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Factors controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic

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Abstract. Planktonic foraminifera preserved in marine sediments archive the physical and chemical conditions under which they built their shells. To interpret the paleoceanographic information contained in fossil foraminifera, the recorded proxy signals have to be attributed to the habitat and life cycle characteristics of individual species. Much of our knowledge on habitat depth is based on indirect methods, which reconstruct the depth at which the largest portion of the shell has been calcified. However, habitat depth can be best studied by direct observations in stratified plankton nets. Here we present a synthesis of living planktonic foraminifera abundance data in vertically resolved plankton net hauls taken in the eastern North Atlantic during 12 oceanographic campaigns between 1995 and 2012. Live (cytoplasm-bearing) specimens were counted for each depth interval and the vertical habitat at each station was expressed as average living depth (ALD). This allows us to differentiate species showing an ALD consistently in the upper 100 m (e.g., *Globigerinoides ruber* white and pink), indicating a shallow habitat; species occurring from the surface to the subsurface (e.g., *Globigerina bulloides*, *Globorotalia inflata*, *Globorotalia truncatulinoides*); and species inhabiting the subsurface (e.g., *Globorotalia scitula* and *Globorotalia hirsuta*). For 17 species with variable ALD, we assessed whether their depth habitat at a given station could be predicted by mixed layer (ML) depth, temperature in the ML and chlorophyll *a* concentration in the ML. The influence of seasonal and lunar cycle on the depth habitat was also tested using periodic regression. In 11 out of the 17 tested species, ALD variation appears to have a predictable component. All of the tested parameters were significant in at least one case, with both seasonal and lunar cyclicity as well as the environmental parameters explaining up to > 50 % of the variance. Thus, *G. truncatulinoides*, *G. hirsuta* and *G. scitula* appear to descend in the water column towards the summer, whereas populations of *Trilobatus sacculifer* appear to descend in the water column towards the new moon. In all other species, properties of the mixed layer explained more of the observed variance than the periodic models. Chlorophyll *a* concentration seems least important for ALD, whilst shoaling of the habitat with deepening of the ML is observed most frequently. We observe both shoaling and deepening of species habitat with increasing temperature. Further, we observe that temperature and seawater density at the depth of the ALD were not equally variable among the studied species, and their variability showed no consistent relationship with depth habitat. According to our results, depth habitat of individual species changes in response to different en-

vironmental and ontogenetic factors and consequently planktonic foraminifera exhibit not only species-specific mean habitat depths but also species-specific changes in habitat depth.

1 Introduction

Planktonic foraminifera record chemical and physical information of the environment in which they live and calcify. Because of their wide distribution in the ocean and good preservation on the seafloor, fossil shells of these organisms provide an important tool for paleoceanographic and paleoclimatic reconstructions. The usefulness of planktonic foraminifera as recorders of past ocean conditions depends on the understanding of their environmental preferences, including the habitat depths of individual species. Compared to the large body of knowledge on the distribution and physiology of planktonic foraminifera species, the complexity of their vertical distribution remains poorly constrained and the existing conceptual models (Hemleben et al., 1989) are not sufficiently tested by observational data. That different species of planktonic foraminifera calcify at different depths was first discovered by geochemical analyses of their shells by Emiliani (1954). These indirect inferences have been confirmed by observations from stratified plankton tows, which provide the most direct source of data on the habitat depth of planktonic foraminifera (Berger, 1969, 1971; Fairbanks et al., 1982, 1980; Bijma and Hemleben, 1994; Ortiz et al., 1995, Schiebel et al., 1995; Kemle-von Mücke and Oberhänsli, 1999).

The existence of a vertical habitat partitioning among planktonic foraminifera species across the upper water column likely reflects the vertical structuring of the otherwise homogenous pelagic habitat. Light intensity, water temperature, oxygen availability, concentration of food, nutrients and predation all change with depth in the ocean, creating distinct ecological niches. If planktonic foraminifera species are indeed adapted to different habitat depths, they must possess some means of reaching and maintaining this depth in the water column. Zooplankton can control their position in the water column mostly by changes in buoyancy (Johnson and Allen, 2005). In the case of passively floating phytoplankton, changes in buoyancy are the only possible mechanism, which is primarily regulated by low-density metabolites or osmolytes (Boyd and Gradmann, 2002). The exact mechanism by which planktonic foraminifera control their position in the water column is not fully understood, but observations indicate that there must be mechanisms allowing for species-specific buoyancy adjustment such that the population of a given species is found concentrated at a given depth. One good example on how planktonic foraminifera control their vertical position in the water column is the case study of *Hastigerinella digitata*. Based on in situ observations of this species using remotely operated vehicle videos in the Monterey Bay (California), Hull et al. (2011) found a consistent and stable dominant concentration of this species in a narrow depth horizon around 300 m, just above the depth of the local oxygen minimum level. The depth of the concentration maximum changed seasonally and this pattern remained stable for 12 years. This example shows that planktonic foraminifera may indeed possess characteristic depth habitats.

When analyzing observations on habitat depth of planktonic foraminifera from plankton tows, one first has to consider the possibility that such data are biased by vertical migration during life. In addition, individuals may be transported up and down the water column by internal waves, suggesting vertical migration, but the amplitude of this effect is likely much smaller than the typical resolution of our sampling (Siccha et al., 2012). Similarly, diel vertical migration is a well-established phenomenon among motile zooplankton (Hutchinson, 1967), but its existence in planktonic foraminifera is unlikely. Day–night abundance variations have been previously reported for planktonic foraminifera, with higher abundance concentrations of foraminifera at the surface during day than at night (Berger, 1969; Holmes, 1982), but the most comprehensive and best replicated test carried out by Boltovskoy (1973) showed no evidence for a systematic day–night shift in abundance. Therefore, plankton tow observations should not be affected by this phenomenon.

However, the existing observational data indicate that the habitat depth of a species is not constant throughout its life. Fairbanks et al. (1980) combined observations from stratified plankton tows with shell geochemistry to demonstrate that calcification depth differs from habitat depth and that at least some species of planktonic foraminifera therefore must migrate vertically during their life. These observations led to the development of the concept of ontogenetic migration (Hemleben et al., 1989; Bijma et al., 1990a). In this model, the vertical distribution of a species at a given time also reflects its ontogenetic trajectory. This trajectory affects "snapshot" observations, such as those from plankton tows, because it interferes with the "primary" environmentally constrained habitat depth. Assuming that reproduction in planktonic foraminifera is synchronized and follows either lunar or yearly cycles (Hemleben et al., 1989; Bijma et al., 1990a; Schiebel et al., 1997), observations on habitat depth from plankton tows must therefore be analyzed in light of the existence of periodic changes synchronized by lunar or yearly cycles.

Considering the distinct geochemical signatures among species, allowing clear ranking according to depth of calcification (e.g., Anand et al., 2003), it seems that the (unlikely) diel vertical migration or ontogenetic migration only operate within certain bounds, defined by the primary depth habitat of each species. The determinants of the primary habitat depth diversity among species of planktonic foraminifera are only partly understood (Berger, 1969; Caron et al., 1981; Watkins et al., 1996; Field, 2004). Next to ambient tem-

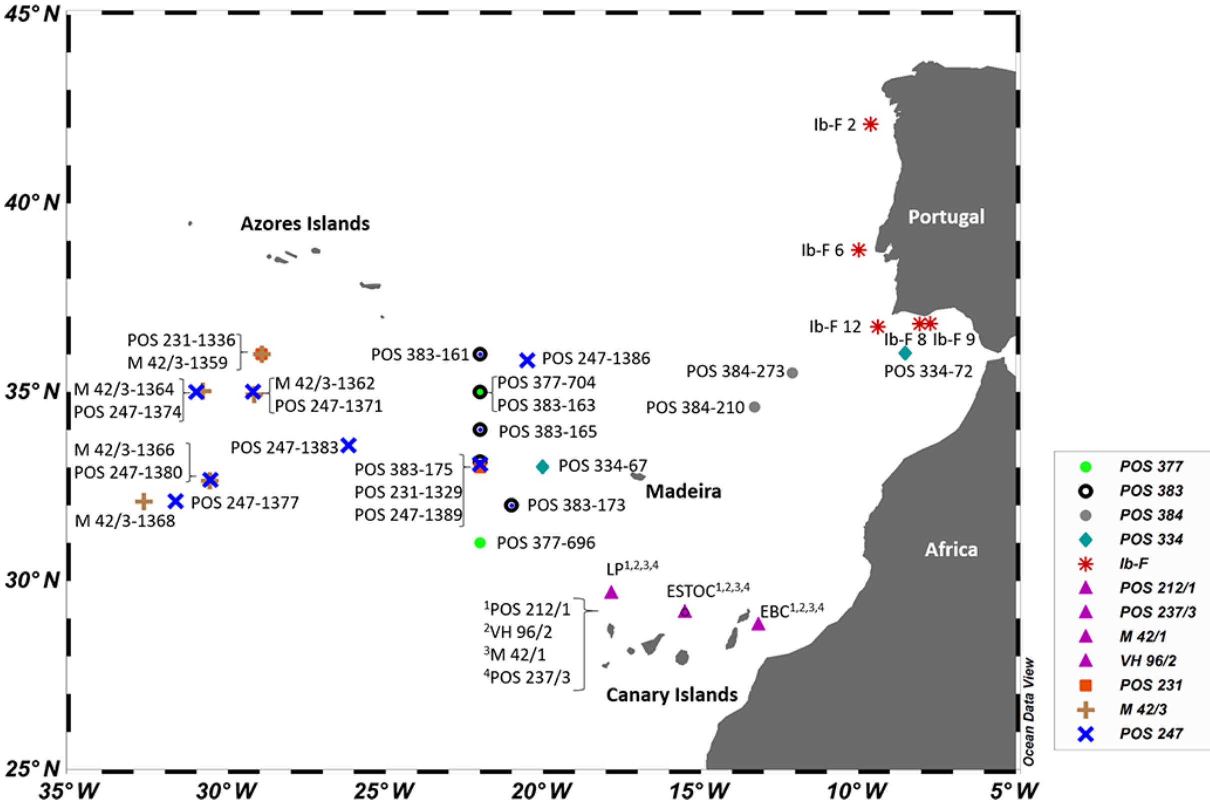


Figure 1. Plankton net stations in the eastern North Atlantic with vertically resolved planktonic foraminifera assemblage counts that were used in this study. The stations are coded by cruises. Superscript and brackets indicate repeated sampling at the same positions (for details see Table 1). Map made with ODV (Schlitzer, 2016).

perature (Fairbanks et al.; 1982; Bijma et al., 1990b), other environmental parameters have been proposed as potential drivers of vertical distribution, such as light for photosymbiotic species (Ortiz et al., 1995; Kuroyagani and Kawahata, 2004), food availability (Schiebel et al., 2001; Salmon et al., 2015) and stratification (Field, 2004; Salmon et al., 2015). In addition, Simstich et al. (2003) analyzed the isotopically derived calcification depths of two species in the Nordic seas and found that each species' calcification depth appeared to follow a particular density layer.

In theory, knowing the primary habitat depth (including calcification depth) of a species should be sufficient to correctly interpret paleoceanographic data based on analysis of fossil planktonic foraminifera. This conjecture assumes that the primary habitat depth (and by inference the calcification depth) is constant. However, the depth habitat of many species may vary in time and at the regional scale, independently of the ontogenetic migration. This phenomenon is known from geochemical studies, indicating large shifts in calcification depth across oceanic fronts or among regions, in absolute terms or relative to other species (Mulitza et al., 1997; Simstich et al., 2003; Chiessi et al., 2007; Farmer et al., 2007). Specifically, it seems that the habitat depth of planktonic foraminifera species is highly variable in mid-latitude settings, such as in the North Atlantic, where large seasonal shifts in hydrography are combined with the presence of steep and variable vertical gradients in the water column (e.g., Schiebel et al., 2001, 2002b). The presence of such steep gradients holds great promise in being able to reconstruct aspects of the surface ocean structure (Schiebel et al., 2002a), as long as the factors affecting the depth habitat of species in this region are understood. Since the concept of a constant primary habitat depth is unlikely to be universally valid, it has to be established how habitat depth varies and whether the variability in habitat depth can be predicted. Although several surveys of planktonic foraminifera distribution in plankton tows have been conducted in the North Atlantic, the majority sampled with limited or no vertical resolution, such as the study by Bé and Hamlin (1967) that only compared 0–10 and 0–300 m vertical hauls, or Cifelli and Bérnier (1976), who sampled only between 0–100 and 0–200 m, Ottens (1991), who analyzed surface pump samples, or limited regional coverage (Schiebel et al., 2001, 2002a, b; Wilke et al., 2009). Importantly, these studies have not covered relevant regions of the eastern North Atlantic that feature in many paleoceanographic studies (e.g., Sánchez Goñi et al., 1999; De Abreu et al., 2003; Martrat et al., 2007; Salgueiro et al., 2010), such that the vertical distribution of

