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Genetic diversity and ecology of the planktonic foraminifers *Globigerina bulloides*, *Turborotalita quinqueloba* and *Neogloboquadrina pachyderma* off the Oman margin during the late SW Monsoon

Kate F. Darling[a,b,*], Christopher M. Wade[c], Michael Siccha[d], Gabriele Trommer[e], Hartmut Schulz[f], Samereh Abdolalipour[f], Atsushi Kurasawa[g]

[a] School of GeoSciences, University of Edinburgh, Edinburgh, UK
[b] School of Geography and Sustainable Development, University of St Andrews, Fife KY16 9AL, UK
[c] School of Life Sciences, University of Nottingham, Nottingham, UK
[d] MARUM, Center for Marine Environ. Sciences, University of Bremen, 28359 Bremen, Germany
[e] Department Biologie II, Ludwig-Maximilians-Universität, D-82152 Planegg-Martinsried, Germany
[f] Department of Geosciences, Universität Tübingen, 72076 Tübingen, Germany
[g] Japan Agency for Marine Earth Science and Technology, Yokosuka 237-0061, Kanagawa, Japan

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ABSTRACT

The tropical waters of the Arabian Sea are among the richest biological areas of the world. The highly complex monsoonal system is particularly challenging for palaeoenvironmental study, which relies heavily upon understanding the modern-day ecology of planktonic foraminiferal assemblages and their geochemical signatures throughout the monsoonal cycle. Major upwelling responders such as *G. bulloides*, *T. quinqueloba* and *N. pachyderma*, typically associated with cooler mid to higher latitude ecosystems, are also found in number in the tropical Arabian Sea. Due to the more usual cooler water affinity of these morphospecies, the oceanographically isolated tropical upwelling ecosystem of the Arabian Sea potentially harbours new ecologically distinct genotypes (ecotypes). Samples were collected off the Oman margin at 15 stations towards the end of the summer monsoon to determine the genetic profiles of these morphospecies in both upwelling and open ocean regimes. Phylogenetic analysis of their small subunit (SSU) rDNA sequences revealed several new genetically distinct ecotypes. Two genetically divergent ecotypes of *G. bulloides* (Types Ia and IIf) were identified along the cruise track. Type Ia, a member of the *G. bulloides* warm water lineage, was found in both the upwelling and open ocean regions. The second genotype (IIf), a member of the *G. bulloides* cool water lineage, was found only in more marginal late upwelling cooler waters. Initial visual assessment of *G. bulloides* images suggests that it may be morphologically cryptic. Two highly divergent genotypes of *T. quinqueloba* (Types Ib and IIe) were also identified, which were largely confined to the eastern and northern Arabian Sea. Type IIe is a new member of the *T. quinqueloba* cool water lineage which points to its potential cool water affinity, but genotyping numbers are too low to confirm a specific association with upwelling. A new highly divergent genotype of *N. pachyderma* (Type VIII) was also identified at the western and southern stations. Comparison of global upwelling system genotype assemblages currently indicate little regional commonality. This complicates regional palaeoproxy understanding, since geochemical calibrations are known to be species and genotype specific. Detailed studies of the ecology and diversity of genotypes within each system should therefore be carried out to ensure the accuracy of palaeorecord interpretation.

1. Introduction

Major research initiatives are directed towards understanding the role of the Arabian Sea and Indian Ocean in Earth's climate system. The tropical waters of the Arabian Sea are among the richest biological areas of the world and make a significant contribution to global ocean productivity and biogenic carbonate burial (Schiebel and Movellan, 2012). The system is highly complex and ecologically variable, being

* Corresponding author at: School GeoSciences, University of Edinburgh, Grant Institute, Kings Buildings, Edinburgh EH9 3FE, UK and School of Geography and Sustainable Development, University of St Andrews, Irvine Building, North Street, KY16 9AL, UK.
E-mail addresses: kate.darling@ed.ac.uk (K.F. Darling), Chris.Wade@nottingham.ac.uk (C.M. Wade), msiccha@marum.de (M. Siccha), gabi.trommer@gmx.de (G. Trommer), hartmut.schulz@uni-tuebingen.de (H. Schulz), samereh.abdolalipour@gmail.com (S. Abdolalipour), atskurasawa@gmail.com (A. Kurasawa).

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subject to seasonally reversing monsoon winds, inverting its circulation completely on a biannual basis (Wyrtki, 1973). The reconstruction of palaeoceanographic environments here is challenging and relies heavily upon understanding the changes in planktonic foraminiferal test assemblages and their geochemical signatures throughout the annual cycle (e.g. Prell and Curry, 1981; Anderson and Prell, 1993; Naidu and Malmgren, 1996a; Ganssen et al., 2011).

The oceanographic circulation in the Arabian Sea annual cycle is controlled by seasonal atmospheric change (Swallow, 1984; Clemens et al., 1991; Schott and McCreary, 2001). The dominating high velocity winds of the South West (SW) summer monsoon (June–September) promote strong upwelling off the coastal regions of Somalia, Yemen and Oman (Schott, 1983; Findlater, 1996; Lee et al., 2000). During the intense upwelling, nutrient rich waters up-dome from depths of 200 m (Smith and Codispoti, 1980) with sea surface temperatures (SSTs) decreasing to between 14–22 °C during peak upwelling (Brown et al., 1980). This results in an enormous increase in primary production (Bauer et al., 1991), which supports a relatively unusual temporal assemblage of planktonic foraminiferal morphospecies. The major upwelling responders (Hutson and Prell, 1980; Conan and Brummer, 2000) are *Globigerina bulloides* accompanied by lower numbers of *Globigerinita glutinata*, *Turborotalita quinqueloba*, *Neogloboquadrina dutertrei*, *Tenuitella iota* and *Neogloboquadrina pachyderma* (previously *N. pachyderma* (sinistral); Darling et al., 2006). Of these, the morphospecies *Globigerina bulloides*, *T. quinqueloba* and *N. pachyderma* are more commonly associated with the cooler waters of higher latitude ecosystems together with *Neogloboquadrina incompta* (previously *N. pachyderma* (dextral); Darling et al., 2006). Interestingly, *N. incompta* is particularly notable for its virtual absence in the western Arabian Sea throughout the year (Conan and Brummer, 2000). During the SE winter monsoon (January–March), the waters off the Oman margin are well stratified with low nutrient levels. *Globigerinoides ruber* dominates the assemblage in these waters, in association with the more tropical and subtropical morphospecies *Globoturborotalita tenella*, *Globigerinella siphonifera*, *Trilobatus sacculifer*, *Globorotalia menardii* and *Neogloboquadrina dutertrei* (Conan and Brummer, 2000). The higher latitude type morphospecies reduce to a minor component of the assemblage during this period in the western Arabian Sea.

The degree of seasonal upwelling provides a measure of monsoonal strength. The morphospecies *G. bulloides* is an ideal proxy for this, as it dominates the nutrient rich upwelling assemblages of the Arabian Sea, but becomes a relatively minor component of the oligotrophic assemblages of the inter-monsoon periods. The presence of *G. bulloides* in the Arabian Sea and its association with regional upwelling is well known (Prell and Curry, 1981; Kroon, 1991; Auras-Schudnagies et al., 1989). Interestingly, the other high latitude type morphospecies *T. quinqueloba* and *N. pachyderma* remained largely unrecorded in early studies, probably due to inappropriate plankton net and sieve mesh sizes (Peeters et al., 1999). For this reason, Bé and Hutson (1977) found *T. quinqueloba* rare in the plankton using a > 202 μm mesh but omnipresent in the sediments using a > 125 μm mesh in the tropical and subtropical regions. More recent sediment and sediment trap studies in the Arabian Sea record their presence in numbers in the > 100 μm fraction (Kroon et al., 1988; Conan and Brummer, 2000), representing as much as 7.4% of the annual sediment trap assemblage and 6.8% in the sediment assemblage. *Neogloboquadrina pachyderma* was first identified in the sediments off the Arabian Sea coast by Hutson and Prell (1980), who considered them part of the regional upwelling assemblage. This was also confirmed by Naidu and Malmgren (1996b) in the sediments off the Oman margin. Sediment trap data off Somalia indicate that *N. pachyderma* exhibits a temporal pattern of two flux peaks in the upwelling assemblage, which tracks those of *G. bulloides*, though at much lower numbers (Conan and Brummer, 2000).

Recent genetic data, based on small subunit ribosomal RNA genotyping, has highlighted the presence of cryptic diversity within the central Arabian Sea mixed layer planktonic foraminiferal assemblage during the SW monsoon (Seears et al., 2012). There is strong evidence from their biogeographic distribution across ecological frontal boundaries, that different genotypes of these morphospecies have independent ecological adaptations (ecotypes). Already, warm water genotypes of the higher latitude morphospecies *G. bulloides* (Type Ia) and *T. quinqueloba* (Type Ib) have been identified in the central Arabian Sea at temperatures as high as 29.5 °C (Darling and Wade, 2008; Seears et al., 2012). Due to their more usual cool water affinity, the divergent upwelling and open ocean ecosystems of the Arabian Sea are likely to harbour different ecotypes of these higher latitude type morphospecies, with potential consequences for palaeoceanographic and palaeoclimate reconstruction there.

The main goal of this study is to determine the genetic profiles of the higher latitude type planktonic foraminifers found within the cool upwelling highly productive waters off the Oman margin and compare them with the warmer, more oligotrophic open ocean environments of the central Arabian Sea. Already, the morphospecies *G. bulloides*, *T. quinqueloba* and *N. pachyderma* are known to represent a series of cryptic ecotypes globally (Darling and Wade, 2008; Morard et al., 2013). The presence of cryptic ecotypes of palaeoceanographically important morphospecies within these divergent ecosystems, complicates our understanding of palaeoproxies used for palaeoclimate reconstruction. To better understand the implication of our findings in the Arabian Sea, the geochemical signatures of *G. bulloides* tests from both plankton and sediment were investigated in parallel (Sadekov et al., 2016). The Arabian Sea results highlight the importance of determining the genetic diversity profiles and ecology of the planktonic foraminiferal assemblages in both upwelling systems and the open ocean.

