ would adversely affect *Globigerinoides sacculifer's*, shallow mesopelagic reproduction-habitat, and intensified stratification would favour *Globigerinoides ruber* over *G. sacculifer.* In addition (calanoid) copepods, part of *G. sacculifer's* dietary preference, today abound in the shallow mesopelagic OMZ in the central Red Sea (Weikert, 1982). Distinct intensification of the OMZ would arguably be detrimental to that zooplankton-niche (cf. Almogi-Labin, 1991).

5.3. Climatological and oceanographic interpretation

Although further validation is needed by multi-proxy studies of a N–S transect of cores, and by numerical circulation modelling of the Red Sea, we believe that sufficient data are available to formulate a working hypothesis regarding the main observed pre-aplanktonic faunal changes in the Red Sea.

The boundary between the southern and northern Red Sea environments is formed by the convergence zone, which develops under the winter NE monsoon regime, and which migrates northward as the NE monsoon intensity increases. Hence, we suggest that the NE monsoon-type configuration became dominant around the MIS-5/4 transition, extending its influences over the entire Red Sea, rather than being limited to the area south of 20°N. Vénec–Peyré and Caulet (2000) suggest that precessional modulation of the SW monsoon intensity continued through MIS-3, and hence we infer that our observations are primarily related to strong intensification of the NE monsoon during MIS-4, 3 and 2. This is also suggested by the observed dramatic latitudinal expansion of its effects, spanning the entire basin. The increase in intensity and/or duration of the NE monsoon started around the MIS-5/4 transition and persisted until the end of the LGM.

Our interpretation of NE monsoon-dominated conditions throughout MIS-4, 3, and 2, corroborates that of Almogi-Labin et al. (2000), who report maximum NE monsoon activity in the Gulf of Aden from about 60 to 13 ka BP. Glacial intensification of the NE monsoon and also weakening/shortening of the SW monsoon has furthermore been described for the wider N. Indian Ocean region (e.g. Van Campo et al., 1982; Duplessy, 1982; Fontugne and Duplessy, 1986; Prell and Van Campo, 1986; Sarkar et al., 1990; Sirocko et al., 1991; Prell et al., 1992; Anderson and Prell, 1993; Emeis et al., 1995). We propose that the mechanism of NE monsoon intensification also presents a suitable explanation for disappearances of *Globigerinoides sacculifer* prior to older glacial maxima. If true, then a “glacial” NE monsoon-dominated regime appears to have developed at least 15 kyr before the onset of each peak glaciation of the last 500,000 years (Table 2).

We interpret the diachronous northward “elimination” of trace-populations of *Globigerinoides sacculifer* as a complex function of (lateral) expansion and intensification of the OMZ towards the north from its “normal” position in the southern Red Sea. In the case of the LGM, there is significant support for this hypothesis. From MIS-4 onwards, increased productivity and intensification/expansion of the OMZ is witnessed by increasing abundances of low-oxygen tolerant benthic foraminifera in all cores investigated (*Bolivinidae* and *Buliminidae*). At the same time, agglutinated benthic foraminifera show a general decline (Almogi-Labin et al., 1996).

OMZ expansion does not seem to be a smooth and unidirectional process, as witnessed by our observations of brief, weak, recoveries of *G. sacculifer* (often with *Limacina inflata*) within MIS-3, which suggest episodes of increased ventilation. Culmination of OMZ expansion/intensification around 40 ka BP completely terminated *G. sacculifer* throughout the basin, and eventually also caused extensive disappearance of mesopelagic pteropods (Almogi-Labin et al., 1986, 1996, 1998; Fenton, 1998; Geiselhart, 1998). These adverse conditions persisted through the LGM.

Gulf of Aqaba bottom water oxygen concentrations, calculated from carbon isotope data, also show strong deterioration of oxygenation from 75 ka BP onwards, persisting until the end of MIS-2 (Reiss and Hottinger, 1984). That study included corroborating evidence from benthic foraminiferal abundance changes in the northernmost Red Sea and Gulf of Aqaba.

6. Conclusions

Aplanktonic zones in full-glacial intervals in Red Sea sediment cores record the N–S diachronous surpassing of the 49 p.s.u. salinity limit. During the last glacial cycle, aplanktonic conditions began at 39 ka BP in the north, where salinities eventually may have reached 55–57 p.s.u. and reached the south-central Red Sea by 22 ka BP. Planktonic foraminiferal faunas continued, albeit in very low abundances and limited diversity ($S \leq 45$ p.s.u.), in the southernmost Red Sea. During MIS-6, the 49 p.s.u. isohaline appears to have resided further north (i.e. in the central Red Sea between cores KL11 and MD921017), which may imply that conditions were not as hypersaline as during MIS-2.

Last glacial maximum salinities in the Gulf of Aqaba seem to have been lower (to $S \leq 45$ p.s.u.) than in the Red Sea, which is completely opposite to the present trend. This apparent anomaly suggests the presence of a significant freshwater-source to the Gulf of Aqaba that is not active today. Validation is needed from further study, but if true, the explanation may have to be sought in intensified influences of Mediterranean climate.

The sequence of species disappearances that was previously known only for the last glacial cycle is found to be systematically present before all glacial maxima of the last 500 kyr. It cannot be related to a general salinity increase, but instead seems to be driven by complex reorganisations in hydrography (stratification), productivity (food availability) and subsurface oxygenation (reproduction-habitats). The sequence-onset results from dramatic expansion of the dominance of NE monsoonal circulation over the entire Red Sea, starting at least 15 kyr before the glacial maxima. Regarding the last glacial cycle, this event started as early as 80 ka BP, culminating around the MIS-4/5 transition (75–70 ka BP). After this major climatic re-organisation, the basin shows intensification of the new conditions. This is especially marked by northward expansion and intensification of the subsurface OMZ. The last glacial cycle shows that this expansion is strongly diachronous from south to north, reaching the central Red Sea around 68 ka BP and the north around 55 ka BP. After that time and until ~40 ka BP, the expanded OMZ conditions were only very occasionally punctuated by weak returns of improved ventilation throughout the basin. Shortly after 40 ka BP, the first aplanktonic conditions began to develop.

Acknowledgements

We thank A. Almogi-Labin and an anonymous reviewer for their extensive and thorough reviews, F.J. Jorissen for his constructive criticism and general support to M.F., and G. Ganssen and H. Vonhof for the stable isotope analyses. Thanks are extended to: NERC for support to M.F.; to the German research Foundation (DFG) for support to Ch.H. (He697-18); and to J.P. Caulet and the National Museum of Natural History in Paris for support to E.J.R. and M.F. during planning and sampling. Full data is available as an online **Background Dataset** or from E.J.R. or Ch.H.[1]

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