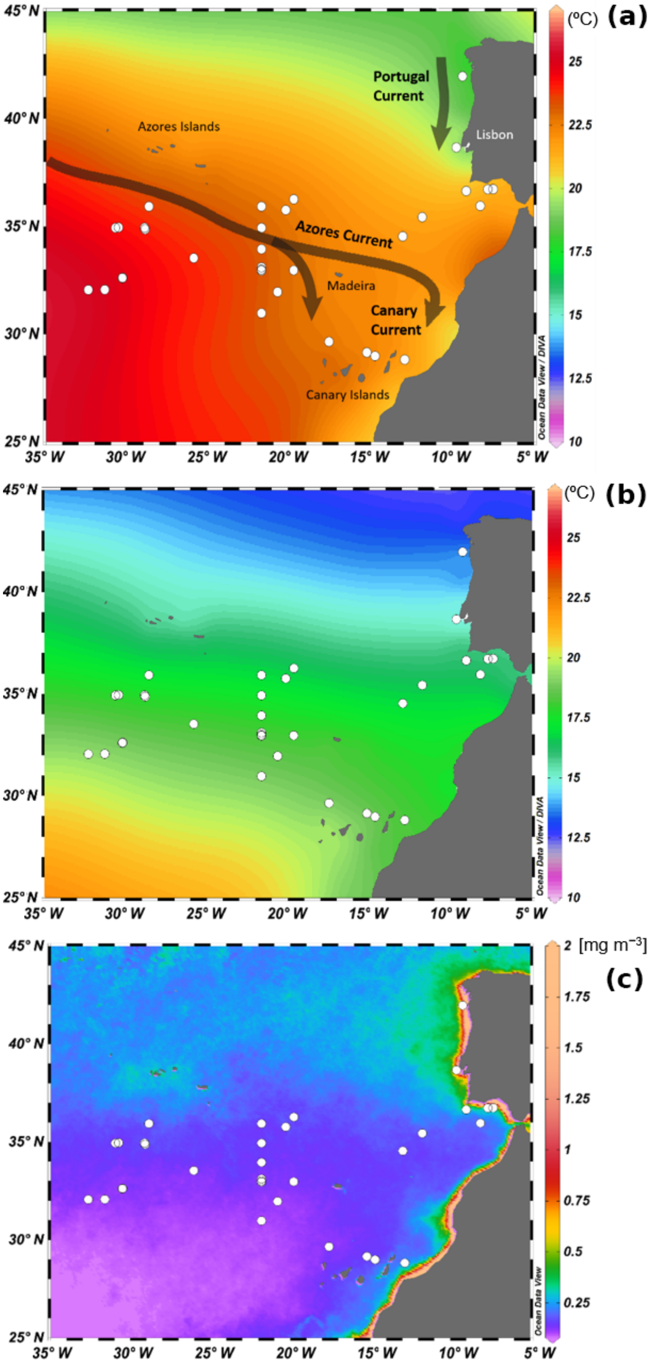


Figure 2. (a) Mean summer (July to September, from 1955 to 2012) SST (sea-surface temperature) (data from World Ocean Atlas 2013) with main surface currents shown by arrows, **(b)** mean winter (January to March, from 1955 to 2012) SST (data from World Ocean Atlas 2013) and **(c)** mean monthly chlorophyll mg m^{-3} data from 2010 to 2015 (data from the Goddard Earth Sciences Data and Information Services Center) in the studied region along with the positions of the studied plankton net stations. Maps made with ODV (Schlitzer, 2016).

planktonic foraminifera along the Iberian Margin and the Canary Islands remains poorly constrained.

To better understand factors affecting vertical distribution of planktonic foraminifera species, facilitating better-constrained proxy calibrations, the variability of their habitat depth has to be studied in a regional context, where it can be directly linked with ambient environmental conditions. To this end, the current study aims to characterize the vertical distribution of living planktonic foraminifera and its potential controlling factors from a compilation of vertically resolved plankton net samples covering a large portion of the eastern North Atlantic (Figs. 1, 2). Data from the Azores Current/Front (Schiebel et al., 2002a, b) and the Canary Islands (Wilke et al., 2009) were combined with new data from the Azores Current/Front and the Iberian Margin. The resulting compilation covers different years and seasons, a range of lunar days and hydrographic conditions, and contains enough stations to facilitate objective analysis of potential controlling factors. In addition, the majority of the counts were exhaustive and considered smaller-sized planktonic foraminifera, providing new information on the ecology of these species as a possible basis for their paleoceanographic application.

2 Regional setting

In the eastern North Atlantic, the subtropical gyre circulation is divided into two different subsystems: the Canary and Iberian upwelling regions (e.g., Barton et al., 1998) (Fig. 2). The discontinuity, caused by the Strait of Gibraltar, helps the exchange between the Mediterranean Outflow Water and North Atlantic Water (Relvas et al., 2007). Modeling studies suggest that the Mediterranean Outflow Water entrainment in the North Atlantic Ocean is a key factor for the establishment of the Azores Current (Jia, 2000; Özgökmen et al., 2001). The Azores Current originates from the southern branch of the Gulf Stream (Sy, 1988), flows southeastward across the Mid-Atlantic Ridge and then extends eastward between 32° and 36° N (Gould, 1985; Klein and Siedler, 1989).

The Azores Current can reach as deep as 2000 m, has a width of 60–150 km (Alves et al., 2002; Gould, 1985) and occurs throughout the year with a variable seasonal transport (Alves et al., 2002). The Azores Current is characterized by strong mesoscale eddies and active meanders (Alves et al., 2002; Fernández and Pingree, 1996; Gould, 1985). Southeast of the Azores Islands, the Azores Current splits into a northern branch that approaches the Portugal Current and a southern branch that connects to the Canary Current (Barton, 2001; Sy, 1988). The latter flows southeastward from the African coast to the North Equatorial Current (Alves et al., 2002), connects to the Caribbean Current and merges with the Gulf Stream (Barton, 2001). The Azores Current's northern limit is defined by a thermohaline front – the Azores Front. It acts as a boundary of water masses, separating the warmer (18 °C), saltier and oligotrophic water mass of the Sargasso Sea from the colder, fresher and more productive water mass of the northern and eastern North Atlantic (Gould, 1985; Storz et al., 2009). Based on the analysis of a 42 year-long time series, the Azores Front's position varied between 30 and 37.5° N and seems to be related to the North Atlantic Oscillation (Fründt and Waniek, 2012). The strong change in temperature (∼ 4 °C) and water column structure across the Azores Front influences the distribution of planktonic organisms including foraminifera (Alves et al., 2002; Schiebel et al., 2002a, b) and increases pelagic biomass and production (Le Févre, 1986).

Far more productive than the seasonal bloom at the Azores Front are the two coastal upwelling regions in the studied area (Fig. 2c). From April to October, when the upper layer becomes more stratified and the northern winds more intense, the conditions are favorable for upwelling (Fiúza, 1983; Wooster et al., 1976; Peliz et al., 2007; McGregor et al., 2007). Off northwest Africa, a major upwelling area is found north of 25° N. The strongest upwelling occurs during summer and autumn, in pace with the seasonal variation of the northeast trade winds. Despite upwelling being usually restricted to the shelf and the upper slope waters, filament structures at specific coastal positions occur off the northwestern African coastline (e.g., Barton et al., 1998).

3 Materials and methods

The analysis of the vertical distribution of planktonic foraminifera is based on data from vertically resolved plankton net hauls collected in the region between 20 to 43° N and 8 to 40° W during 12 oceanographic campaigns between 1995 and 2012 (Table 1; Fig. 1b). In all cases, the sampling was done using either a Hydro-Bios Midi or Maxi multiple closing net (100µm mesh size, opening 50 × 50 cm) hauled vertically with a velocity of $0.5\,m\,s^{-1}$. The multiple closing net used in this study provides vertical resolution at five levels during one haul or nine levels for two consecutive hauls. Because of different oceanographic settings in the studied regions and because of different time constraints during the cruises, the vertical sampling scheme varied (Table 1). At 16 out of the 43 stations, the water column distribution was resolved to nine levels (two hauls). Five vertical levels were resolved at 23 stations and four vertical levels at the four stations from the western Iberian Margin. At stations with less than nine levels, the vertical sampling scheme was adjusted to capture the structure of the regional thermocline. At all stations, sampling was carried out to at least 300 m (275 m in one case) and although planktonic foraminifera are known to live deeper than 300 m (e.g., Peeters and Brummer, 2002), the population size below this depth is small and the counts used in this study should reflect the main portion of the standing stock of the analyzed species at each station.

After collection, net residues from each depth were concentrated on board, preserved with 4 % formaldehyde or using a saturated $HgCl_2$ solution, buffered to a pH value of 8.2 with hexamethylenetetramine ($C_6H_{12}N_4$) to prevent dissolution and refrigerated. Specimens of planktonic foraminifera were picked completely from the wet samples under a binocular microscope and air dried. All individuals in the fraction, either above 100 or 125 µm (specified in Table 1), were counted and identified to species level according to the taxonomy of Hemleben et al. (1989), Brummer and Kroon (1988) and Spezzaferi et al. (2015). Living foraminifera (cytoplasm-bearing) were distinguished from dead specimens (partially or entirely free of cytoplasm). Some "cryptic species" (Darling and Wade, 2008), such as those subsumed in the morphospecies concepts of *G. ruber* and *G. siphonifera*, are morphologically different in adult specimens, but their characteristic features are not well developed among pre-adult individuals that are abundant in the plankton tows. Therefore, this level of taxonomic resolution was not possible in our study. Juvenile and adult stages were not distinguished in individuals identified as belonging to the same species. The concentration, expressed as number of individuals per unit volume (m^3), was determined by dividing the counts in each depth interval by the volume of water filtered during the plankton net corresponding to the depth interval, i.e., multiplying the area of the square-shape net opening with the length of the towed interval. The underlying assumption is that the hauls were carried out vertically and that the filtered volume was not affected by the vertical movement of the vessel during hauling. This assumption was tested by comparison with direct measurements of filtered water volume from a flow meter available for some of the stations. In those hauls, the sampled water volume was very close to 100 % and hence the same procedure was applied to all stations.

In situ water column properties, including temperature, salinity and fluorescence (calibrated to chlorophyll *a* concentration), were measured with a conductivity–temperature–depth (CTD) device before each plankton tow (Table 2). These data were used to determine the base of the mixed layer (the depth where in situ temperature decreased by more than 0.5 °C compared to the surface) (Monterey and Levitus, 1997). This value was considered to represent mixed layer depth (MLD) and all readings within the mixed layer defined in this way were used to calculate the mean temperature in the mixed layer (TML) and chlorophyll *a* concentration in the mixed layer (CML). Stations for which in situ fluorescence profiles were not available (Table 2), CML was approximated from chlorophyll *a* satellite values at the ocean surface at the same day whenever available or using the 8-day or monthly composite always, using the best approximation to the date of collection and the nearest available coordinates from NASA's Ocean Color Web database (http://oceancolor.gsfc.nasa.gov/cms/). For cruises performed in 1995, 1996 and 1997 (VH 96/2, POS 212/1 and POS 231-1329), no CTD data were available and chlorophyll *a* data

Table 1. Cruise and stations, location, time (day/month/year), depth intervals, method used for preservation of the sample, counting size and person, who did the taxonomy of the planktonic foraminifera.

Cruise	Station	Latitude	Longitude	Time	Date	DOY[a]	Lunar day	MLD[b] (m)	TML[c] (°C)	CML[d] ($mg\,m^{-3}$)	Depth intervals	Preservation method[e]	Counts size	Taxonomy[f]
Poseidon 212/1	LP	29.667	−17.833	11:25 LT	22/9/95	265	28	55.59	24.076	N/A	0–50, 50–150, 150–300, 300–500, 500–800	2	> 125 µm	H. M.
	ESTOC	29.167	−15.500	07:48 LT	24/9/95	267	30	47.60	23.776	N/A	0–50, 50–150, 150–300, 300–500, 500–800	2	> 125 µm	H. M.
	EBC	28.833	−13.167	01:00 LT	26/9/95	269	2	38	20.015	N/A	0–50, 50–150, 150–300, 300–500, 500–800	2	> 125 µm	H. M.
	EBC	28.833	−13.167	14:17 LT	26/9/95	269	2	38	20.015	N/A	0–25, 25–50, 50–100, 100–200, 200–275	2	> 125 µm	H. M.
Victor Hensen 96/2	ESTOC	29.167	−15.500	13:15 LT	24/1/96	24	5	140	18.922	N/A	0–25, 25–50, 50–150, 150–300, 300–440	2	> 125 µm	H. M.
	EBC	28.833	−13.167	19:40 LT	25/1/96	25	6	N/A	N/A	N/A	0–25, 25–50, 50–150, 150–300, 300–440	2	> 125 µm	H. M.
	LP	29.667	−17.833	21:50 LT	29/1/96	29	10	N/A	N/A	N/A	0–25, 25–50, 50–150, 150–300, 300–440	2	> 125 µm	H. M.
Poseidon 231/3	1329	33.000	−21.999	11:12 LT	6/8/97	218	4	32.45	23.101	N/A	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100 µm	R. S.
	1336	36.000	−28.934	06:46 LT	14/8/97	226	12	24	24.224	0.005	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100 µm	R. S.
Poseidon 237/3	EBC	28.833	−13.167	22:03 LT	4/4/98	94	8	98	19.443	0.204	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.
	ESTOC	29.167	−15.500	00:10 LT	5/4/98	95	9	76	19.599	0.150	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.
	LP	29.667	−17.833	12:13 LT	8/4/98	98	12	44	20.011	0.132	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.
Meteor 42/1	EBC	28.833	−13.167	09:44 LT	28/6/98	179	5	20	20.808	0.156	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.
	ESTOC	29.167	−15.500	19:18 LT	1/7/98	182	8	50	21.151	0.113	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.
	LP	29.667	−17.833	19:20 LT	5/7/98	18	12	30	22.209	0.088	0–25, 25–50, 50–150, 150–300, 300–500	2	> 125 µm	H. M.