2. Material and methods

2.1. Sampling locality and collection

Stratified vertical plankton tows were collected at 30 stations along the cruise track of FS Meteor (cruise M74-1b; 19/09-04/10) off the Oman margin at the end of the summer monsoon in 2007 (Fig. 1, Supplementary Table S1). CTD stations were also carried out using a SEABIRD electronic underwater unit equipped with additional oxygen and fluorescence sensors. Early in the cruise, upwelling was found to be still active and temperature profiles, water chemistry and surface phytoplankton blooms along the coast revealed upwelling patchiness, with SSTs within the coastal upwelling of 23.5 °C at station 944 and 24.0 °C at station 946 (Fig. 2). This pattern progressively changed towards the eastern Arabian Sea, where SSTs rose to 28 °C, with low nutrient surface waters, a deep mixed layer and much lower phytoplankton concentrations typical of inter-monsoon conditions (Fig. 2; METEOR-Berichte 10-3, Cruise Report No. 74, 2010). The most easterly station (953) had no living plankton in the water column (Supplementary Table S1). On the east-west leg of the cruise, the inter-monsoon oceanic conditions continued to the coast, indicating that the upwelling had finished by the end of the cruise.

Specimens of *G. bulloides*, *T. quinqueloba* and *N. pachyderma* were collected at all 15 stations along the cruise track (Fig. 1). Both shallow net hauls (0–100 m at 5 depth intervals) and deep net hauls (0–700 m at 5 depth intervals) were carried out at each station using a multi plankton sampler (Hydro Bios, Kiel, 50 × 50 cm opening, 100 μm mesh size). In total, 30 vertical multinet hauls were successfully processed.

2.2. Sample processing

For genetic analysis, specimens of *G. bulloides* (n = 153), *T. quinqueloba* (n = 71) and *N. pachyderma* (n = 131) were individually picked from the plankton samples and digitally imaged. Specimens were then transferred into 1.5 ml Eppendorf vials containing 25 μl of DOC buffer (Holzman and Pawlowski, 1996; Darling et al., 1999) and incubated with gentle shaking at 60 °C for one hour. Samples were

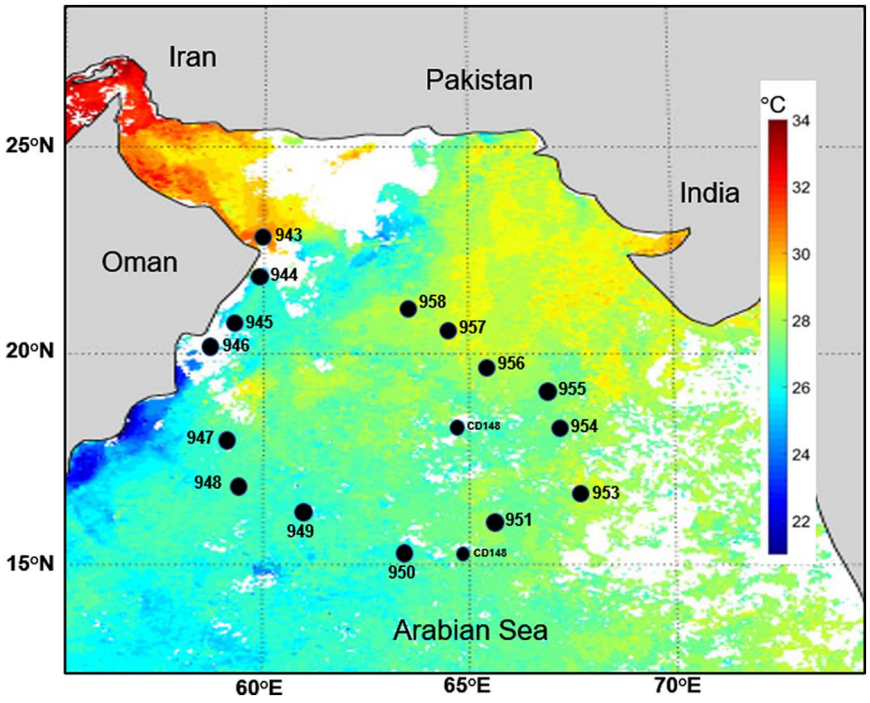

Fig. 1. Cruise track of FS Meteor M74-1b off the Oman margin towards the end of the summer monsoon in 2007. Plankton samples were collected at 15 stations along the cruise track (Table 1). Two further stations are also shown, sampled during RRV Charles Darwin cruise CD 148 in July 2003. Background colours are the Aqua MODIS mean Sea Surface Temperatures (11 μ daytime) from the 22nd to the 29th of September 2007 (NASA Ocean Biology (OB. DAAC), 2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stored at room temperature for transportation and SSU rDNA genotyping in the laboratory, since continual freezing and thawing has been found to result in DNA deterioration (Weiner et al., 2016). Following genotyping, samples were then frozen at 20 °C for longer term storage. A further 3 specimens of *G. bulloides* and 7 specimens of *T. quinqueloba* were also successfully extracted in a urea buffer (Weiner et al., 2016; Table 1). The relative proportion or number of specimens collected for genotyping does not reflect the standing stock of each morphospecies in the assemblage.

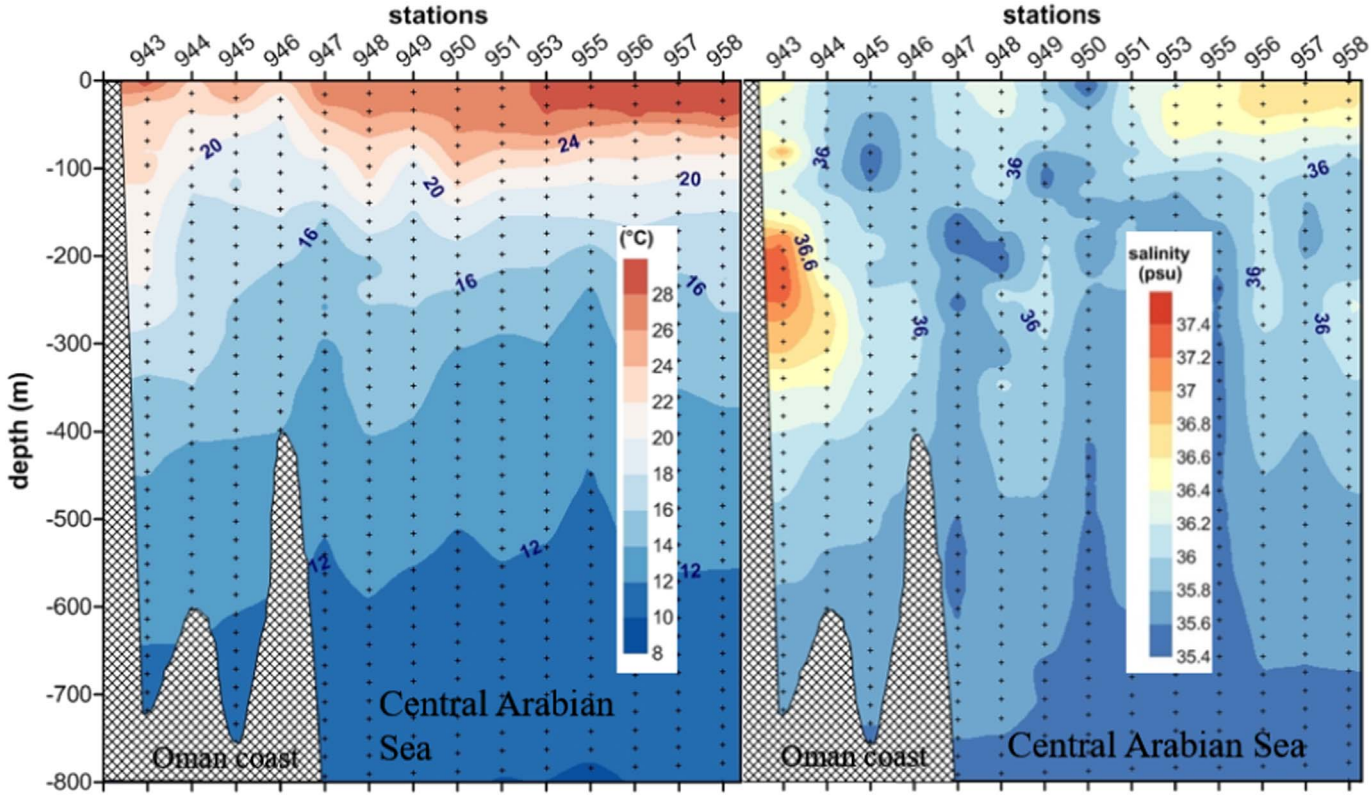

Fig. 2. (a) Temperature and (b) salinity profiles (0–800 m) along the cruise track of FS Meteor M74-1b. At the early stations (944–946), upwelling was still active and temperature profiles, water chemistry and surface phytoplankton blooms along the coast revealed upwelling patchiness. This pattern progressively changed towards the eastern Arabian Sea, where SSTs rose to 28 °C, with low nutrient surface waters and a deep mixed layer. Inter-monsoon oceanic conditions then prevailed on the east-west cruise leg.

Table 1
Multinet stations with hydrographic data and SSU rRNA genotypes of *G. bulloides*, *T. quinqueloba* and *N. pachyderma* identified along the cruise track of M74/1b.