Table 1. Continued.

Cruise	Station	Latitude	Longitude	Time	Date	DOY[a]	Lunar day	MLD[b] (m)	TML[c] (°C)	CML[d] ($mg\,m^{-3}$)	Depth intervals	Preservation method[e]	Counts size	Taxonomy[f]
Meteor 42/3	1359	35.997	−28.930	09:14 LT	29/8/98	272	8	17	25.328	0.066	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1362	34.930	−29.170	20:51 LT	29/8/98	272	8	21	25.689	0.071	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1364	35.020	−30.800	07:14 LT	30/8/98	273	9	17	25.956	0.074	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1366	32.650	−30.580	11:17 LT	30/8/98	273	9	28	26.483	0.069	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500	1	> 100 µm	R. S.
	1368	32.100	−32.670	07:39 LT	31/8/98	274	10	23	26.019	0.069	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
Poseidon 247/2	1371	35.002	−29.204	13:33 LT	17/1/99	17	1	122	19.209	0.199	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100 µm	R. S.
	1374	35.000	−31.001	04:25 LT	18/1/99	18	2	110	18.910	0.208	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1377	32.103	−31.654	06:33 LT	19/1/99	19	3	118	19.908	0.191	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1380	32.669	−30.553	23:13 LT	19/1/99	19	3	102	19.504	0.198	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1383	33.582	−26.167	05:32 LT	21/1/99	21	5	150	19.369	0.249	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1386	35.833	−20.501	21:27 LT	22/1/99	22	6	112	18.177	0.167	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.
	1387	33.083	−21.999	22:03 LT	24/1/99	24	8	170	18.766	0.182	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	R. S.

Table 1. Continued.

Cruise	Station	Latitude	Longitude	Time	Date	DOY[a]	Lunar day	MLD[b] (m)	TML[c] (°C)	CML[d] ($mg\,m^{-3}$)	Depth intervals	Preservation method[e]	Counts size	Taxonomy[f]
Poseidon 334	67	33.010	−20.011	09:03 LT	18/3/06	83	19	213	17.586	0.302	0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–300	1	> 100µm	I. F.
	72	36.025	−8.503	09:28–14:55 LT	24/3/06	79	25	81.23	16.112	0.348	0–20, 20–40, 40–100, 100–200, 200–300	1	> 100µm	A. R.
Poseidon 377	696	31.000	−22.000	11:04 LT	11/12/08	346	14	113	20.310	0.323	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
	704	35.000	−22.000	00:48 LT	13/12/08	348	16	74	19.516	0.330	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
Poseidon 383	161	36.000	−22.000	10:10 LT	22/4/09	112	27	49	18.090	0.305	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
	163	35.000	−22.000	02:03 LT	23/4/09	113	28	85	18.274	0.289	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
	165	34.000	−22.000	13:40 LT	23/4/09	113	28	29	18.580	0.1161	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
	173	32.000	−21.000	19:03 LT	25/4/09	115	30	88	17.906	0.474	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
	175	33.150	−22.000	11:52 LT	26/4/09	116	1	45	18.383	0.089	0–100, 100–200, 200–300, 300–500, 500–700	1	> 100µm	A. R.
Poseidon 384	210	34.600	−13.290	07:05 LT	12/5/09	132	18	40	18.158	0.046	0–100, 100–200, 200–300, 300–400, 400–700	1	> 100µm	A. R.
	273	35.500	−12.090	20:51 LT	21/5/09	141	27	51	17.834	0.052	0–100, 100–200, 200–300, 300–400, 400–500	1	> 100µm	A. R.
Iberia-Forams	2	42.090	−9.50	01:09 LT	11/9/12	255	26	20	19.707	0.228	0–25, 25–80, 80–200, 200–300	1	> 100µm	A. R.
	6	38.760	−9.98	17:07 LT	12/9/12	256	27	9	20.077	0.119	0–70, 70–140, 140–240, 240–340, 240–540	1	> 100µm	A. R.
	8	36.800	−8.04	16:11 LT	13/9/12	257	28	13	21.701	0.115	0–60, 60–120, 120–240, 240–400	1	> 100µm	A. R.
	9	36.810	−7.71	21:11 LT	13/9/12	257	28	12	22.426	0.252	0–90, 90–180, 180–270, 270–360	1	> 100µm	A. R.
	12	36.720	−9.37	12:04 LT	15/9/12	259	30	21	20.998	0.170	0–100, 100–200, 200–350, 350–550	1	> 100µm	A. R.

[a] DOY is days of year. [b] MLD is mixed layer depth. [c] TML is temperature in the mixed layer. [d] CML is chlorophyll a in the mixed layer. [e] Preservation method: 1 = formaldehyde 4 % buffered with hexamethylenetetramine; 2 = saturated $HgCl_2$ solution [f] taxonomy; H.M. = Helge Meggers; R.S.: Ralf Schiebel; I.F.: Igaratza Fraile; A.R.: Andreia Rebotim. N/A: not available.

Table 2. Cruises with references for the temperature and chlorophyll data.

Cruise	Temperature	Chlorophyll
Poseidon 212/1	Knoll et al. (1998)	Ocean Color Data[c]
Victor Hensen 96/2	Neuer (1997)[a] Ocean Color Database[b]	Ocean Color Data[c]
Poseidon 231/3	Waniek (1997)	Ocean Color Data[c,d,e]
Poseidon 237/3	Knoll et al. (1998)	Ocean Color Data[d]
Meteor 42/1	Pfannkuche et al. (1998)	Ocean Color Data[d]
Meteor 42/3	Pfannkuche et al. (1998)	Ocean Color Data[d]
Poseidon 247/2	Müller (1999)[e]	Ocean Color Data[d]
Poseidon 334	Schulz (2006)[f]	Ocean Color Data[d]
Poseidon 377	Waniek et al. (2009a)	Waniek et al. (2009a)
Poseidon 383	Waniek et al. (2009b)	Waniek et al. (2009b) Ocean Color Data[d]
Poseidon 384	Christiansen (2009)	Christiansen (2009)
Iberia-Forams	Voelker et al. (2015)	Voelker (2012)

[a] Station EBC. [b] stations ESTOC and LP. [c] MODIS-Aqua data from 2003 to 2013. [d] MODIS-Aqua data for the exact position and day of sampling. [e] Station 1329.

could not be derived from the satellite observations. Therefore, mean monthly chlorophyll *a* data from 2003 to 2013 (MODIS-Aqua, NASA's Ocean Color Web database) were used (Table 2).

Although for each station, data on the abundance vertical profile for each species are available, the variable vertical resolution among the stations makes a common analysis prone to bias. Therefore, we have decided to reduce the information on the vertical distribution profile into a single robust parameter. Specifically, for each station and species, the depth distribution has been expressed as average living depth (ALD), calculated as the average of the mean depths of the sampling intervals where the species occurred weighted by the species concentration in those intervals (ind m^{-3}):

$$\mathrm{ALD} = \frac{\sum \mathrm{Ci} \times \mathrm{Di}}{\sum \mathrm{Ci}},$$

where Di denotes a depth interval and Ci is concentration of a species in that depth interval. ALD was only determined at stations where at least five individuals of a given species were counted. The vertical dispersion (VD) of the population around the ALD was determined as the mean distance of the population from the ALD (Fig. 4):

$$\mathrm{VD} = \frac{\sum (|\mathrm{ALD} - \mathrm{Di}| \times \mathrm{Ci})}{\sum \mathrm{Ci}}.$$

The 95 % confidence intervals of ALD and VD were calculated for each species based on the corresponding standard error and assuming a normal distribution.

For species where ALD values varied, the predictability of the ALD under given environmental parameters was assessed using a generalized linear model (GLM). We used GLM since it is a flexible ordinary linear regression method that allows for non-normally distributed responses and has the option of using a link function. In contrast to a simple individual regression that considers the explanatory variables together, a GLM allows one to identify the most important explanatory variables with the limitation of assuming that the observations are uncorrelated. In our case, the ALD was linked to the environmental variables of mixed layer (ML) depth, TML or chlorophyll *a* concentration in the ML (CML) using a logarithmic function. ML depth was tested because it is presumed that (a) the deeper the ML depth the deeper the ALD or (b) if there are species that have a habitat that is independent of the ML depth (straddles the ML or live below), then the stronger the stratification (thin ML) the more stratified the habitat of the species. Further, we tested TML as a factor because in regions with a warmer ML the potentially warmer subsurface and thus reduced stratification might affect a species' ALD. In the case of the CML, we assume that higher productivity brings symbiont-bearing species closer to the surface because of light limitation, whilst it allows deeper-dwelling species to live deeper because more food will be arriving below the photic zone. For the GLM, only samples for which all three variables from in situ measurements are available were included in the analysis (Table 3).

In addition, we explored the possibility that the depth habitat of planktonic foraminifera species reflects ambient conditions at the ALD and not only the state of the ML. Assuming that species abundance is strongly linked to temperature changes, we extracted temperature at the ALD for species. Further, we also calculated the seawater density at the ALD from CTD profiles. To test if some species show more variance in their temperature or seawater density at ALD than others, we used a Levene's test (test for equality of variances; Levene, 1960). In addition, we analyzed the relationship between ALD and temperature/density at ALD by plotting their interquartile range against the interquartile range of ALD expressed as a percentage of the mean ALD. This was done for all the species, except *P. obliquiloculata* since the few stations where this species was present include the Canary stations, from which we do not have in situ CTD data for all stations. A similar test could not be performed for chlorophyll *a* concentration, since vertical profiles of this parameter are not available at most of the studied stations (Table 2).

The existence of vertical migration of a species during a seasonal and lunar cycle was tested using a periodic regression. For that, the date of sample collection was transformed to day of year (365 days) regarding seasonality and lunar day for the lunar cycle (29.5 days) (Table 1). Both circular variables were converted to phase angles and the significance of a multiple regression of the sine and cosine of the phase angle with the logarithm of ALD was determined (Bell, 2008).

4 Results

To analyze the habitat depth of planktonic foraminifera species in the eastern North Atlantic region, species abundances were determined in a total of 43 vertically resolved plankton net hauls. The counts are provided in the elec-

Table 3. Analysis of the influence of time of collection and environmental parameters at the time of collection on the average living depth of 17 species with variable vertical habitat (Fig. 6). Shown is variance explained by the model (periodic regression or GLM) and significance of the tested parameters.

				Yearly cycle			Monthly cycle			Predictability by environmental conditions, GLM						
											p of individual parameters					
Species	*N*	ALD	SD ALD	R^2	*p*	Day of year	R^2	*p*	Lunar day		MLD		TML		CML	
		(m)	(m)			of max ALD			of max ALD	Pseudo- R^2	DC	*p*	DC	*p*	DC	*p*
G. falconensis	15	92.9	53.4	0.07	0.64		0.29	0.13		0.28		0.16		0.25		0.42
G. siphonifera	24	83.8	36.0	0.10	0.34		0.02	0.82		0.16		0.12		0.50		0.14
G. bulloides	29	102.3	58.1	0.04	0.55		0.03	0.63		0.07		0.65		0.35		0.55
G. inflata	21	104.4	46.5	0.20	0.12		0.14	0.27		0.02		0.64		0.74		0.69
G. ruber white	36	57.8	18.4	0.02	0.69		0.00	0.95		0.06		0.69		0.67		0.67
T. quinqueloba	17	143.9	82.3	0.19	0.23		0.30	0.08		0.21		0.09		0.73		0.70
G. scitula	25	224.3	95.9	0.41	0.00	168	0.06	0.49		0.14		0.20		0.16		0.72
T. parkerae	14	137.3	70.7	0.49	0.02	259	0.26	0.18		0.62		0.36		0.05	–	0.02
N. incompta	24	80.9	40.1	0.36	0.01	195	0.06	0.55		0.27		0.10		0.87		0.49
G. hirsuta	16	176.5	120.4	0.79	0.00	192	0.27	0.13		0.42	–	0.00		0.07		0.92
G. truncatulinoides	20	96.3	51.2	0.71	0.00	174	0.48	0.00	23	0.35	–	0.01	–	0.01		0.94
G. glutinata	39	78.6	43.4	0.18	0.03	156	0.30	0.00	25	0.36	–	0.00	–	0.00		0.55
T. sacculifer	30	60.7	45.0	0.27	0.01	141	0.28	0.01	25	0.50	–	0.00	–	0.00		0.88
G. calida	18	73.3	22.8	0.26	0.10		0.10	0.46		0.61		0.21	+	0.00		0.66
G. rubescens	22	107.4	74.6	0.17	0.18		0.01	0.91		0.22		0.79	+	0.03		0.26
T. humilis	15	92.0	58.4	0.33	0.09		0.27	0.15		0.51	–	0.00		0.26		0.06
G. tenellus	12	52.2	19.3	0.22	0.32		0.04	0.81		0.36	+	0.02	–	0.04		0.88

N is number of occurrences. ALD is average living depth. max is maximum. *p* is *p* value. R^2 is coefficient of determination of the periodic regression. GLM is generalized linear model. MLD is mixed layer depth. TML is temperature mixed layer. CML is chlorophyll mixed layer. DC is direction of the correlation. Pseudo-$R^2 = 1 - [rd/nd]$ with rd = residual deviance and nd = null deviance.

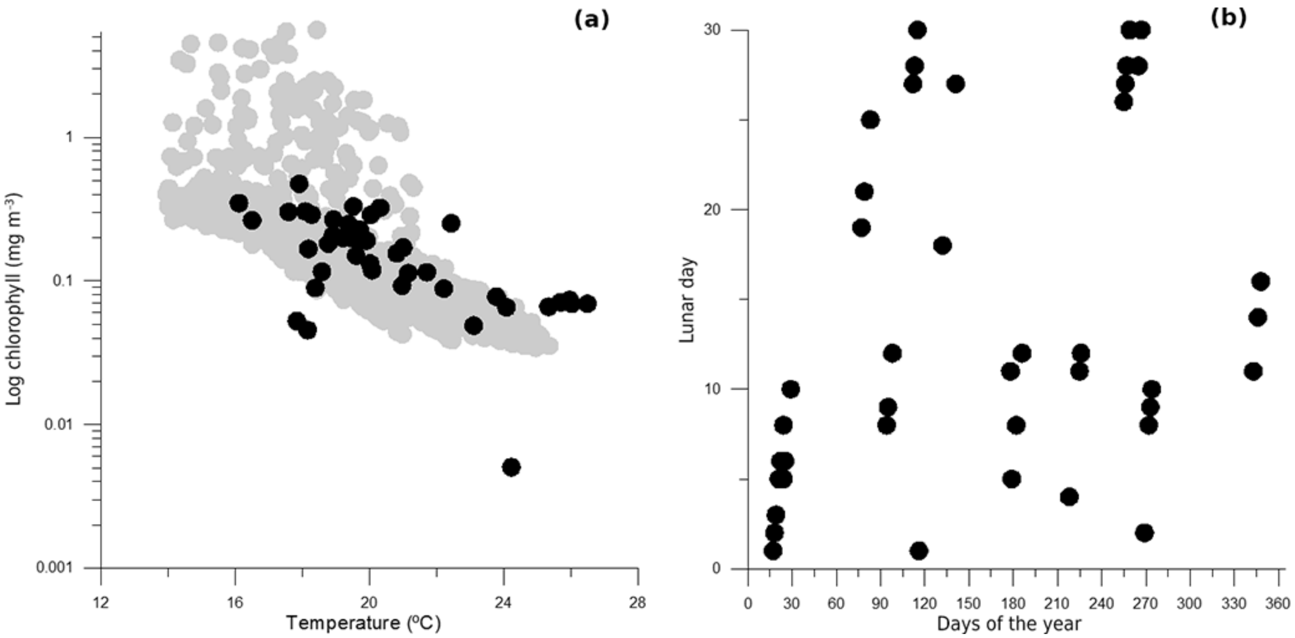


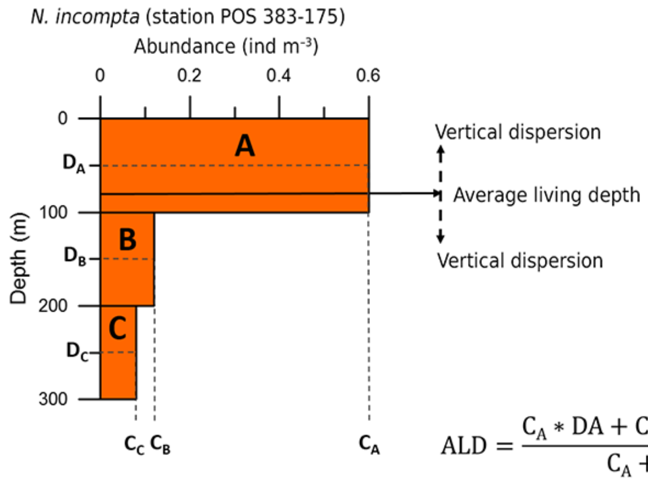
Figure 3. Coverage of the ecological space of planktonic foraminifera in the studied region by the sampled stations. **(a)** Gray symbols show the covariance between mean monthly SST (sea-surface temperature) (MIMOC: Monthly Isopycnal/Mixed-layer Ocean Climatology; Schmidtko et al., 2013) and chlorophyll (MODIS-Aqua 2003–2013 Data, NASA) concentration for every grid at 2° × 2° resolution in the studied region (Fig. 1). Dark symbols show the in situ values for the two parameters at the time of sampling for the studied plankton net stations. **(b)** Seasonal coverage of the lunar cycle by the studied sampling stations.

tronic supplement and all the data will be available online through www.pangaea.de. The total of 39 203 counted individuals could be attributed to 34 species. The stations included in the analysis cover a large portion of the environmental gradients in the studied region (Figs. 2, 3). However, our sampling does not cover the cold end of the temperature range, represented by the winter situation north of the Azores Front and we have no samples representing the most intense coastal upwelling characterized by chlorophyll *a* values above 0.6 mg m^{-3} (Fig. 3). The cruises occurred scattered with respect to season and lunar day, and all combinations of these parameters are represented in the data (Fig. 3).

An inspection of the data set reveals that we observe distinct vertical distribution patterns with most of the species showing unimodal distribution that can be expressed effectively by the ALD and VD concepts (Fig. 4). Next to clear differences among species, we see evidence for strong changes in ALD within species, which may reflect seasonal shifts, environmental forcing or ontogenetic migration with lunar periodicity (Fig. 5).

4.1 Absolute abundance and vertical distribution of living foraminifera

Due to different oceanographic settings in the studied area, three distinct regions were considered to present the absolute abundances and vertical distribution of living foraminifera. Because only selected species have been quantified at 14 of the studied stations, only data from 29 stations can be used to analyze the standing stock of total planktonic foraminifera and their vertical distribution (Fig. 6). At those stations, in the 0 to 100 m sampling interval, the abundance of living planktonic foraminifera ranged from less than 1 ind m^3 to 486 ind m^3 (Fig. S1 in the Supplement). The highest abundance was observed at stations close to the Canary Islands (stations EBC: Eastern Boundary Canary and ESTOC: European Station for Time-series in the Ocean) during winter. Numbers increase only slightly when the entire population in the water column down to 800 m is considered (1 to 517 ind m^3), indicating that at most stations the living specimens occupied the surface layer. Indeed, the ratio of population size between 0 and 100 and > 100 m was well above 1 at 18 stations reaching up to a ratio of 22 (Fig. 6). The highest ratios coincide with highest total abundance, whereas ratios below 1, indicating a higher abundance deeper than 100 m, were recorded at stations with the lowest total abundance of foraminifera and representing the oligotrophic summer conditions in the Canary Islands region. The standing stock of foraminifera seems to be higher in samples with lower temperature and higher productivity, but the highest standing stocks were observed at intermediate values of both parameters in stations in the Canary Islands region and along the Iberian Margin (Fig. 6). The vertical partitioning of the population also shows a pattern, with low ratios indicating sim-



$$\mathrm{ALD} = \frac{C_A * DA + CB * DB + CC * DC}{C_A + CB + CC} = 85.00\ \mathrm{m}$$

$$\mathrm{VD} = \frac{C_A|D_A - \mathrm{ALD}| + CB|D_B - \mathrm{ALD}| + CC|D_C - \mathrm{ALD}|}{C_A + CB + CC} = 52.5\ \mathrm{m}$$

Figure 4. An example of a vertical distribution of live specimens of *Neogloboquadrina incompta* in the upper three sampling intervals (indicated as A, B and C) of station POS 383-175. The diagram is used to illustrate how the vertical habitat of a species is expressed by average living depth (ALD), calculated as the average of the sampling depths (D_A, D_B and D_C) weighted by the abundance concentration at these depths (C_A, C_B and C_C), and vertical dispersion (VD), calculated as the mean distance of the population from the ALD.

ilar abundances deeper and shallower than 100 m typically associated with low temperatures (Fig. 6).

4.2 Vertical distribution of planktonic foraminifera species

Of the 34 species recorded, 28 occurred in sufficient abundance to allow for the quantification of their habitat depth with confidence (Table 4, Fig. 7). The results confirm the existence of large differences in depth habitat among the studied species, with species' mean ALD varying from less than 50 m to almost 300 m (Table 4). We also observe a considerable range of ALD values within species. Some species, such as *T. sacculifer*, *G. hirsuta* and *G. rubescens*, show a widespread in the observed ALD values, whereas species like *G. ruber* pink and *T. iota* show a more restricted ALD range, in relation to their ALD median (50 % of the ALD). When ranked by their arithmetic mean ALD, the species seem to display three depth habitat preferences (Fig. 7):

1. Apparent surface dwellers show narrow ALD ranges. These species appear to be consistently concentrated in the surface layer and the majority of their observed ALD values is < 50 m. These species include *G. ruber* pink and white, *G. tenellus*, *P. obliquiloculata*, *G. crassaformis* and *T. sacculifer.*

2. Surface to subsurface dwellers show a broader range of ALD values, with most of their observed ALD values being between 100 and 50 m. These species include *O. universa*, *T. fleisheri*, *G. calida*, *N. incompta*, *G. glutinata*, *N. dutertrei*, *G. rubescens*, *G. siphonifera*, *T. humilis*, *G. inflata*, *G. bulloides*, *G. falconensis* and *N. pachyderma*.

3. Subsurface dwellers also exhibit a large range of ALD values, but most of their observed ALD values are > 100 m. These species include *B. pumilio*, *T. parkerae*, *T. quinqueloba*, *H. pelagica*, *G. hirsuta*, *T. clarkei*, *G. scitula* and *T. iota*.

Higher values of ALD seem to be associated with higher VD of the population, resulting in a positive correlation between mean ALD of a species and its mean VD (Fig. 8). This pattern may be caused by an uneven vertical sampling resolution in the surface and subsurface layers, but most likely reflects the lognormal property of depth as a variable with a bounding value of 0 m. However, there is a distinct reversal in the relationship between mean ALD and mean VD such that the deepest dwelling species are characterized by smaller vertical dispersion than expected, and *T. iota*, having the deepest ALD, shows a smaller VD than many surface species (Fig. 8). Overall, the plot of species ALD and VD values shows three different patterns: species with the shallowest ALD and lowest VD (surface dwellers), species having the deepest ALD as well as the highest VD values (except for *T. iota*) (subsurface dwellers) and species that have intermediate ALD and VD values (surface to subsurface dwellers).

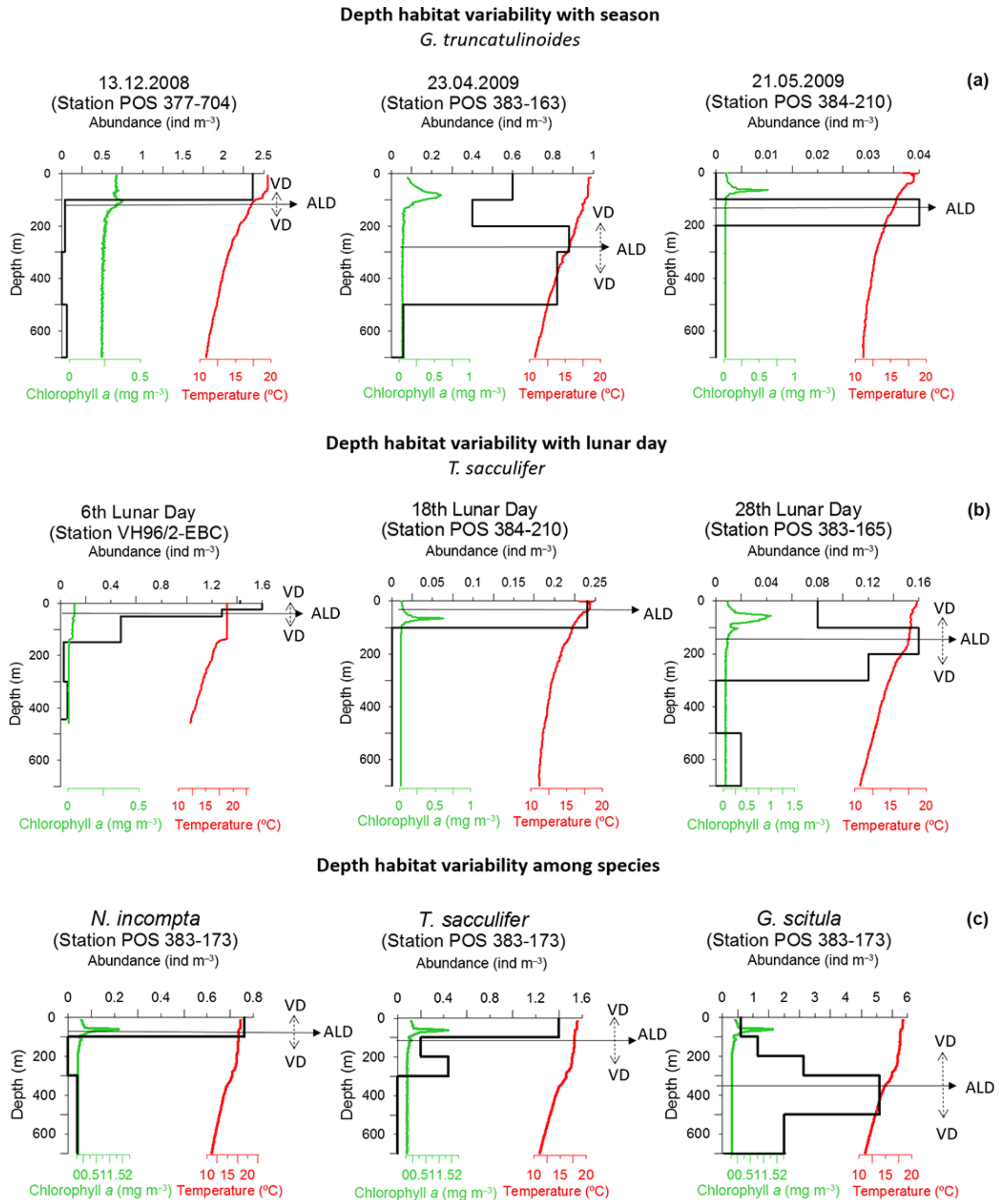


Figure 5. Examples of potential environmental parameters affecting vertical habitat of planktonic foraminifera in the studied region. **(a)** Vertical distribution of one species in the Azores region at different times of the year, showing apparent changes in ALD with season. Also plotted is the in situ temperature and chlorophyll *a* concentration (where available). **(b)** Vertical distribution of one species in the Azores region sampled at different times of the lunar cycle, showing apparent changes in ALD with lunar phase. **(c)** Vertical distribution of three species at the same station, showing different vertical habitats.