Date of collection	Multinet station	Station latitude	Station longitude	Water depth (m)	Sampling depth (m)	Temperature (°C)	Salinity (psu)	Preservation method	Cruise specimen#	Edinburgh specimen #	Morphospecies	Genotype
20-09-07	943	22°37.00′N	59°41.50′E	789	100–80	23.00	36.06	DOC	3062	OM08	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	100–80	23.00	36.06	DOC	3066	OM09	*G. bulloides*	BUL Ia
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	DOC	3103	OM23	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	60–40	23.77	36.31	DOC	3105	OM25	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	60–40	23.77	36.31	DOC	3106	OM26	*T. quinqueloba*	QUI IIe
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU07	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU09	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU15	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU16	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU22	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU28	*T. quinqueloba*	QUI Ib
20-09-07	943	22°37.00′N	59°41.50′E	789	40–20	25.97	36.30	UREA	–	OMU32	*T. quinqueloba*	QUI Ib
21-09-07	944	21°55.97′N	59°48.15′E	651	40–20	22.12	36.17	DOC	3116	OM36	*G. bulloides*	BUL IIf
21-09-07	944	21°55.97′N	59°48.15′E	651	40–20	22.12	36.17	DOC	3117	OM37	*G. bulloides*	BUL IIf
21-09-07	944	21°55.97′N	59°48.15′E	651	40–20	22.12	36.17	DOC	3121	OM40	*G. bulloides*	BUL IIf
21-09-07	944	21°55.97′N	59°48.15′E	651	60–40	21.05	36.15	DOC	3130	OM48	*G. bulloides*	BUL Ia
21-09-07	945	20°43.72′N	59°23.89′E	781	500–300	12.89	35.80	DOC	3191	OM86	*N. pachyderma*	PAC VIII
21-09-07	945	20°43.72′N	59°23.89′E	781	20–0	27.29	36.03	DOC	3193	OM87	*T. quinqueloba*	QUI Ib
21-09-07	945	20°43.72′N	59°23.89′E	781	700–500	11.60	35.78	DOC	3249a	OM113 (a)	*N. pachyderma*	PAC VIII
21-09-07	945	20°43.72′N	59°23.89′E	781	700–500	11.60	35.78	DOC	3249b	OM113 (b)	*G. bulloides*	BUL IIf
21-09-07	945	20°43.72′N	59°23.89′E	781	700–500	11.60	35.78	DOC	3285	OM132	*G. bulloides*	BUL IIf
21-09-07	945	20°43.72′N	59°23.89′E	781	700–500	11.60	35.78	DOC	3292	OM135	*G. bulloides*	BUL IIf
21-09-07	945	20°43.72′N	59°23.89′E	781	20–0	27.29	36.03	DOC	3315	OM148	*G. bulloides*	BUL Ia
21-09-07	945	20°43.72′N	59°23.89′E	781	20–0	27.29	36.03	UREA	–	OMU51	*G. bulloides*	BUL Ia
21-09-07	945	20°43.72′N	59°23.89′E	781	20–0	27.29	36.03	UREA	–	OMU57	*G. bulloides*	BUL Ia
23-09-07	947	18°00.02′N	59°00.24′E	3577	40–20	25.97	36.30	DOC	3320	OM152	*N. pachyderma*	PAC VIII
23-09-07	947	18°00.02′N	59°00.24′E	3577	40–20	25.97	36.30	DOC	3321	OM153	*N. pachyderma*	PAC VIII
23-09-07	947	18°00.02′N	59°00.24′E	3577	200–100	16.96	35.87	DOC	3351	OM179	*G. bulloides*	BUL IIf
24-09-07	949	16°26.00′N	61°14.99′E	3985	40–20	25.97	36.30	DOC	3557	OM259	*T. quinqueloba*	QUI IIe
24-09-07	949	16°26.00′N	61°14.99′E	3985	60–40	24.31	23.77	DOC	3570	OM263	*N. pachyderma*	PAC VIII
24-09-07	949	16°26.00′N	61°14.99′E	3985	100–80	20.19	36.06	DOC	3589	OM277	*G. bulloides*	BUL Ia
24-09-07	949	16°26.00′N	61°14.99′E	3985	700–500	11.87	35.86	DOC	3602	OM280	*N. pachyderma*	PAC VIII
24-09-07	949	16°26.00′N	61°14.99′E	3985	700–500	11.87	35.86	DOC	3611	OM285	*G. bulloides*	BUL Ia
24-09-07	949	16°26.00′N	61°14.99′E	3985	300–200	16.02	36.21	DOC	3642	OM296	*N. pachyderma*	PAC VIII
24-09-07	949	16°26.00′N	61°14.99′E	3985	200–100	17.97	35.98	DOC	3651	OM303	*T. quinqueloba*	QUI IIe
24-09-07	949	16°26.00′N	61°14.99′E	3985	200–100	17.97	35.98	DOC	3653	OM304	*N. pachyderma*	PAC VIII
24-09-07	949	16°26.00′N	61°14.99′E	3985	200–100	17.97	35.98	DOC	3655	OM305	*N. pachyderma*	PAC VIII
24-09-07	949	16°26.00′N	61°14.99′E	3985	40–20	25.97	36.30	UREA	–	OMU93	*G. bulloides*	BUL Ia
25-09-07	950	15°14.99′N	63°30.01′E	3916	20–0	27.29	36.03	DOC	3659	OM308	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	20–0	27.29	36.03	DOC	3660	OM309	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	20–0	27.29	36.03	DOC	3662	OM311	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3680	OM318	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3683	OM319	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3686	OM321	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3688	OM323	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3697	OM326	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3702	OM327	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3703	OM328	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3709	OM329	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	40–20	25.97	36.30	DOC	3712	OM330	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	500–300	12.81	35.78	DOC	3728	OM331	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	300–200	15.42	35.90	DOC	3729	OM332	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	100–80	20.19	36.06	DOC	3739	OM340	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	60–40	23.77	36.31	DOC	3745	OM342	*N. pachyderma*	PAC VIII
25-09-07	950	15°14.99′N	63°30.01′E	3916	60–40	23.77	36.31	DOC	3746	OM343	*G. bulloides*	BUL Ia
25-09-07	950	15°14.99′N	63°30.01′E	3916	60–40	23.77	36.31	DOC	3747	OM344	*G. bulloides*	BUL Ia
26-09-07	951	16°07.80′N	65°44.50′E	3705	40–20	27.24	36.38	DOC	3788	OM352	*N. pachyderma*	PAC VIII
26-09-07	951	16°07.80′N	65°44.50′E	3705	80–60	25.06	36.20	DOC	3840	OM384	*G. bulloides*	BUL Ia
26-09-07	951	16°07.80′N	65°44.50′E	3705	100–80	22.55	36.17	DOC	3846	OM389	*G. bulloides*	BUL Ia
26-09-07	951	16°07.80′N	65°44.50′E	3705	100–80	22.55	36.17	DOC	3847	OM390	*G. bulloides*	BUL Ia
26-09-07	951	16°07.80′N	65°44.50′E	3705	100–80	22.55	36.17	DOC	3850	OM391	*N. pachyderma*	PAC VIII
26-09-07	951	16°07.80′N	65°44.50′E	3705	700–500	11.43	35.77	DOC	3852	OM393	*N. pachyderma*	PAC VIII
26-09-07	951	16°07.80′N	65°44.50′E	3705	500–300	12.84	35.84	DOC	3854	OM395	*N. pachyderma*	PAC VIII
26-09-07	951	16°07.80′N	65°44.50′E	3705	500–300	12.84	35.84	DOC	3855	OM396	*N. pachyderma*	PAC VIII
26-09-07	951	16°07.80′N	65°44.50′E	3705	500–300	12.84	35.84	DOC	3856	OM397	*N. pachyderma*	PAC VIII
28-09-07	954	18°16.00′N	67°34.00′E	3414	20–0	28.48	36.48	DOC	3895	OM406	*T. quinqueloba*	QUI Ib
29-09-07	955	19°06.00′N	67°06.00′E	3258	20–0	28.50	36.06	DOC	3913	OM408	*T. quinqueloba*	QUI Ib
29-09-07	955	19°06.00′N	67°06.00′E	3258	20–0	28.50	36.06	DOC	3915	OM409	*T. quinqueloba*	QUI Ib
29-09-07	955	19°06.00′N	67°06.00′E	3258	20–0	28.50	36.06	DOC	3918	OM411	*T. quinqueloba*	QUI Ib
29-09-07	955	19°06.00′N	67°06.00′E	3258	40–20	28.10	36.70	DOC	3931	OM414	*T. quinqueloba*	QUI Ib
29-09-07	955	19°06.00′N	67°06.00′E	3258	200–100	18.07	35.97	DOC	3945	OM417	*T. quinqueloba*	QUI Ib
29-09-07	956	19°53.00′N	65°53.00′E	3140	20–0	29.02	36.00	DOC	3988	OM419	*T. quinqueloba*	QUI Ib
29-09-07	956	19°53.00′N	65°53.00′E	3140	60–40	24.37	36.62	DOC	4015	OM421	*T. quinqueloba*	QUI Ib

2.3. Isolation and sequencing of SSU genes

DNA extraction, amplification by polymerase chain reaction and automated sequencing of an ~1000 base pair region of the terminal 3′ end of the foraminiferal SSU rRNA gene were as described previously (Darling et al., 2000; Seears et al., 2012). Specimens of *G. bulloides* and *T. quinqueloba* were directly sequenced, but a degree of intra-individual variation was detected in the *N. pachyderma* specimens and they were cloned prior to sequencing. Cloning was undertaken using a PCR 2.1 TOPO TA cloning kit (Invitrogen).

2.4. Genotyping success

A total of 73 specimens were successfully genotyped from the Oman margin sample set of 355 specimens in total (Table 1). This was an unusually low success rate (20%), which was most likely due to the deoxygenation of the concentrated plankton sample during and following sampling at the eutrophic coastal upwelling stations, which were dominated by diatom blooms. In addition, low background oxygen levels were present in samples collected from below 75 m depth due to the shoaling oxygen minimum zone, which would have contributed to the poor preservation potential of the plankton sample DNA. A combination of low nutrient and low oxygen conditions were also encountered in the water column towards the eastern most stations of the cruise track (METEOR-Berichte 10-3, Cruise Report No. 74, 2010), which would also have affected the viability of samples. However, a sufficient number of specimens were genotyped to provide an overview of their biogeographical distribution along the cruise track.

2.5. Phylogenetic analysis

Partial SSU rDNA sequences were aligned manually within version 2.2 of the Genetic Data Environment (GDE) package (Smith et al., 1994). Phylogenetic trees for *G. bulloides* were based on 666 unambiguously aligned nucleotide sites and rooted on the subtropical *G. bulloides* Type I genotypes. For *T. quinqueloba*, phylogenies were based on 748 sites and rooted on the subtropical *T. quinqueloba* Type I genotypes. Phylogenetic trees for *N. pachyderma* were based on 666 sites (including all Neogloboquadrinid taxa sequenced to date) and 811 sites (excluding the highly divergent *N. incompta* lineage) and rooted on the globorotaliid *Globorotalia inflata*, as in previous studies (Darling et al., 2004, 2007). Phylogenetic trees were constructed using the neighbour-joining (NJ), Fitch-Margoliash (FM), maximum likelihood (ML) and maximum parsimony (MP) methods within Paup* version 4.0d64 (Swofford, 2003). For the NJ, FM and ML methods a general time reversible (GTR) model was used, with rate-heterogeneity between sites accounted for by incorporating gamma-distributed rates in the model (Γ). The rate matrix, base frequencies and shape parameter (α) of the gamma distribution (based on 16 rate categories) were estimated using likelihood by iteration from an initial neighbour-joining tree. Genetic distances were estimated using the GTR + Γ model. Bootstrap resampling (1000 replicates) was employed to assign support to branches in the trees (Felsenstein, 1985). Bayesian inference (BI) was performed using the MrBayes (version 3.0B4) package (Huelsenbeck and Ronquist, 2001). A GTR + Γ model (16 rate categories) was used and the tree space was explored using four chains of a Markov Chain Monte Carlo algorithm for 1 million generations, sampling every 100 generations. A consensus tree was built using the last 1000 trees (burnin = 9001 samples). The new sequences used in the phylogenetic study are deposited in GenBank under the accession numbers KX576651, KX576652, KX576653 and sequences from every individual specimen (accession numbers XXX-XXX) are included in the PFR^2 data base (Morard et al., 2015).