4.3 Environmental factors controlling vertical distribution

Of the 28 species analyzed, four species exhibit a stable vertical habitat with a small range of ALD values (*G. ruber* pink, *O. universa*, *H. pelagica*, and *T. iota*) and seven species with variable depth habitat were represented by too few cases (Table 4). In the remaining 17 species, potential factors affecting the ALD variability among stations were analyzed. The influence of ontogenetic migration in association with a yearly or lunar reproduction on the ALD was assessed using a periodic regression and the effect of TML, MLD and CML was tested using a GLM (Table 3).

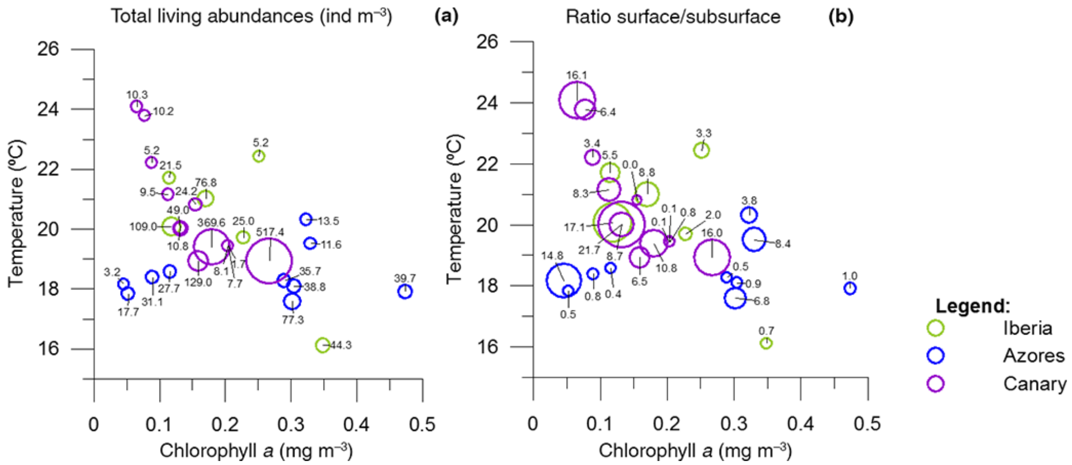


Figure 6. Total abundance given by circles size in the three regions from the study area of **(a)** living planktonic foraminifera and **(b)** the partitioning of the living population between surface and subsurface at the studied stations (Fig. 1) as a function of in situ mixed-layer interval mean temperature and mixed-layer interval mean chlorophyll *a* concentration. Samples from cruises M42/3, POS247/2, POS231/1 (Table 1) were not used, since only some species were counted in these samples and total living planktonic foraminifera abundances are not available. The depth partitioning of the population was calculated as the ratio of living planktonic foraminifera in the top 100 m (or 150 m where finer resolution was not available) and below.

The periodic regression analysis reveals that *G. scitula*, *T. parkerae*, *N. incompta*, *G. hirsuta*, *G. truncatulinoides*, *G. glutinata* and *T. sacculifer* exhibit apparent seasonal cycle in their ALD. Most of the species show the deepest ALD in May–July with the exception of *T. parkerae* that reveals the deepest ALD in September. The seasonal signal is strongest in *G. truncatulinoides*, where it explains > 70 % of the variance (Table 3). In addition to the yearly cycle, *G. truncatulinoides*, *G. glutinata* and *T. sacculiffer* show a significant apparent lunar cycle in their ALD, all reaching the deepest ALD around new moon. However, we note that only in *G. glutinata* and *T. sacculifer* the lunar model explains more variability than the annual model (Table 3; Fig. 9).

Besides showing significance towards the yearly or lunar cycle or both, the GLM analysis reveals that the ALD of *G. hirsuta*, *G. truncatulinoides*, *G. glutinata* and *T. sacculifer* exhibits a negative correlation with MLD, whereas the latter three also show significant relationship with temperature in the ML (Table 3; Fig. 9). No periodic signal in habitat depth was found for *T. humilis*, *G. calida*, *G. rubescens* and *G. tenellus*, but the values of these species are significantly correlated to other environmental parameters. While the ALD of *T. humilis* correlates negatively with MLD, *G. calida* and *G. rubescens* exhibit a positive relationship between ALD and the temperature in the ML and *G. tenellus* shows weak correlation between ALD and both MLD and temperature in the ML (Table 3; Fig. 9). Finally, *T. parkerae* is the only species that displays a relationship between ALD and chlorophyll *a* in the ML (Table 3; Fig. 9). In contrast, to the before mentioned species, the ALD variability of *G. falconensis*, *G. siphonifera*, *G. bulloides*, *G. inflata*, *G. ruber* white and *T. quinqueloba* does not appear to be predictable by any of the tested environmental parameters nor does it appear to vary in response to either of the tested cycles (Table 3; Fig. S2).

In order to assess if the vertical distribution of the analyzed species reflects in situ temperature or if the species are following a specific density surface, we compiled data on in situ temperature and density at ALD of each species at all stations with sufficient data (Fig. 10, Table 4). Levene's tests revealed significance differences among species with respect to the variance of in situ temperature at ALD ($p = 0.04$) and in situ seawater density at ALD ($p = 0.00$). Species like *G. tenellus* and *G. scitula* show a small range of temperature at ALD, whereas *G. ruber* pink and *O. universa* show a broad range of temperatures in their preferred depth habitat (Fig. 10). Regarding seawater density at ALD, *G. siphonifera* and *T. humilis* exhibit a narrow range, in contrast with *G. ruber* pink and *T. quinqueloba* that have a wider spread.

To assess whether variability of ALD reflects the adjustment of the habitat of a given species to a narrow range of in situ temperature or seawater density, the interquartile range of in situ temperature at ALD and in situ seawater density at ALD were compared with interquartile range of ALD (Table 5; Fig. 10). Species showing a large range of ALD but a small range of either of the in situ parameters can be considered to adjust their ALD to track a specific habitat. First, we note that the behavior of the studied species with respect to in situ temperature at ALD and in situ seawater density at ALD differs, with most species showing a large range in temperature than seawater density (Fig. 10). Second, we note that the variability of environmental parameters at ALD appears not related to depth habitat (Fig. 10).

Table 4. The 34 species found within the 43 counted stations are listed below sorted by the number of occurrences within the samples, including concentrations lower than 5 ind m^{-3} per station, stations where the maximum abundance were observed, average ALD and VD, interpretation of each species depth habitat and its corresponding variability or stability.

Species (34)	*N*	Maximum abundance within stations (ind m^{-3})	ALD (m)	ALD standard error 95 % confidence (m)	Average VD (m)	VD standard error 95 % confidence (m)	Depth habitat	Depth habitat variability
Globigerinita glutinata	42	75.90[b]	78.62	13.63	57.79	11.42	Surface–subsurface	Variable
Globigerinoides ruber white	40	21.31[b]	57.84	6.00	35.04	9.05	Surface	Variable
Globigerina bulloides	40	23.08[c]	102.35	21.14	67.38	10.93	Surface–subsurface	Variable
Trilobatus sacculifer	39	68.54[e]	60.71	16.10	35.45	10.18	Surface	Variable
Globigerinella siphonifera	38	1.52[f]	83.78	14.41	42.29	11.91	Surface–subsurface	Variable
Globorotalia scitula	37	13.04[k]	224.28	37.58	85.30	19.16	Subsurface	Variable
Turborotalita quinqueloba	34	14.46[g]	143.90	39.14	69.72	20.53	Subsurface	Variable
Globoturborotalita rubescens	34	52.73[b]	107.41	31.19	79.85	27.61	Surface–subsurface	Variable
Globorotalia inflata	33	2.44[c]	104.35	19.90	61.52	10.73	Surface–subsurface	Variable
Globorotalia. truncatulinoides	32	19.70[a]	96.36	22.42	64.67	11.48	Surface–subsurface	Variable
Globorotalia hirsuta	27	6.40[g]	167.24	58.25	79.60	27.08	Subsurface	Variable
Globigerinoides ruber pink	27	5.84[c]	39.51	5.24	24.09	6.60	Surface	Stable
Globigerinella calida	27	9.48[g]	73.33	10.55	47.60	11.00	Surface–subsurface	Variable
Turborotalita humilis	25	203.8[g]	91.98	29.55	56.83	23.81	Surface–subsurface	Variable
Orbulina universa	24	1.70[e]	79.00	13.75	40.39	13.09	Surface–subsurface	Stable
Neogloboquadrina incompta	24	70.04[a]	80.93	16.05	50.32	11.57	Surface–subsurface	Variable
Hastigerina pelagica	23	0.28[i]	202.45	45.48	112.50	24.57	Subsurface	Stable
Globigerina falconensis	21	26.94[a]	92.92	27.01	57.67	21.46	Surface–subsurface	Variable
Tenuitella parkerae	19	0.80[j]	137.28	37.05	89.15	22.19	Subsurface	Variable
Neogloboquadrina pachyderma	18	1.37[h]	113.35	50.88	44.42	23.82	Surface–subsurface	*
Globigerinoides tenellus	16	0.32[a]	52.16	10.90	35.46	7.25	Surface	Variable
Berggrenia pumillio	13	6.87[h]	137.61	66.07	77.57	39.11	Subsurface	*
Pulleniatina obliquiloculata	11	29.87[a]	44.51	13.16	30.99	8.37	Surface	*
Neogloboquadrina dutertrei	11	6.00[a]	62.69	22.06	22.78	6.40	Surface	*
Tenuitella fleisheri	9	1.01[h]	81.14	24.80	44.60	23.76	Surface–subsurface	*
Globorotalia crassaformis	9	0.6[d]	48.33	14.85	15.52	13.35	Surface	*
Tenuitella iota	7	3.96[g]	276.81	32.46	49.68	20.78	Subsurface	Stable
Globigerinita minuta	6	0.46[n]	14.71	0.00	9.23	0.00	*	*
Dentigloborotalia anfracta	5	5.44[a]	12.50	0.00	0.00	0.00	*	*
Turborotalita clarkei	4	1.44[h]	217.98	117.32	70.27	2.43	Subsurface	*
Hastigerinella digitata	2	0.08[l]	*	*	*	*	*	*
Globorotalia menardii	2	0.02[m]	*	*	*	*	*	*
Globigerinita uvula	1	0.08[a]	*	*	*	*	*	*
Beella digitata	1	0.11[b]	*	*	*	*	*	*

N is number of occurrences. ALD is average living depth. VD is vertical dispersion. * Not enough data to analyze a – VH 96/2-ESTOC, b – VH 96/2-EBC, c – POS 212/1-EBC, d – Ib-F 8, e – Ib-F 6, f – POS 383-175, g – POS 334-67, h – POS 334-72, i – POS 383-161, j – POS 383-161, k – POS 383-163, l – POS 212/1-LP, m – M 42/1-EBC, n – POS 247-1380.