2.6. Hydrographic data analysis

CTD-casts with a *SBE 911plus* (Sea-Bird Electronics) were performed at all plankton sampling stations. Parameters were transformed to TEOS-10 standards using the Gibbs-Seawater Oceanographic Toolbox (McDougall and Barker, 2011) and binned to 1 m intervals. For the comparison of hydrographic parameters in Figs. 4b and 6b, all sampled water column intervals where the respective genotypes were identified, were merged. The intervals were weighted for interval length (20 m vs. 100 m intervals) but not for the number of genotypes obtained.

2.7. Nomenclature

The nomenclature system used to delineate genetic types follows that described in Darling and Wade (2008). It has been developed over several years and is well established in the literature. It forms the basis of the new taxonomy initiative for the planktonic foraminifera, proposed by Morard et al. (2016).

3. Results

3.1. The general assemblage profile along the cruise track

Although this study specifically focuses on the higher latitude types of planktonic foraminifers, the assemblage profile and turnover provides an important guide to the changing water column conditions along the cruise track (Fig. 1). Descriptive notes were therefore made of the major morphospecies observed during sample processing at each station (Supplementary Table S1). The first station 943 was situated in the warm high salinity waters of the Arabian Gulf (Fig. 2), where relatively few small and mostly immature morphospecies dominated, including *T. quinqueloba*. There were very low numbers of *G. bulloides* in the assemblage at this station. However, in the actively upwelling waters at the following station 944 off the Oman margin, the assemblage was completely dominated by *G. bulloides*, with very few other morphospecies in the water column. At station 945, the assemblage also reflected very recent upwelling, where *G. bulloides* was present in very high numbers, but together with *G. siphonifera*, *G. menardii*, *N. dutertrei*, *G. sacculifer*, *G. ruber* and possibly a first small *N. pachyderma*. Similar high numbers of *G. bulloides* were also found further offshore at station 947, together with numbers of *N. pachyderma* (20–40 m) and a diverse assemblage of other morphospecies to depth. Between station 948–951, a similar profile of morphospecies was observed, but *G. bulloides* numbers progressively decreased to very low numbers, with *N. pachyderma* only observed at depth. As noted above, the most easterly station 953 had no living plankton in the water column. The character of the water column changed on the return leg of the cruise (stations 954–958), where stations were influenced by the Arabian Gulf outflow (Fig. 2). Here low numbers of small morphospecies such as *T. quinqueloba*, *G. rubescens* and *G. tenella* dominated the upper levels with very few living forams at depth. There was a slight increase in diversity at the last station 958, with the appearance of low numbers of *N. dutertrei* and *G. sacculifer*.

3.2. Phylogenetic relationships and global biogeography of G. bulloides

The global biogeographical distribution of *G. bulloides* genotypes identified to date and their evolutionary inter-relationships are shown in Fig. 3a and b. Within the SSU rDNA ML phylogeny (666 nucleotide sites), the *G. bulloides* genotypes fall into two clear highly divergent groups related to their ecologies (Darling and Wade, 2008). The Type I genotypes are associated with warmer waters with four distinct genotypes identified to date. Type Ia was found in the Coral Sea (Darling et al., 1999), the Northwest Pacific (Kurasawa et al., n.d., unpublished sequence in GenBank; PFR^2, Morard et al., 2015), the central Arabian Sea (Darling and Wade, 2008; Seears et al., 2012) and now the western

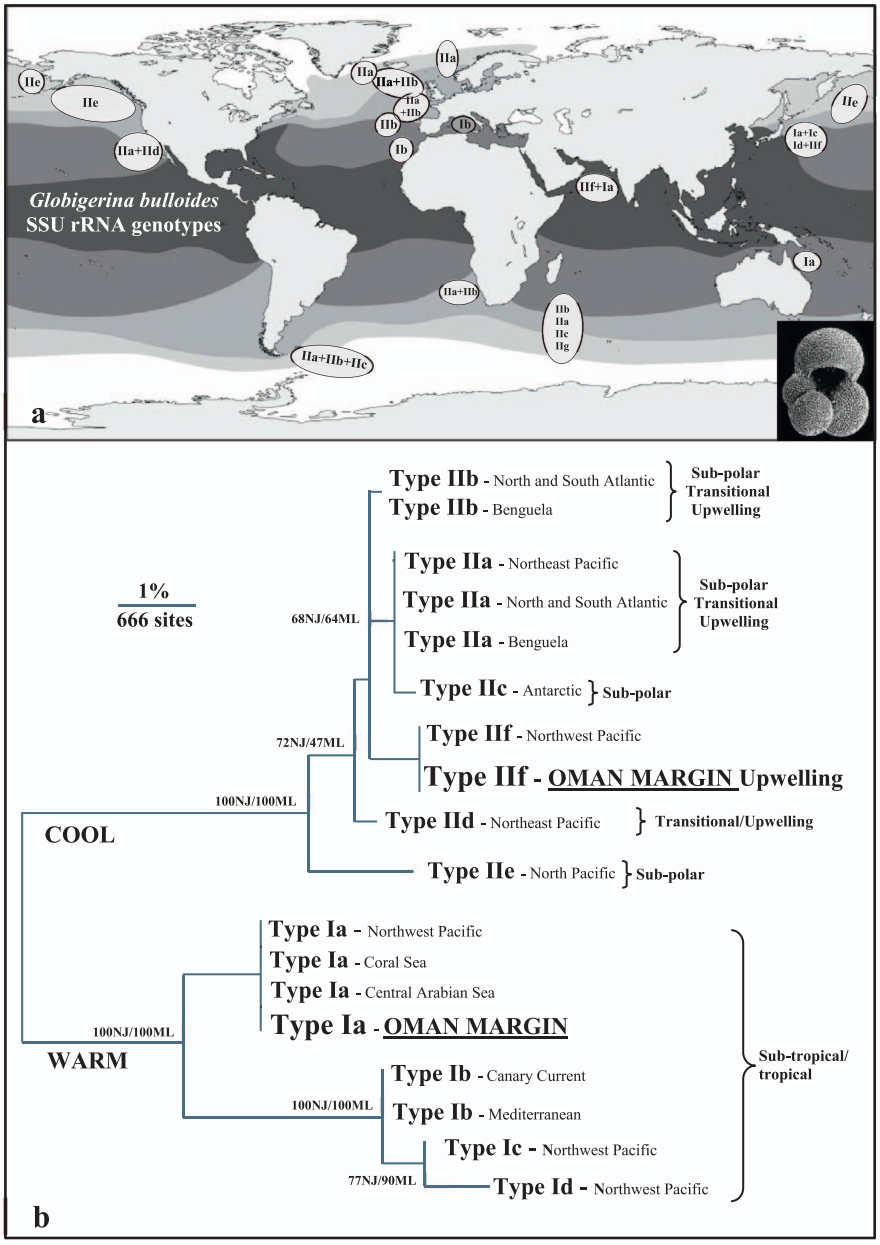

Fig. 3. (a) Map with background shading showing the five major planktonic foraminiferal faunal provinces (modified from Bé and Tolderlund, 1971), which largely correspond to the main hydrographic regions of the global ocean (tropical, subtropical, transitional, subpolar and polar). Each province occurs reciprocally in both hemispheres. The global biogeographical distribution of *G. bulloides* genotypes identified to date are shown (b) Maximum likelihood (ML) phylogenetic tree showing the evolutionary relationships among *G. bulloides* genotypes. The tree is based on analysis of 666 nucleotide sites of the 3′ terminal end of the SSU rRNA gene and is rooted on the subtropical *G. bulloides* Type I genotypes. Bootstrap values (NJ/ML), expressed as a percentage, indicate support for branches in the tree. Bootstrap values are only shown for branches that are strongly supported in ~70% of bootstrap replicates. There was insufficient sequence length to include *G. bulloides* Type IIg (Morard et al., 2013) in the ML phylogeny, but shorter gene fragment phylogenies indicate that it clusters with subpolar Antarctic Type IIc (data not shown).

Arabian Sea off the Oman margin (n = 13). Type Ib was found in subtropical waters of the North Atlantic (Darling and Wade, 2008) and the Mediterranean (de Vargas et al., 1997) and Types Ic and Id were found in subtropical/transitional waters of the Northwest Pacific (Kurasawa et al., n.d., unpublished sequence GenBank; PFR^2, Morard et al., 2015). This increases the total number of warm water cluster genotypes identified to date to four. The Type II genotypes (Types IIa–IIe) are associated with cooler high latitude and transitional upwelling waters (Darling and Wade, 2008). A further member of this cool-water group (Type IIf, n = 7) was identified in the Arabian Sea off the Oman margin in this study and at the subtropical/transitional interface of the Kuroshio Current in the Northwest Pacific (Fig. 3a and b; Kurasawa et al., n.d., unpublished sequence GenBank; PFR^2 - Morard et al., 2015). An additional cool water genotype (Type IIg) was also identified in the southern Indian Ocean (Fig. 3a; Morard et al., 2013), but there was insufficient sequence length to include Type IIg in the phylogenetic analysis used in this publication. The recently identified genotypes Type IIf (this study) and Type IIg (Morard et al., 2013) increase the number of genotypes within the cool water cluster to seven. The full temperature-specific range of the *G. bulloides* genotypes identified to date is shown in Sadekov et al. (2016) and Supplementary Fig. S1.

The distribution of *G. bulloides* genotypes (n = 20) identified along the M74/1b cruise track is shown in Fig. 4a, Table 1 and Supplementary Table S2. Also included are five further genotyped specimens of *G. bulloides*, collected during RRV Charles Darwin cruise CD 148 in July 2003 from the central Arabian Sea, which also coincided with the SW monsoon (Darling and Wade, 2008; Seears et al., 2012). As mentioned above, the number of specimens chosen for genotyping does not reflect the standing stock of the assemblage. The cruise descriptive notes (Supplementary Table S1) indicate that *G. bulloides* was very common in the foraminiferal assemblage at the stations influenced by upwelling and progressively reduced in number to much lower levels at the later stations. Stations with the highest numbers of *G. bulloides* are underlined. Assemblage counts (> 100 μm; 0–20 m; data not shown) carried out at stations 945 and 947 indicate that *G. bulloides* was present in much greater numbers at station 945 (88.95% of the assemblage) than at station 947 (10.34% of the assemblage), confirming that the

contribution of *G. bulloides* to the planktonic foraminiferal assemblage had strongly diminished by station 947.

A total of 18 specimens of *G. bulloides* Type Ia were genotyped along the cruise tracks at both upwelling and non-upwelling stations (Fig. 4a). Although one live *G. bulloides* specimen was collected and genotyped from 600 m depth (Supplementary Table S2), this should not be considered as being part of their natural habitat depth range. This could have been a specimen which had failed to reproduce, as several intact live specimens were found at depth between stations 944–949. Mean depth and temperature values therefore only include sampling depths above 150 m (Supplementary Table S2). The Type Ia genotype was associated with a mean water temperature of 26 °C (range 20–29.5 °C) at a mean depth of 39 m (range 5–90 m). A total of 7 specimens of the new genotype of *G. bulloides* Type IIf were also identified within the region of late summer upwelling at stations 944, 945 and 947 (Fig. 4a). Again, 3 specimens were found at 600 m depths (Supplementary Table S2) and therefore depth and temperature values only include the four specimens sampled above 150 m. This genotype was only associated with the cooler upwelling water with a mean temperature of 21 °C (range 17–22 °C) at a mean depth of 60 m (range 30–150 m). No specimens of Type IIf were found in waters outside the upwelling zone. Box plots comparing conservative temperature Θ between the sampled water column intervals where genotypes Ia and IIf were found are shown in Fig. 4b. Statistical analysis demonstrates that there is a significant difference between *G. bulloides* Type Ia and Type IIf in their temperature distribution in the water column (WILCOXON signed rank test; $p = 5.473e-9$), which supports their ecological distinction.

3.3. Phylogenetic relationships and global biogeography of *T. quinqueloba*

The global biogeographical distribution of *T. quinqueloba* genotypes identified to date and their evolutionary inter-relationships are shown in Fig. 5a and b. As for *G. bulloides*, *T. quinqueloba* genotypes fall into two clear highly divergent groups with very different ecologies (Darling and Wade, 2008). The Type I genotypes are associated with warmer waters, with two distinct genotypes identified to date. Type Ia was found in the Coral Sea (Darling et al., 2000) and Type Ib in the central Arabian Sea (Darling and Wade, 2008; Seears et al., 2012). The Type Ib genotype has now also been identified in the western Arabian Sea (this study). In contrast, the Type II genotypes (Types IIa–IId) are associated with cooler high latitude and transitional waters (Fig. 5a) and a new member of this cool-water group (Type IIe) has been identified off the Oman margin in this study (Fig. 5b).

The distribution of *T. quinqueloba* genotypes (n = 23) identified along the M74/1b cruise track is shown in Fig. 6a (Supplementary Table S3). The data set includes a single specimen of *T. quinqueloba* genotyped during cruise CD 148 (Seears et al., 2012; see above). The cruise descriptive notes (Supplementary Table S1) indicate that *T. quinqueloba* was most common in the foraminiferal assemblage at the first station 943 and again at the more northerly stations 955–958, where small morphospecies dominated a low diversity assemblage. Stations with the highest numbers of *T. quinqueloba* are underlined. Assemblage counts (> 100 μm; 0–20 m; assemblage data not shown) carried out at the upwelling station 945 indicated that *T. quinqueloba* constituted a minor component of the upwelling assemblage (0.71%).

A total of 20 specimens of the warm water *T. quinqueloba* genotype Type Ib were identified along the cruise tracks (Fig. 6a). Type Ib was most common in the waters off the Oman margin towards the north and northeast sections of the transect (stations 943 and 955), where the smaller foraminifera dominated the water column assemblage (Supplementary Table S1). Type Ib was associated with a mean water temperature of 25.7 °C (range 18–29.5 °C) at a mean depth of 34 m (range 5–150 m; Supplementary Table S3). Three specimens of the newly identified cool water genotype Type IIe were also found at stations 943 and 949 (Fig. 6a). Although station 943 is close to the cooler water upwelling station 944, *T. quinqueloba* was found to be relatively rare within the upwelling station assemblages. In addition, the two other specimens of Type IIe were found further offshore at station 949, within a high diversity assemblage. The new genotype of *T. quinqueloba* Type IIe was associated with a mean water temperature of 22 °C (range 18–25 °C) at a mean depth of 77 m (range 30–150 m). Box plots comparing conservative temperature Θ between the sampled water column intervals where genotypes Ib and IIe were found are shown in Fig. 6b. Although Type IIe clearly clusters within the cool water *T. quinqueloba* clade (Fig. 5b), it is not possible to conclude that this genotype is predominantly associated with the cooler waters of the Arabian Sea, due to the low numbers of successful amplifications of *T. quinqueloba*.

3.4. Phylogenetic relationships and global biogeography N. pachyderma

The global biogeographical distribution of *N. pachyderma* genotypes identified to date and their evolutionary inter-relationships are shown in Fig. 7a and b. The phylogeny (Fig. 7b) includes *N. dutertrei* and *Pulleniatina obliquiloculata*, the warmer water members of the Neogloboquadrinid clade together with the cooler water *N. pachyderma* (previously *N. pachyderma* (sinistral); Darling et al., 2006). The tree (811 nucleotide sites) is rooted on *G. inflata* and includes all the genotypes of *N. pachyderma* published to date (Darling and Wade, 2008). The new *N. pachyderma* genotype (Type VIII) found in the waters off the Oman margin falls within the *N. pachyderma* clade in the molecular phylogenies, albeit on a long branch (Fig. 7b).

The predominantly right coiling genotypes of *N. incompta*

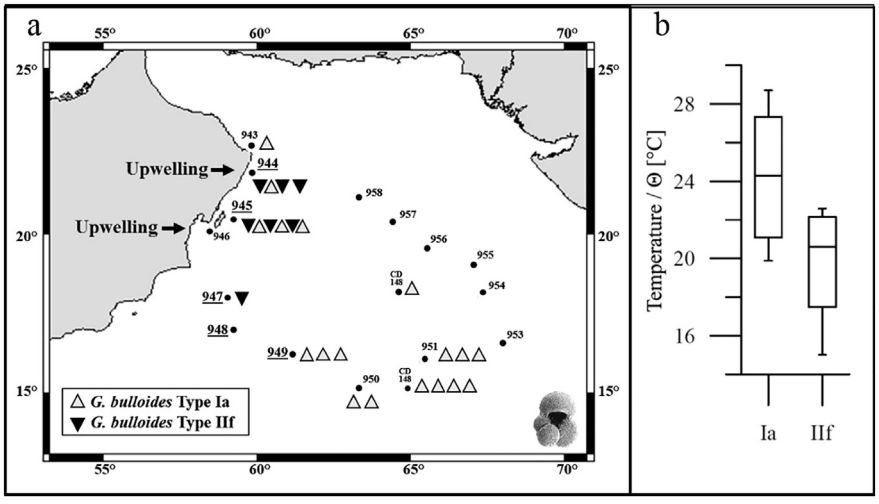

Fig. 4. (a) The distribution of individual *G. bulloides* Types Ia and IIf specimens along the cruise tracks of M74/1b and CD148. *G. bulloides* was very common in the foraminiferal assemblage at the stations influenced by upwelling, but transitioned to very low numbers by station 950. Stations with the highest numbers of *G. bulloides* are underlined. (b) Box plots showing a comparison of conservative temperature Θ between the sampled water column intervals where genotypes Ia (n = 18) and IIf (n = 7) were found.

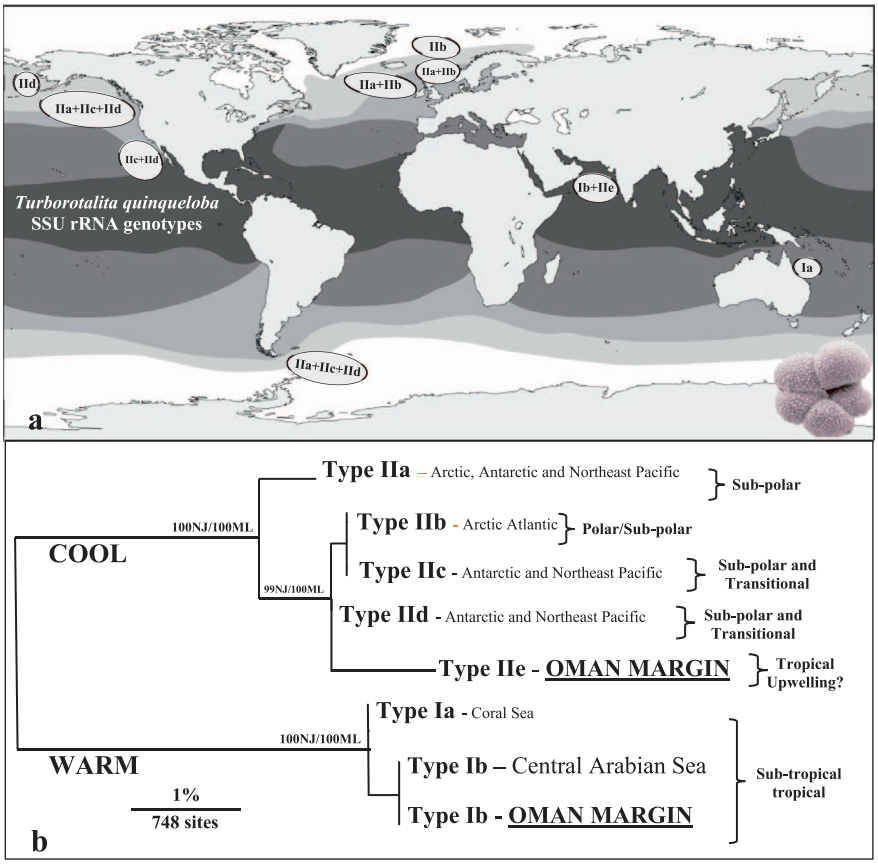

Fig. 5. (a) Map with background shading showing the five major planktonic foraminiferal faunal provinces (see Fig. 3 legend). The global biogeographical distribution of *T. quinqueloba* genotypes identified to date are shown. (b) Maximum likelihood (ML) phylogenetic tree showing the evolutionary relationships among the *T. quinqueloba* genotypes. The tree is based on analysis of 748 nucleotide sites of the 3′ terminal end of the SSU rRNA gene and is rooted on the subtropical *T. quinqueloba* Type I genotypes. Bootstrap values (NJ/ML), expressed as a percentage, indicate support for branches in the tree. Bootstrap values are only shown for branches that are strongly supported in ~70% of bootstrap replicates.