5 Discussion

In terms of species composition, the assemblages that were observed in the current study are comparable to the fauna reported in previous studies from the eastern North Atlantic (e.g., Bé and Hamlin, 1967; Cifelli and Bénier, 1976; Ottens, 1992; Schiebel and Hemleben, 2000; Storz et al., 2009). An exception is given by the here consistently reported occurrences of the smaller species like *T. clarkei*, *T. parkerae*, *T. fleisheri*, *T. iota* and *B. pumilio*. These species are typically smaller than 150 µm and, because the fraction < 150 µm is usually not considered in paleoceanographic studies CLIMAP Project Members, 1976), only a few observations on their distribution in the plankton exist (e.g., Peeters et al., 2002; Schiebel et al., 2002b). The observed total standing stocks and the tendency of higher abundance towards the surface (Fig. 6) also compare well with values reported in previous studies from similar settings (e.g., Schiebel et al., 2002b; Watkins et al., 1998). The analysis of the vertical distribution revealed that some species consistently inhabit a narrow depth habitat either at the surface or below, whereas other species showed considerable variation in their ALD among the stations (Fig. 7). If the depth habi-

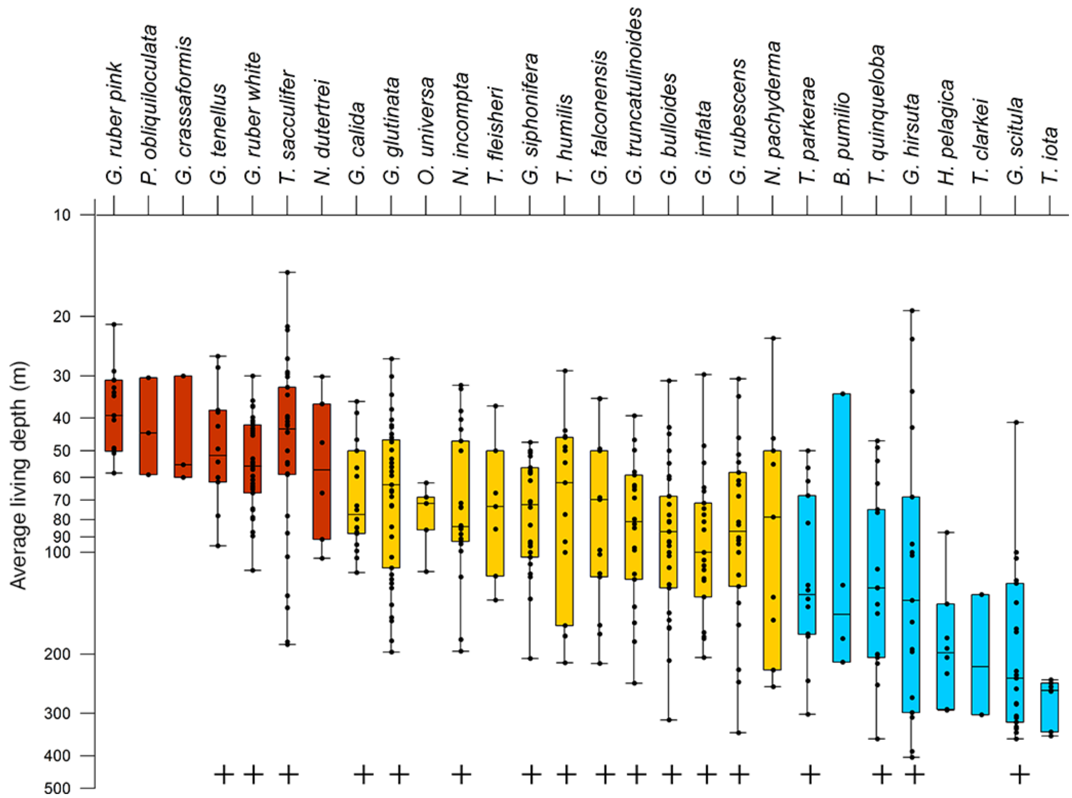


Figure 7. Average living depths of the 28 most abundant species of planktonic foraminifera obtained from analysis of 43 vertically resolved plankton hauls (Fig. 1, Table 1). Values are only shown for stations where at least five individuals of a given species have been counted. The box and whiskers plots are highlighting the median and the upper and lower quartiles. The species are ordered according to their mean ALD. Dots represent individual observations. Colors are used to highlight species with similar depth preferences; changes in color coding reflect large and consistent shifts in ALD. Crosses underneath the box plots indicate species with variable living depth and sufficient number of observations, such that they could be included in an analysis of factors controlling their living depth.

tat of the studied species would be determined by processes like rapid (diel) vertical migration or water column mixing or differential horizontal advection, we should not observe such differentiated depth habitats among the species. Therefore, we conclude that the patterns we observe likely reflect differences in the primary habitat depth and/or differences in ontogenetic and seasonal migration.

Nevertheless, when considering observations on habitat depth of planktonic foraminifera from plankton tows one has to consider potential sources of bias. The main uncertainty derives from the identification of living cells by the presence of cytoplasm. This causes a bias towards greater ALD, because dead cells with cytoplasm sinking down the water column still appear as living and their occurrence will shift ALD to greater depth. This means that all ALD values likely have a bias towards deeper ALD, which is largest for species where only a few specimens were found. However, the magnitude of the ALD overestimation via this effect is likely small since maximum mortality among the juvenile specimens likely occurs in size classes smaller than the mesh size used in this study. Second, the ALD estimates are affected by unequal sampling intervals and unequal maximum sampling depths among the stations (Table 1). Uneven sampling intervals will increase the noise in the data, whereas uneven maximum sampling depths will cause an underestimation of the ALD of deep-dwelling species at stations with shallower sampling. In addition, plankton tows only represent a snapshot in time and space of the pelagic community, and the data we present are affected by low counts for some of the species. Whilst these factors should not overprint the main ecologically relevant signal in the data, they likely contribute to the scatter in the data, affecting the predictive power of our statistical tests.

5.1 Standing stock of living planktonic foraminifera

The pattern of standing stocks of planktonic foraminifera (Fig. 6) can be best explained when the geographical position of the samples is considered. The highest and lowest abundances of living planktonic foraminifera among all the studied samples were recorded in the same region off the northwestern African coast and the Canary Islands. The highest abundances were observed in the nearshore station (EBC) in

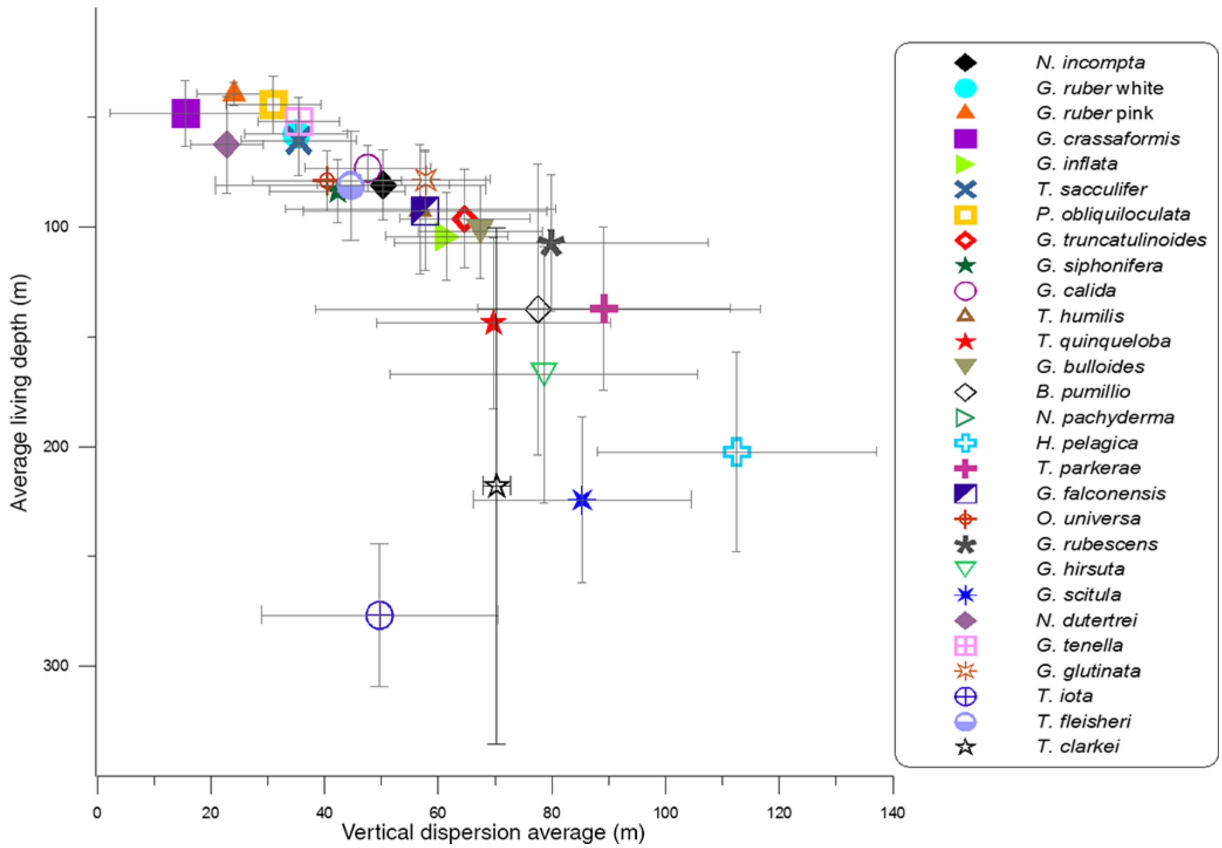


Figure 8. Relationship between the mean ALD and the mean vertical dispersion of the habitat of the 28 most abundant species of planktonic foraminifera analyzed in this study. Symbols are showing mean values, bars indicate 95 % confidence intervals and colored ellipses are used to highlight species with similar depth preferences (see Fig. 7).

winter, whereas the lowest standing stocks were recorded at all three stations in the area (EBC, ESTOC and La Palma) during spring and early summer (Fig. 6). The same samples were previously analyzed by Meggers et al. (2002) and Wilke et al. (2009), who attributed this pattern to the influence of eutrophic waters from the upwelling (Santos et al., 2005). Even though the EBC station is located outside of the upwelling zone, it is influenced by the Cape Yubi's upwelling filament (Parilla, 1999).

In addition to the seasonal upwelling in the Canary Islands region, wind-driven deep vertical mixing occurs in winter, resulting in an increase of nutrients in the euphotic zone and consequently an increase in productivity (Neuer et al., 2002). Therefore, the flux of planktonic foraminifera in EBC station shows a bimodal seasonal pattern with maxima in winter (mixing) and summer/autumn (upwelling) (Abrantes et al., 2002). This bimodal pattern is reflected in our observations, which cover all seasons in this station, showing high-standing stocks during winter (mixing) and autumn (upwelling). In winter the fauna is more diverse with high occurrences of *N. incompta*, *G. ruber* white, *P. obliquiloculata*, *G. truncatulinoides*, *G. glutinata*, *T. humilis*, *T. quinqueloba*, *G. falconensis*, *N. dutertrei* and *G. rubescens*, whereas in the autumn the fauna is dominated almost exclusively by *G. ruber* pink and white, *G. glutinata* and *G. bulloides*.

The highest standing stock values recorded in this region do not necessarily correspond to the highest chlorophyll *a* concentrations among the studied stations (Fig. 6). This could reflect the lack of CTD measurements for some of the Canary Islands stations or indicate that the abundances are not exclusively related to chlorophyll *a* concentrations. Alternatively, it could represent a small temporal delay between phytoplankton and zooplankton bloom, caused by different rates of reproduction in these groups (Mann and Lazier, 2013). Schiebel et al. (2004) made a similar observation in the Arabian Sea, attributing it to a decline of symbiont-bearing species caused by increased turbidity and consequent decrease in light in the upwelling center. This observation agrees with the great reduction in the faunal diversity observed in our samples from the Canary Islands stations during fall.

The second highest standing stocks of planktonic foraminifera were observed in the Iberian region at stations Ib-F 6 and Ib-F 12, where hydrographic data indicate a situation with warm water, strong stratification and intermediate chlorophyll *a* concentration. Although no upwelling

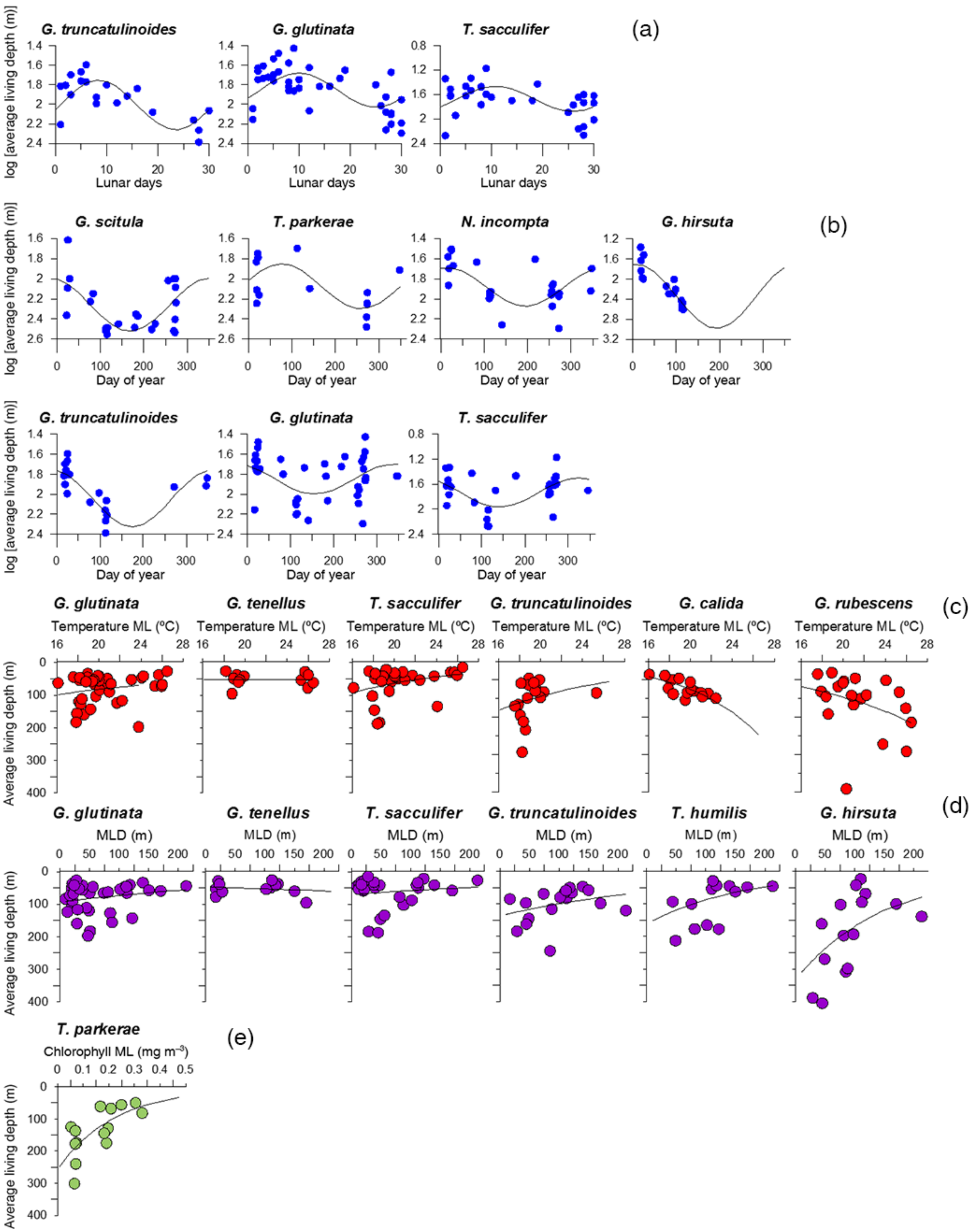


Figure 9. Comparison of modeled and observed ALD in species where ALD appears to be predictable ($p < 0.05$, Table 3) by **(a)** lunar cycle, **(b)** yearly cycle, **(c)** mean temperature in the mixed layer interval, **(d)** mixed layer depth and **(e)** mean chlorophyll *a* concentration in the mixed layer interval.