(previously *N. pachyderma* (dextral); Darling et al., 2006) also fall on an exceptionally long branch in the Neogloboquadrinid tree (Darling et al., 2006), making it impossible to resolve their evolutionary relatedness to the other members of the Neogloboquadrinid clade. This highlights the divergent nature of *N. incompta* from all the other Neogloboquadrinids. To conclusively allay doubts that the new genotype of *N. pachyderma* is not a left coiling *N. incompta*, we have included an inset with a *Neogloboquadrina* phylogeny that included *N. incompta* (Fig. 7c). The new *N. pachyderma* Type VIII genotype conclusively falls in the same position in this phylogeny (666 nucleotide sites) within the *N. pachyderma* clade, as it does in the 811 nucleotide site phylogeny which excludes *N. incompta*. Although it is not possible to be confident of the ancestry of *N. pachyderma* Type VIII due to its divergent nature, it is consistently associated with the *N. pachyderma* subpolar/transitional/upwelling group in both phylogenies and not with the two polar *N. pachyderma* genotypes (Type I and IV). It is interesting to note that globally to date, all *N. pachyderma* genotypes appear confined to the regional water column in which they were identified (Fig. 7a). Interestingly, *N. incompta* specimens were not found in the water column at any of the stations. This is consistent with the study of Ivanova et al. (1999) off Somalia, where they found only very few specimens in the water column. These specimens were most likely *N. pachyderma* (dex) (Darling et al., 2006).

The distribution of *N. pachyderma* Type VIII genotypes (n = 31), identified along the M74/1b cruise track, is shown in Fig. 8. The cruise

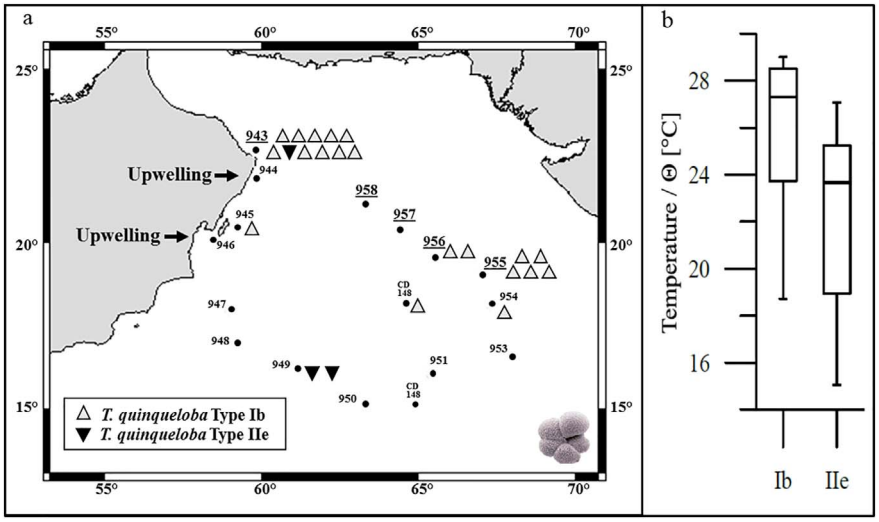

Fig. 6. (a) The distribution of individual *T. quinqueloba* Types Ib and IIe specimens along the cruise tracks of M74/1b and CD148. *T. quinqueloba* was most common in the foraminiferal assemblage at the most northerly station 943 and the north-eastern stations 955–958, where small morphospecies dominated a low diversity assemblage. Stations with the highest numbers of *T. quinqueloba* in the assemblage are underlined. (b) Box plots showing a comparison of conservative temperature Θ between the sampled water column intervals where genotypes Ib (n = 20) and IIe (n = 3) were found.

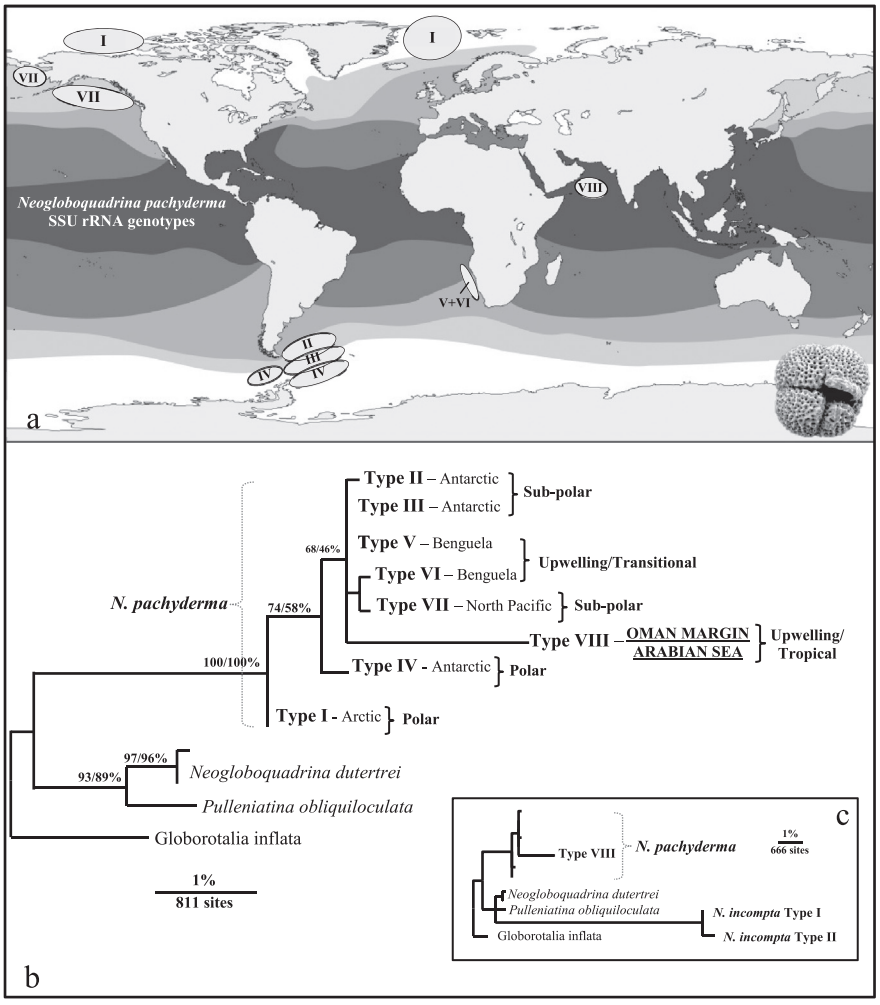

Fig. 7. (a) Map with background shading showing the five major planktonic foraminiferal faunal provinces (see Fig. 3 legend). The global biogeographical distribution of *N. pachyderma* genotypes identified to date are shown (b) Maximum likelihood (ML) phylogeny showing the evolutionary relationships among *N. pachyderma* genotypes. The tree is based on analysis of 811 nucleotide sites of the SSU rRNA gene and *G. inflata* was used as an outgroup. (c - insert) Neighbour-Joining (NJ) phylogeny (666 sites) was constructed to demonstrate that the Arabian Sea *N. pachyderma* Type VIII falls within the *N. pachyderma* clade and not within the highly divergent *N. incompta* clade. Bootstrap values (NJ/ML), expressed as a percentage, indicate support for branches in the tree. Bootstrap values are only shown for branches that are strongly supported in ~70% of bootstrap replicates.

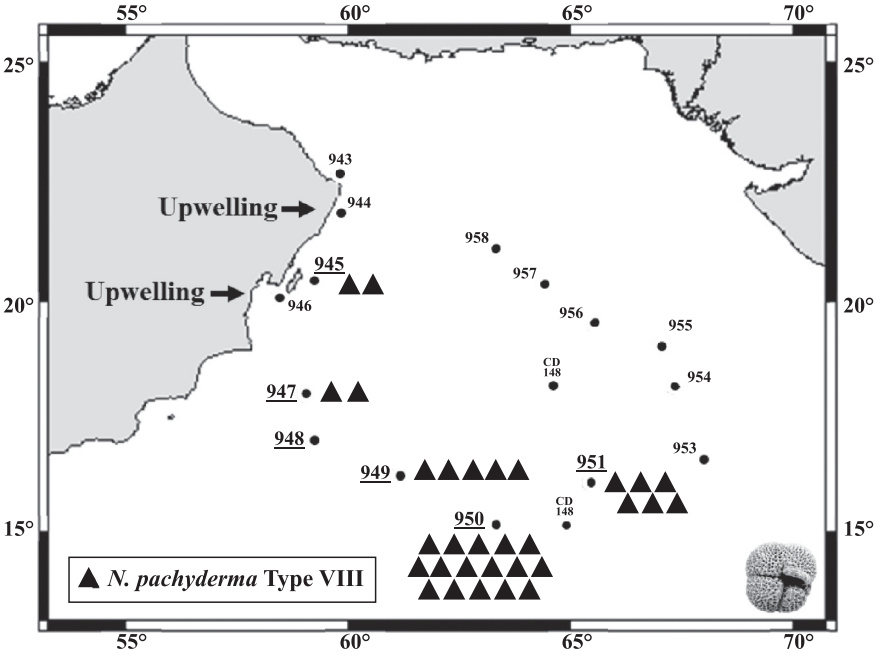

Fig. 8. The distribution of individual *N. pachyderma* Type VIII specimens along the cruise track of FS Meteor cruise M74/1b. *N. pachyderma* did occur in the upwelling assemblage in relatively low numbers, but was found most commonly offshore at the southerly stations (Supplementary Table S5). Stations with the highest numbers of *N. pachyderma* in the assemblage are underlined.

descriptive notes (Supplementary Table S1) indicate that, although *N. pachyderma* does occur in the upwelling assemblage as described by Ivanova et al. (1999) and Conan and Brummer (2000), *N. pachyderma* was found more commonly in the foraminiferal assemblage offshore during cruise M74/1b (Supplementary Tables S4 and S5). Stations with the highest numbers of *N. pachyderma* are underlined. Assemblage

counts (Supplementary Table S5) show that *N. pachyderma* occupied the whole water column between 0–700 m, but was more common at depth, consistent with Ivanova et al. (1999) and Peeters and Brummer (2002). A significant proportion of specimens were genotyped at depth (400–600 m; Supplementary Table S4) indicating that they were alive and it is highly likely that most of the deep *N. pachyderma* were alive and not empty shells. *N. pachyderma* was identified in the upwelling assemblage water column at station 944 (mean = 0.16 specimens/m^3), station 945 (mean = 2.24 specimens/m^3) and station 947 (mean = 0.62 specimens/m^3). These values are consistent with those numbers found in the upwelling water column off Somalia during the SW monsoon by Ivanova et al. (1999). However, progressively increasing concentrations of *N. pachyderma* were also found further offshore in the open ocean at stations 948 (mean = 2.46 specimens/m^3), 949 (mean = 4.8 specimens/m^3) and 950 (mean = 4.02 specimens/m^3). Concentrations then progressively reduced again at stations 951 (mean = 1.79 specimens/m^3), 953 (mean = 0.05 specimens/m^3) and 955 (mean = 0.04 specimens/m^3), occurring very rarely at later stations.

4. Discussion

4.1. Foraminiferal upwelling assemblages

The absolute abundance and depth habitat of planktonic foraminifers is thought to be related to mixed layer depth, thermocline depth, integrated primary productivity and light levels (Ravelo and Fairbanks, 1992; Watkins and Mix, 1998). However, within upwelling systems, these physical and biological features are highly unstable and their physical and biological character is regionally specific. It is not surprising therefore, that the accumulating foraminiferal assemblage data associated with upwelling systems indicate that the planktonic foraminiferal assemblages are unique to each system. Interestingly, there is also a prevailing presence of cooler water more high latitude type morphospecies within the upwelling systems. For example, the Western Arabian Sea upwelling systems have a very high percentage of *G. bulloides* within the upwelling core compared with the other major upwelling responders *N. pachyderma*, *N. dutertrei* and *G. glutinata*, with *N. incompta* notable for its absence (Conan and Brummer, 2000). On the other hand, the Benguela upwelling system off Namibia has a very high percentage of *N. pachyderma* within the upwelling core, with *G. bulloides* and *N. incompta* being more confined to the margins where the upwelled and oligotrophic offshore waters mix (Giraudeau, 1993; Ufkes et al., 1998). Upwelling systems are also strongly seasonal and as the deep vertical mixing decays and entrained nutrients are consumed, only the more oligotrophic open ocean assemblages are left to occupy the water column.

Such regionally unique habitats also present the opportunity for planktonic foraminifera to specialise by adapting to live within them. Such specialisation may remain hidden at the morphospecies level, since many genotypes of the cool water morphospecies remain cryptic (Darling and Wade, 2008). Indeed, this has already been demonstrated in the Benguela upwelling system, where two distinct *N. pachyderma* genotypes (Type VI and VII) have been identified within the upwelling off Namibia (Darling et al., 2007). Here they live at temperatures as high as 14 °C, while their Southern Ocean counterparts (Types II and III; Fig. 7b) inhabit subpolar waters at temperatures 5 °C lower. The data presented in this study confirms that there are also specialist genotypes of morphospecies associated with the Arabian Sea upwelling system.

4.2. Globigerina bulloides

4.2.1. The global phylogeography of G. bulloides

The morphospecies *G. bulloides* has a bipolar distribution, occurring in high abundance in the subpolar and transitional zones (Bé and Tolderlund, 1971; Bé, 1977) and also often characterises the cool nutrient rich upwelling systems of the transitional and lower latitudes such as the Peru/Chile Current (Hebbeln et al., 2000), N-W Africa (Thiede and Junger, 1992), San Pedro Basin, California (Thunell and Reynolds-Sautter, 1992) and Arabian Sea (Prell and Curry, 1981). The presence of this higher latitude morphospecies in more tropical/subtropical waters such as the Arabian Sea led workers to the conclusion that its distribution is primarily controlled by food availability rather than specific temperature range. This conclusion was of course made without the knowledge that the *G. bulloides* morphospecies in reality currently represents eleven genetically distinct cryptic genotypes (Fig. 2b; Darling and Wade, 2008; Morard et al., 2013; this study). Whether this number of genotypes represents an equivalent number of extant species remains to be resolved (André et al., 2014). Their biogeographic distribution has been found to be based on both their genetic isolation (Darling et al., 2007) and divergent adaptations (Darling and Wade, 2008; Morard et al., 2013).

The global *G. bulloides* SSU rRNA genotype distribution found to date is shown in Fig. 3a. Within the warm water cluster (Types Ia–Id; Fig. 3b), there appears to be a major division between Type Ia, which has been found throughout the Indo-Pacific (Coral Sea, North Pacific and Arabian Sea) and Type Ib, which has only been found to date in the North Atlantic and Mediterranean. Interestingly, although Type Ib has yet to be identified within the Indo-Pacific, its sister taxa Types Ic and Id do occur there (Fig. 3a). These genotypes are genetically distinct, but their ecology is as yet unknown. Whether *G. bulloides* Types Ia and Ib are truly isolated remains in question, since there are many regions of the tropical/subtropical ocean remaining to be sampled. To date, the Type II genotypes have only been reported in the higher latitudes and transitional zones (Fig. 3a). This study now reports the presence of a Type II genotype (IIf) in the tropics. Type IIf falls on a separate small branch within the molecular phylogeny and clusters, albeit with very low support, with the subpolar and transitional genotypes of the North and South Atlantic rather than those of the Northeast Pacific (Fig. 3b).

4.2.2. The distribution and ecology of G. bulloides genotypes in the Arabian Sea

The conditions encountered along the cruise track spanned the late upwelling period to the termination (Fig. 1). Upwelling was still active, with both physical and biological indicators revealing upwelling patchiness along the Oman margin (Fig. 2). This pattern progressively changed towards the eastern Arabian Sea where more typical inter-monsoon conditions were encountered (see Methods Section 2.1). The sea conditions in this study therefore allowed a direct comparison to be made between the genetic profiles of *G. bulloides* within the late upwelling eutrophic waters off the Oman margin, the nutrient-rich waters of the divergence zone and the more oligotrophic inter-monsoonal conditions of the central Arabian Sea.

Sediment trap data off Somalia in 1992/93 showed that *G. bulloides* dominated the SW monsoon > 100 μm assemblage (Conan and Brummer, 2000) together with *G. glutinata*, *N. dutertrei*, *N. pachyderma*, *G. ruber*. Two distinct genotypes of *G. bulloides* (Types IIa and IIf) were found along the cruise transect in this study. The molecular phylogeny provides several significant clues to their expected ecology and biogeography. The *G. bulloides* genotypes split principally into two main ecological groups, where Type I genotypes have only been found in subtropical and tropical waters to date while the Type II genotypes were found within cool subpolar, transitional and transitional upwelling waters (Fig. 3b). Consistent with being a member of the subtropical and tropical lineage, *G. bulloides* Type Ia was found at 8 different stations along the transects of cruises M74/1b and CD 148 in water with an average temperature of 26 °C. During cruise M74/1b, Type Ia was also found at the upwelling stations (944 and 945) together with the genotype Type IIf (Fig. 4a). As opposed to Type Ia however, Type IIf was only found in these cooler upwelling waters and also at a lower average temperature of 21 °C. This is consistent with being an end member of the cooler water lineage, albeit at higher temperatures than

Type II genotypes have previously been found (Supplementary Fig. S1). It is highly likely that if genotyping had been more successful, it would have shown large numbers of the Type IIf genotype at the upwelling station 944 and 945 where *G. bulloides* constituted nearly 90% of the assemblage in the top 20 m. A specimen of Type IIf was also found at station 947, where *G. bulloides* still represented over 10% of the assemblage in the top 20 m. No further Type IIf were found in the mixed foraminiferal assemblages at the following stations (Supplementary Table S2), where *G. bulloides* Type Ia characterised the assemblage further offshore (Fig. 4a). Here *G. bulloides* would have represented a relatively minor component of the open ocean assemblage (Schiebel et al., 2004).

Sediment trap data record that *G. bulloides* represents at least 5% of the assemblage during the inter-monsoon non-upwelling period at sites of regional upwelling off Somalia (Conan and Brummer, 2000). Since the inter-monsoon sea surface temperatures are > 26 °C, it is most likely that the inter-monsoon *G. bulloides* will be Type Ia. Spread over several months, this flux, together with the significant component of Type Ia observed in the upwelling cells at stations 944 and 945, suggests that *G. bulloides* Ia must represent an important fraction of the *G. bulloides* specimens within the sediments below the upwelling. However, the overall majority fraction is most likely to be represented by the genotype Type IIf, when sea temperatures fall to 20 °C or below within the upwelling cell and the *G. bulloides* component increases to as much as 70% of the assemblage (Conan and Brummer, 2000).

Globigerina bulloides is one of the most commonly used planktonic foraminiferal morphospecies used in palaeoclimate reconstructions. The discovery of the two ecologically distinct genotypes in the Arabian Sea within a traditionally recognized morphospecies, has potential repercussions for palaeoclimate reconstructions. Morphologically, they appear to have few distinguishing features (Supplementary Fig. S2), though high resolution examination has yet to be carried out. However, there have been no reports of divergent morphotypes of *G. bulloides* within Arabian Sea sediment assemblages, although they have been extensively studied throughout the region. Geochemical analyses of individual *G. bulloides* shells from both core top and living assemblages of *G. bulloides* in the Arabian Sea demonstrate a bimodal distribution for both the $\delta^{18}O$ and Mg/Ca values which cannot be explained solely by seawater parameters or environmental signals (Sadekov et al., 2016). It is thought that the bimodality reflects the presence of both warm lineage Type Ia and cool lineage Type IIf genotypes in the sample sets and is attributed to genotype-specific biological controls on their shell geochemistry.

4.3. *Turborotalita quinqueloba*

4.3.1. *The global phylogeography of T. quinqueloba*

Early ecological surveys suggested that the spinose morphospecies *T. quinqueloba* is a shallow dwelling largely bipolar species with a temperature range of between 1 and 21 °C, predominantly occurring in waters colder than 12 °C (Bé and Tolderlund, 1971). However, the introduction of smaller sieve and plankton net mesh sizes led to the identification of *T. quinqueloba* in tropical waters, at temperatures even higher than 28 °C (Bé and Hutson, 1977; Kroon, 1991; Conan and Brummer, 2000).

This study increases the number of SSU rRNA genotypes of *T. quinqueloba* identified globally to seven (Fig. 5a and b). However, there are considerable gaps in the sampling coverage in the tropical/subtropical regions. It is quite possible that further warm-water genotypes will be identified when the tropical/subtropical regions have been more rigorously sampled, particularly in the Atlantic and western Pacific. As in *G. bulloides*, genotypes clearly fall into two genetically divergent and ecologically distinct clades (Fig. 5a and b), with members of the Type I clade associated with the warm tropics/subtropics and the Type II clade being associated with the cooler waters of the higher latitudes (Darling and Wade, 2008). Although genetically distinct, the Arabian Sea warm water clade genotype Type Ib shares a close common ancestor with Type Ia from the Coral Sea (Fig. 5b; Darling and Wade, 2008; Seears et al., 2012). Due to the current state of under sampling of this small morphospecies in subtropical/tropical waters, it is not possible to determine whether the two genetically distinct genotypes (Ia and Ib) are adapted to different environments or whether they are biogeographically isolated between the Coral Sea and the Arabian Sea.