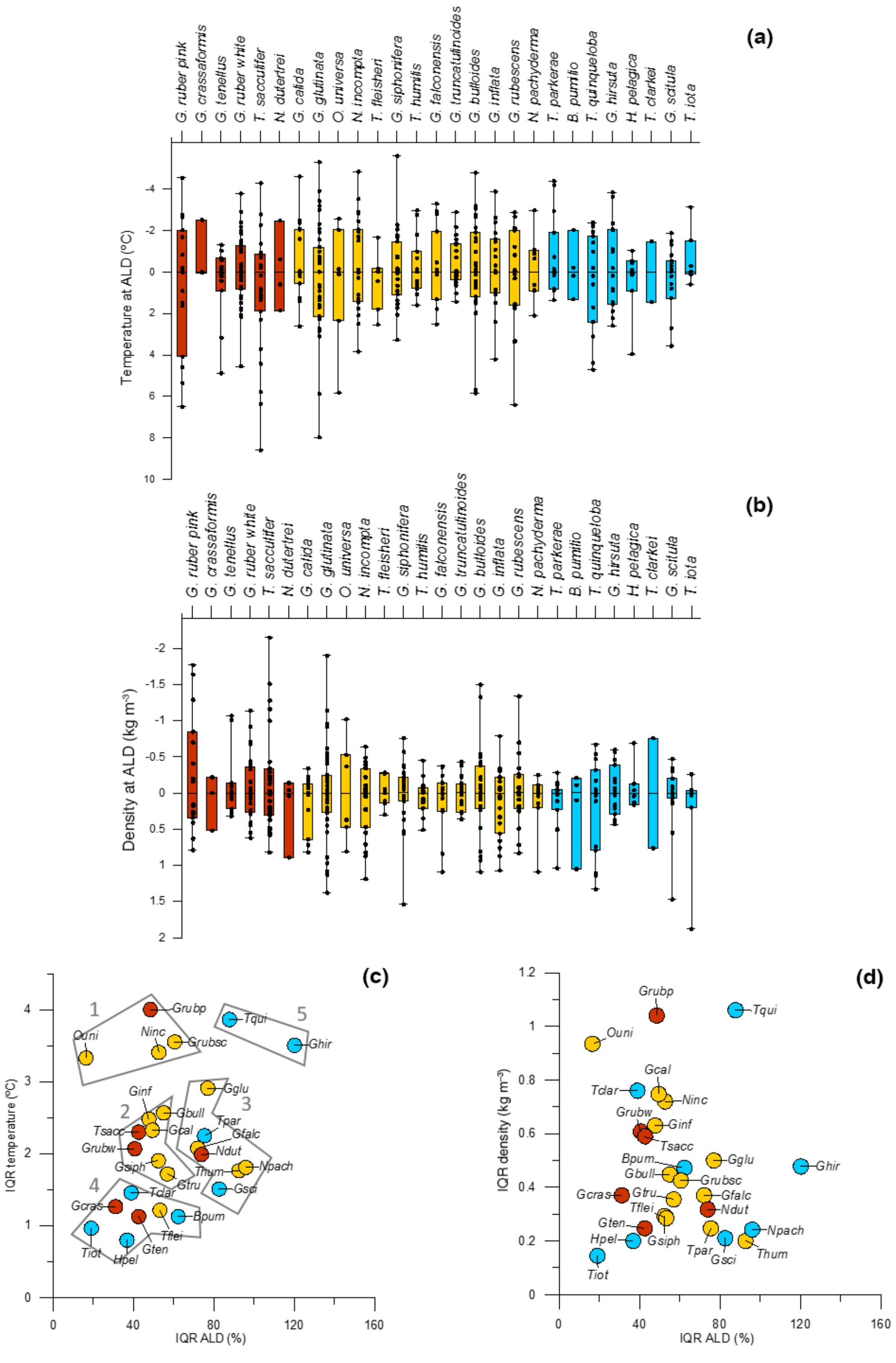


Figure 10. **(a)** Average temperature (°C) at ALD and **(b)** average seawater density (kg m^{-3}) at ALD for the 27 most abundant species normalized to the median value for each species and **(c)** relationship between the interquartile range of temperature (°C) at ALD (kg m^{-3}) and interquartile range of ALD expressed as percentage of mean ALD for each species, whereas the group numbers stand for 1 – species showing a large spread in temperature at the ALD (average living depth) but a small relative ALD range; 2 – species showing an intermediate spread in T_{ALD} and narrow relative ALD range; 3 – species with intermediate T_{ALD} range and variable relative ALD; 4 – species with narrow T_{ALD} and narrow relative ALD; 5 – species with variable T_{ALD} and variable ALD and **(d)** the same for seawater density at ALD. The species are ordered by their mean ALD mean and colored according to their habitat depth preferences (Fig. 7). Dots represent individual observations. Only species with sufficient number of observations are shown.

Table 5. Seawater density and temperature at ALD and respective variance for the 28 most abundant species. The abbreviations for each species are also shown.

Species	Species abbreviations	Density at ALD ($Kg\,m^{-3}$)	Temperature at ALD (°C)	Variance of density at ALD ($Kg\,m^{-3}$)	Variance of temperature at ALD (°C)
N. incompta	Ninc	1026.64	17.46	0.23	4.70
G. ruber white	Grubw	1026.23	19.01	0.17	2.76
G. ruber pink	Grubp	1025.82	20.55	0.59	9.41
G. inflata	Ginf	1026.79	16.59	0.21	3.41
G. crassaformis	Gcras	1026.64	17.22	0.10	1.40
T. sacculifer	Tsacc	1026.20	18.82	0.47	7.67
P. obliquiloculata	Pobli	1026.33	19.10	–	–
G. truncatulinoides	Gtru	1026.35	18.43	0.05	1.34
G. glutinata	Gglu	1026.35	18.42	0.41	6.75
G. siphonifera	Gsiph	1026.50	17.73	0.19	3.13
G. calida	Gcal	1026.71	17.15	0.14	3.10
T. humilis	Thum	1026.40	18.00	0.06	1.95
T. quinqueloba	Tqui	1026.96	16.38	0.42	5.52
T. iota	Tiot	1027.00	14.96	0.46	1.42
G. bulloides	Gbull	1026.52	17.63	0.32	5.42
B. pumillio	Bpum	1026.89	16.15	0.25	1.44
N. pachyderma	Npach	1026.70	16.88	0.15	2.16
H. pelagica	Hpel	1026.55	16.40	0.07	2.11
T. parkerae	Tpar	1026.53	17.31	0.11	3.29
G. falconensis	Gfalc	1026.67	17.35	0.17	3.07
T. fleisheri	Tflei	1026.47	18.19	0.04	1.63
O. universa	Ouni	1026.68	15.98	0.41	8.00
G. rubescens	Grubsc	1026.52	17.71	0.22	5.25
G. hirsuta	Ghir	1026.49	17.08	0.11	3.98
G. scitula	Gsci	1026.84	15.25	0.16	2.26
N. dutertrei	Ndut	1026.66	17.08	0.17	2.55
T. clarkei	Tclar	1027.63	14.16	0.58	2.12
G. tenellus	Gten	1025.92	19.96	0.19	2.97

event was observed in the week prior to and during the Iberia-Forams cruise in September 2012 (Voelker, 2012), the western Iberia upwelling typically occurs in late spring and summer (Wooster et al., 1976), with filaments of cold and nutrient-rich water that extend up to 200 km off the coast (Fiúza, 1983). Off Cape S. Vicente, at the southwestern extremity of Portugal, the upwelled waters often circulate eastward and flow parallel to the southern coast (Sousa and Bricaud, 1992), which could be a source of food at both stations and therefore a possible explanation for the high-standing stock of planktonic foraminifera.

Both the Gulf of Cadiz and the Canary Basin are influenced by the Azores Current (Klein and Siedler, 1989; Peliz et al., 2005). The Azores Current is associated with the Azores Front, where cold and more eutrophic waters from the north are separated from warmer and oligotrophic waters in the south. This front was crossed during the cruise POS 247/2 in 1999 and POS 383 in spring 2009, yet only for the second cruise standing stock data are available. The highest standing stock of planktonic foraminifera was observed in the northernmost station of POS 383 cruise. While this result was expected, since the waters in the north are more productive (Gould, 1985) as supported by the chlorophyll *a* measured at the site (0.3 mg m^{-3}), a second abundance maximum was observed in the southernmost station during this cruise. At this station, the mixed layer was substantially deeper, reaching to 88 m. According to Lévy et al. (2005), the deepening of the ML allows for the entrainment of nutrients, which agrees with the 0.5 mg m^{-3} measured at station 173, and therefore could explain the high abundance of planktonic foraminifera found in this subtropical gyre station.

The depth of the ML could also account for the differences in productivity and foraminifera standing stocks among the remaining stations in the region south of the Azores Front. In this region, the mixed layer deepens from late summer to February (100–150 m) and during March it shoals to 20–40 m and stratification evolves rapidly (Waniek et al., 2005). Consequently, in late summer, the primary production is very low. During autumn, the ML starts to deepen to 100–150 m between December and February along with an increase in primary productivity (Waniek et al., 2005). The model developed by Waniek et al. (2005) predicts higher phytoplankton concentrations and primary productivity at the surface between January and March, occasionally with early phytoplankton growth during December, which also agrees with Lévy et al. (2005). This supports the greater chlorophyll *a* concentrations and standing stocks of living planktonic foraminifera observed at station POS 334-69 in early spring (March) compared to the lower values at station POS 384-210 in May. In addition, there are many upwelling and downwelling cells associated to the Azores Current and Azores Front, which induce local changes in productivity and thereby planktonic foraminifera standing stocks (Schiebel et al., 2002b).

Overall, the highest standing stocks of planktonic foraminifera appear to coincide with higher chlorophyll *a* concentrations and lower temperatures, which are associated with a deeper mixed layer. According to our data, in the eastern North Atlantic either seasonal upwelling or deep vertical mixing in winter may stimulate productivity by entrainment of nutrients (Neuer et al., 2002; Waniek et al., 2005) resulting in a more even partitioning of the planktonic foraminifera standing stock shallower and deeper than 100 m. Both situations are associated with lower temperatures. Conversely, an uneven standing stock, with high concentration only at the surface (shallower than 100 m), appears to coincide with a more stratified water column, which usually occurs in summer when temperature is higher.

5.2 Habitat depth of individual species

5.2.1 Surface species

The species that were found to live consistently shallower than 100 m, with a median ALD between 40 and 60 m, were *G. ruber* pink and white, *G. tenellus*, *P. obliquiloculata*, *G. crassaformis*, *T. sacculifer* and *N. dutertrei* (Figs. 7, 8). Among these, *T. sacculifer*, both varieties of *G. ruber* and *N. dutertrei* are symbiont-bearing species (Gastrich, 1987; Hemleben et al., 1989), which could explain their consistent affinity towards the surface where light availability is greater. The existence of symbionts in *P. obliquiloculata* and *G. tenellus* is not well constrained and *G. crassaformis* is likely a non-symbiotic species.

The ALD of *G. ruber* pink was consistently shallower than 60 m, which agrees with Wilke et al. (2009), who observed the abundance maximum of this species in the upper 50 m near the Canary Islands during summer/autumn (warmer seasons). A surface layer habitat of this species is also consistently inferred from $\delta^{18}O$ of sedimentary specimens (e.g., Rohling et al., 2004; Chiessi et al., 2007). The white variety of *G. ruber* showed a typical ALD of 45 to 70 m, which agrees with previous studies in the eastern North Atlantic (Bé and Hamlin, 1967; Schiebel et al., 2002b) and in the tropical waters from the Panama Basin (Fairbanks et al., 1982). In the subtropical to tropical waters of the central equatorial Pacific and southeast Atlantic, *G. ruber* white occurred mostly in the upper 50–60 m (Kemle-von Mücke and Oberhänsli, 1999; Watkins et al., 1996), whereas in the temperate to subtropical waters from the seas around Japan it inhabited the upper 200 m (Kuroyanagi and Kawahata, 2004). Half of the observed ALD of *T. sacculifer* autumn in the interval from 30 to 60 m, which agrees well with a habitat in the upper 80 m described by Watkins et al. (1996). The ALD of this species varied between 15 and 200 m, which compares well with observations by Kuroyanagi and Kawahata (2004).