Again, as in *G. bulloides*, this study reports the presence of a new *T. quinqueloba* cool-water clade genotype (Type IIe) in the tropics which also falls on a separate branch within the cool-water clade (Fig. 5b). It clusters with significant support with the South Atlantic and Northeast Pacific genotypes which are bipolar in the Pacific, but not the Atlantic (Darling and Wade, 2008). This cluster also includes Type IIb (Stewart et al., 2001), which may be confined to the cooler waters of the North Atlantic, as is observed in *N. pachyderma* Type I. This cluster is relatively distant from the cosmopolitan bipolar *T. quinqueloba* genotype IIa. The branch length of Type IIe indicates a degree of isolation of the Arabian Sea cool water genotype, hinting that it may have been there for a period of time. However, further extensive sampling will be required before any suggestion can be made of the potential isolation of Type IIe within the Arabian Sea.

4.3.2. *The distribution and ecology of T. quinqueloba genotypes in the Arabian Sea*

The cruise descriptive notes (Supplementary Table S1) indicate that *T. quinqueloba* was most common in the foraminiferal assemblage at the most northerly station 943 (Fig. 6a) and again at the more north-eastern stations 955–958, where small morphospecies dominated a low diversity assemblage. This region of the Arabian Sea is associated with high salinity (Fig. 2), suggesting that *T. quinqueloba* may have a preference for high temperature and salinity waters in the Arabian Sea. However, in the present study, assemblage counts (> 100 μm; 0–20 m) carried out at the upwelling station 945 indicate that *T. quinqueloba* also constituted a minor component of the upwelling assemblage, but was absent in the assemblage at the non-upwelling station 947 further offshore (Fig. 6a). This is consistent with the findings of Conan and Brummer (2000) and Peeters and Brummer (2002), who found *T. quinqueloba* in both sediment trap and multinet assemblages in the upwelling off Somalia and Oman. During the inter-monsoon, *T. quinqueloba* was virtually absent (Peeters and Brummer, 2002) from these waters. Since upwelling is associated with lower temperatures and salinities, the *T. quinqueloba* found in the upwelling must have completely different ecological adaptations from those in the northern Arabian Sea. Peeters and Brummer (2002) speculated that two populations of *T. quinqueloba* most likely exist in the Arabian Sea, one being adapted to the cool upwelling and the other to the warm surface waters.

The present study suggests that Peeters and Brummer (2002) are correct. Although sample numbers are too low to conclusively confirm their affinity and distribution, potentially two different ecotypes of *T. quinqueloba* do inhabit the waters of the Arabian Sea (Fig. 6b). The majority of *T. quinqueloba* specimens found in the warmer more saline north-eastern waters were genotype Type Ib. This distribution is consistent with this genotype being a member of the warm water clade (Fig. 5b). Specimens of *T. quinqueloba* were found in too low numbers to determine the true distribution of genotype Type IIe at the upwelling and southern stations. However, all other members of the cool water clade have consistently been associated with cooler water (Darling and Wade, 2008).

4.4. *Neogloboquadrina pachyderma*

4.4.1. *The global phylogeography of N. pachyderma*

The sedimentary fossil record shows that *N. pachyderma* is the dominant morphospecies within the Arctic and Antarctic polar provinces (Bé and Tolderlund, 1971; Kennett, 1968) and also constitutes a significant proportion of the subpolar assemblage (Darling and Wade,

2008). In addition, it is found within the offshore upwelling systems and cool-water boundary currents such as the Benguela Current (Ufkes and Zachariasse, 1993), the Peru-Chile Current (Marchant et al., 1998), the Western Arabian Sea (Naidu and Malmgren, 1996b), the California Current (Ortiz and Mix, 1992) and the Kuroshio Current off Japan (Arikawa, 1983). It is highly likely that all lower latitude eutrophic upwelling systems harbour *N. pachyderma*. Apart from its presence in these systems, it is absent from the subtropical and tropical provinces, exhibiting an anti-tropical bipolar distribution.

Even though *N. pachyderma* is clearly capable of long-distance dispersal throughout the global ocean, genotypes consistently exhibit regional genetic and ecological distinction in the present day (Fig. 7a; Darling et al., 2004; Darling and Wade, 2008). Although the Arabian Sea *N. pachyderma* Type VIII has an exceptionally long branch, it consistently falls within the subpolar/transitional/upwelling group, using all tree construction methods (see Section 2; Fig. 7b). Although it is not possible to be confident of its ancestry, this suggests that Type VIII could have been seeded from either the southern hemisphere or North Pacific genotypes. It has a high temperature tolerance, which would facilitate its passage from either gene pool. Type VIII is the first *N. pachyderma* genotype found to exhibit such a high evolution rate but it is not the first Neogloboquadrinid to do so. The two genotypes of *N. incompta* also fall on an exceptionally long branch in the Neogloboquadrinid tree (Fig. 7c), diverging only at the tip. It is most likely that very low numbers of founding specimens established the population of *N. pachyderma* Type VIII and they may have remained in isolation since.

4.4.2. The distribution and ecology of *N. pachyderma* genotypes in the Arabian Sea

In the present study, only a single SSU rRNA genotype was found in the Arabian Sea out of 31 specimens sequenced. Numbers may not therefore be sufficient to conclude that only a single genotype exists in the region, but *N. pachyderma* Type VIII were found in both upwelling and open ocean environments. For a high latitude morphospecies, *N. pachyderma* has proved full of surprises. It ranges from being an extremophile species in the Antarctic winter sea ice (Type IV; Darling et al., 2004), to being a tropical species, able to tolerate equally extreme temperatures as high as 28 °C (Type VIII in this study). It is clearly not temperature that controls the dispersal of *N. pachyderma*, although each genotype has an adaptive temperature range. Also surprising is that it is not restricted to shallow depths like most other planktonic foraminifers. For example, in the Benguela System off Namibia (Darling et al., 2004), large numbers of *N. pachyderma* were found in waters < 70 m in depth. Yet, in the Arabian Sea it is found in high numbers at depths as great as 400–600 m (Ivanova et al., 1999; this study). The common theme throughout all studies on *N. pachyderma* genotypes, is their seasonal association with high levels of primary productivity in the water column. This is consistent with the views of Reynolds and Thunell (1986) and Ufkes and Zachariasse (1993) who suggested that the distribution of *N. pachyderma* is mainly controlled by the seasonal availability of food.

Sediment traps off Yemen/Oman show that *N. pachyderma* is present throughout the year in low numbers, but grows and reproduces in the months associated with upwelling (Conan and Brummer, 2000). The highest flux of *N. pachyderma* is observed at the end of June/July; a period characterised by falling SST's, the development of an upwelling gyre and increased primary production. Since the majority of specimens are found at depth in the Arabian Sea (Ivanova et al., 1999), the majority would have to be feeding at these depths on detrital material if alive. Conan and Brummer (2000) believe their presence in high numbers at depth may represent a resting stage related to their reproductive cycle, which would have been preceded by a short reproductive period near the surface. Alternatively, they could be predominantly empty shells, the product of an earlier reproduction bloom at the surface. Both scenarios are supported by isotope data from both sediment trap and sediment, which indicates that they mostly calcify around 25 m water depth. In this study, nine *N. pachyderma* specimens were genotyped from deep nets (300–700 m), indicating that they were still alive. Whether they were living and feeding at depth is unknown.

5. Conclusions

Planktonic foraminiferal morphospecies assemblage structure not only differs between upwelling systems, but the genotypes of common morphospecies also vary between systems. The morphospecies *G. bulloides* is represented by Types IIa and IId in the Santa Barbara Channel upwelling (Darling et al., 2003), by Types IIa and IIb in the Benguela upwelling system (Darling and Wade, 2008), and Type Ia and Type IIf in the Oman margin upwelling (this study). The morphospecies *T. quinqueloba* is represented by Types IIc and IId in the Santa Barbara Channel upwelling and potentially by Type IIe in the Oman margin upwelling (this study). The morphospecies *N. pachyderma* is represented by Types V and VI in the Benguela upwelling (Darling et al., 2007) and by Type VIII in the Oman margin upwelling (this study).

Where sympatric genotypes occur, it is highly likely that they represent divergent ecotypes driven by ecological partitioning (Seears et al., 2012). It has been suggested that some of the genotypes of *G. bulloides* may be over-split and may not correspond to genuine species (André et al., 2014). However, this only applies to those very closely related sibling genotypes within the same clade. The two *G. bulloides* genotypes (Type Ia and Type IIf) are genetically highly distinct, are members of different ecological clades and also have very different ecologies. They should certainly be considered as different species. The same rationale could also apply to *T. quinqueloba* Types Ia and IIf, since they are also genetically highly distinct and members of different ecological clades.

Both the newly characterised genotypes of *T. quinqueloba* Type IIe and *N. pachyderma* Type VIII exhibit proportionately long branch lengths in their phylogenies (Figs. 4b and 6b), suggesting that they may be genetically isolated in the Arabian Sea. Only extensive global sampling will confirm whether this is the case. Surveying the ocean for undiscovered genotypes is now an achievable task, due to the global metabarcoding approach that has been developed to genetically characterise planktonic foraminifera using SSU rRNA gene short sequences as barcodes (de Vargas et al., 2015). The upwelling genotype of *G. bulloides* (Type IIf) found in this study is not isolated, since it has also been identified in the subtropical waters of the Northwest Pacific off Japan (Kurasawa et al., n.d., unpublished sequence; Morard et al., 2015). Interestingly, it was not found by Darling et al. (2003) in the Northeast Pacific (Santa Barbara Channel).

The stable isotopic and elemental composition of foraminiferal shells reflects the physiochemical environment in which they are formed. Currently, reconstruction of oceanic and climatic conditions in the past relies heavily upon these geochemical signatures (Kucera, 2007). It is therefore essential to obtain a clear understanding of the relationship between the ecology of individual foraminiferal morphospecies and their shell geochemistry in the present day water column. This relationship has been traditionally based on the assumption that each foraminiferal morphospecies represents a genetically continuous species with a unique habitat preference. However, the genetic and ecologically divergent nature of the new genotypes identified off the Oman margin is highly suggestive of species level distinction. This makes the use of a general morphospecies concept inappropriate for this region, since many geochemical proxies used for palaeoenvironmental studies are known to be species specific (Bemis et al., 1998, 2002). As mentioned above, geochemical analyses of individual *G. bulloides* shells from both core top and living assemblages in the Arabian Sea, demonstrate a bimodal distribution which cannot be explained solely by seawater parameters or environmental signals (Sadekov et al., 2016). This is attributed to genotype-specific biological controls on their shell geochemistry, highlighting the requirement for regional genetic characterisation and geochemical calibration.

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