N. dutertrei showed an ALD interquartile range from 35 to 90 m, which corresponds well with the results from other plankton tow studies, where the species was found mostly in the upper 100 m (Fairbanks et al., 1982; Kemle-von Mücke and Oberhänsli, 1999; Watkins et al., 1996). In these studies, the typical depth habitat of the species has been associated with the thermocline. However, in our data, we observe the species mainly in the mixed layer. Among the stations where this species was abundant, CTD data are available for the Canary Islands station EBC visited in winter 1996. These data imply a mixed layer depth of 140 m, but all specimens of this species at that station were found in the top 50 m, meaning that this species was more abundant above the thermocline depth.

Peeters and Brummer (2002) observed *G. tenellus* mostly in the upper 50 m in the Arabian Sea, whereas in the Indian Ocean it was found in the upper 200 m of the water column (Duplessy et al., 1981). The interquartile range of the ALD between 40 and 60 m agrees well with the first study, but our data do suggest that this species inhabits a wider vertical range in agreement with Duplessy et al. (1981). *P. obliquiloculata* showed an ALD from 30 to 60 m, which is comparable to a habitat in the top 80 m and 126 m reported by Watkins et al. (1996) and Wilke et al. (2009), respectively. However, in our samples most of the specimens identified as *P. obliquiloculata* were juveniles, so that the observed depth range most likely reflects the habitat of the juveniles, whereas the adult habitat and the calcification depth could be different.

In the current study, the occurrence of *G. crassaformis* was shallower (ALD 30–60 m) than in previous studies in the eastern equatorial Atlantic and northern Caribbean where it was found deeper than 100 m down to 300 m (Bé and Hamlin, 1967; Kemle-von Mücke and Oberhänsli, 1999; Schmuker and Schiebel, 2002b). In agreement with our results, the species was observed between 25 and 50 m in the very particular hydrographic setting of the outer edge of the Angola-Benguela Front (Kemle-von Mücke and Oberhänsli, 1999), which is the boundary of two distinct water masses similarly to the Azores Front in our region where the higher abundances for this species were recorded. In general, *G. crassaformis* was rare at all stations, and more observations are thus needed to better constrain its habitat depth in this area.

5.2.2 Surface to subsurface species

Living typically between 50 and 200 m are the species *O. universa*, *T. fleisheri*, *G. calida*, *G. siphonifera*, *T. humilis*, *G. glutinata*, *G. falconensis*, *N. pachyderma*, *G. truncatulinoides*, *N. incompta*, *G. bulloides*, *G. rubescens* and *G. inflata* (Fig. 7). According to previous studies, *O. universa*, *G. siphonifera*, *G. glutinata*, *G. inflata* and *T. humilis* are considered to harbor algal symbionts, the latter three facultatively (Spero and Parker, 1985; Gastrich, 1987; Hemleben et al., 1989). Given their phylogenetic position, the presence of symbionts is likely in *G. calida* and *G. rubescens*. The depth habitat of these species should thus be largely limited to the euphotic zone. This is not necessarily at odds with our observation of a partly subsurface habitat of these species as in the studied region the euphotic zone can reach deeper than 100 m. Algal symbionts have not been reported in any of the other species of this group. The depth habitat of these species is thus independent of light availability.

Among the symbiont-bearing species, *O. universa* only occurred in low abundances; thus, it is hard to constrain its habitat and its variability precisely. Its ALD was mainly between 70 and 90 m, which is consistent with observations by Field (2004) in the eastern Pacific. Fairbanks et al. (1980) also indicated a surface to subsurface habitat of this species. *G. siphonifera* showed a typical ALD between 55 and 100 m, which agrees with Watkins et al. (1996) and Fairbanks et al. (1980). The ALD of *G. glutinata* was variable, ranging between 30 and 200 m, with most of the observations between 50 and 120 m. This agrees well with occurrence in the upper 200 m in a study performed in the seas around Japan (Kuroyanagi and Kawahata, 2004) and with the presence of *G. glutinata* deeper than 150 m in some of the sites studied in the southeast Atlantic (Kemle-von Mücke and Oberhänsli, 1999). In the eastern North Atlantic the species was observed shallower than 100 m (Schiebel et al., 2001), and in the central equatorial Pacific it was found between 0 and 120 m (Watkins et al., 1996). A variable depth habitat for this species is thus confirmed by observations from different regions. The species *G. inflata* and *T. humilis* also show a large variability in their ALD with values reaching well deeper than 100 m. Fairbanks et al. (1980) and van Raden et al. (2011) reported the highest abundances of *G. inflata* in the top 100 m, with a significant part of the population living deeper than this depth. Loncaric et al. (2006) also observed the same general pattern in the South Atlantic. The data for *T. humilis* reported here (including observations already discussed in Schiebel et al., 2002b) appear to provide some of the first constraints on the depth habitat of this species (Table 4). In the current study, the ALD of *G. rubescens* was variable, with most values between 50 and 150 m. In previous studies from the northeast and southeast Atlantic, it was found more restricted towards the surface layer (Bé and Hamlin, 1967; Kemle-von Mücke and Oberhänsli, 1999). In the Indian Ocean this species was found from 30 to 200 m (Duplessy et al., 1981), confirming the here observed large range in its depth habitat. Finally, *G. calida* occurred mostly with an ALD between 50 and 90 m, which agrees with a maximum abundance of this species in the upper 100 m of the water column in the Bay of Biscay (Retailleau et al., 2011).

Among the presumably symbiont-barren species, the depth habitat of *G. bulloides* was variable, with many of the observed ALD values deeper than 100 m. Such deep habitat was already reported by Schiebel et al. (2001) and Wilke et al. (2009), but it appears deeper compared to the results by Bé and Hamlin (1967) in the same area, where it was described as being more frequent in the surface (0–10 m) than deeper tows (0–300 m) and of van Raden et al. (2011) in the Mediterranean and Field (2004) in the eastern Pacific, who found the species being restricted to the top 100 m. Mortyn and Charles (2003) also reported a variable habitat depth for this species in the Southern Ocean. Similarly variable is the inferred depth habitat of *G. falconensis*. This species showed a typical ALD between 45 and 120 m, which falls in the depth interval (50–100 m) where Peeters and Brummer (2002) found the highest abundances of this species in the northwestern Arabian Sea. The ALD of *N. incompta* was between 30 and 200 m, with most of the observations between 50 and 120 m. This agrees well with observations around Japan (Kuroyanagi and Kawahata, 2004) and in the South Atlantic (Mortyn and Charles, 2003; Kemle-von Mücke and Oberhänsli, 1999). In the North Atlantic, the habitat of this species was studied by Schiebel et al. (1997), who also reported a broad vertical range for this species, although most of the population appeared shallower than 60 m. The even larger ALD interquartile range obtained for *N. pachyderma* of 50–220 m is consistent with previous observations (Ortiz et al., 1996; Bergami et al., 2009). However, this species was rare in the studied area precluding more detailed inferences. The depth habitat of *G. truncatulinoides* was also variable, with ALD ranging from within the mixed layer to 250 m. Whilst the habitat of the species is often reported as subsurface (100 to 300 m in the Caribbean, Schmuker and Schiebel, 2002), a broad range of depth is consistent with observations by Fairbanks et al. (1980), Loncaric et al. (2006) and Mortyn and Charles (2003).

5.2.3 Subsurface species

Species with median ALD ranging from 130 to 230 m are *B. pumilio*, *T. parkerae*, *T. quinqueloba*, *H. pelagica*, *G. hirsuta*, *T. clarkei*, *T. iota* and *G. scitula* (Fig. 7). With most of the observed ALDs deeper than 70 m, the vertical distribution of these species indicates a habitat in subsurface waters. Except for *H. pelagica* (Alldredge and Jones, 1973), there is no unequivocal evidence that any of these species harbor algal symbionts (Hemleben et al., 1989), but little literature is available regarding the species *T. clarkei*, *T. iota*, *B. pumilio* and *T. parkerae*. Our results on their subsurface habitats indicate that these species live below the photic zone and therefore they are likely symbiont-barren.

The depth habitat is best known for *G. scitula*, which is consistently described as inhabiting subsurface depths (Ortiz et al., 1996; Schiebel and Hemleben, 2000). In the Indian Ocean, *G. scitula* was reported as inhabiting preferentially the depth below the mixed layer (30–80 m) until 200 m (Duplessy et al., 1981). In the eastern Pacific, highest abundances were also found below the thermocline with peak abundances deeper than 250 m (Field, 2004), and in the western Pacific no specimens were found shallower than 300 m (Itou et al., 2001). While the distribution of the ALDs of this species in our study is wide (∼ 40–350 m) it is skewed towards greater depths and it is one of the few species that shows ALDs over 300 m. Our observations thus confirm the truly deep habitat of this species. *G. hirsuta* is the other species in our study where an ALD > 300 m was observed multiple times (Fig. 7). However, even though its median ALD is deeper than 100 m this species shows the widest ALD range (∼ 400 m) in our study and can therefore not be considered as a strict subsurface dweller. This wide vertical range is in agreement with observation from the Indian Ocean (Duplessy et al., 1981). In our study *T. quinqueloba* showed a typical ALD between 70 and 180 m, ranging from 50 to 350 m. In the Fram Strait (Artic Ocean) this species was present throughout the upper 200 m (Carstens et al., 1997; Pados and Spielhagen, 2014). In the eastern North Atlantic, *T. quinqueloba* was found at variable depths down to 500 m (Schiebel et al., 2001).

The depth habitat of *H. pelagica* is known to range from the surface to the subsurface, but the vertical distribution differs among the three known cryptic genetic types of this species (Weiner et al., 2012). In the eastern North Atlantic *H. pelagica* was found to live deeper than 60 m (Schiebel et al., 2002b) and it is reported as preferring waters deeper than 100 m (Bé and Hamlin, 1967; Bé and Tolderlund, 1971). This range is in agreement with the occurrence of all three genetic types in the studied region as reported by Weiner et al. (2012). The fact that many of the observed ALD of this species indicate a subsurface habitat implies a dominance in the studied region of the deep-dwelling (deeper than 100 m) type IIa Weiner et al. (2012).

Little is known about the depth habitat of *T. parkerae*, *T. clarkei*, *T. iota* and *B. pumilio*. Most of these species are rare in our study and only *T. parkerae* was observed at more than five stations (Fig. 7). A previous study in the northeast Atlantic showed that *T. parkerae* occurred throughout the water column, but with highest abundances shallower than 100 m (Schiebel et al., 2002b). Our observations indicate a median ALD of this species of ∼ 130 m and an ALD range extending down to 300 m, thus suggesting that the species occupies a wider depth habitat than previously thought. Similarly, our observations on *T. iota* also extend its known vertical range. In a study performed in the northwestern Arabian Sea *T. iota* was found mostly within the upper 100 m (Peeters and Brummer, 2002). Our observations however indicate a considerably deeper ALD with narrow range between 250 and 350 m. *B. pumilio* and *T. clarkei* were observed at four and two stations, respectively. While the observed ALD range of the latter agrees with previous work in the southeastern Atlantic (Kemle-von Mücke and Oberhänsli, 1999), the rarity of the two species precludes a robust delineation of their depth habitat.

5.3 Variability of habitat depth

The species *G. ruber* pink, *O. universa*, *H. pelagica* and *T. iota* appear to consistently exhibit a narrow range of ALD in the studied region (Figs. 7, 10), suggesting that these species are able to successfully maintain a specific preferred depth habitat. Therefore, these species could serve – at least in the studied region – as paleoclimate proxy carriers that are relatively unaffected by depth habitat variability. Despite a general affinity among the other species to a certain typical depth habitat, they showed a considerable range in their ALD (Fig. 7). This means that, depth habitat is not constant within a species, but varies presumably as a function of local environmental conditions and ontogeny. As a first approximation, we hypothesize that the depth habitat of such species reflects a thermal and/or density optimum niche, where the environmental conditions should result in a higher reproduction and growing success. In this case, the temperature or density at the ALD of such species would show a relatively narrow range, despite a large range of ALD. In order to assess if this is the case, we compared the interquartile ranges (IQR) of these two environmental parameters with the IQR of the ALD expressed as a fraction of the mean ALD (Fig. 10). The latter was done to account for the lognormal distribution of depth and sampling intervals.

The results indicate that the studied foraminifera species can be roughly divided into five groups when the IQR of temperature at the ALD (T_{ALD}) is considered:

1. Species showing a large spread in T_{ALD} but a small relative ALD range would appear in the studied area to maintain a specific narrow depth habitat independent of temperature. Most of these species (e.g., *G. ruber* pink) harbor algal symbionts and their light dependence is probably more important in determining their depth habitat than other environmental factors.

2. Species showing an intermediate spread in T_{ALD} and narrow relative ALD range indicate that temperature may play a role in determining their depth habitat, but that other factors such as light or food availability might be more important as well. An example for this behavior is *T. sacculifer*.

3. Species with intermediate T_{ALD} range and variable relative ALD, such as *G. glutinata* could be considered to follow an optimum temperature range and adjust their depth habitat accordingly.

4. Species with narrow T_{ALD} and narrow relative ALD, such as *H. pelagica*, indicate that they consistently occur in a similar habitat. Many of the species from this group occur in the subsurface, where temperature variability is muted. Alternatively, the same behavior would be expected for species tracking the same habitat seasonally.

5. Finally, species with variable T_{ALD} and variable ALD, such as *G. hirsuta*, must vary their habitat depth in response to other factors than temperature.

The variability of seawater density at ALD (Fig. 10) provides a further key to constrain the habitat depth. Compared to the more even distribution of the variability of temperature at ALD, we observe that the variability of seawater density at ALD within species (expressed as interquartile range) is skewed towards lower values (Fig. 10). This could be an indication that density is more important than temperature in determining the depth habitat of planktonic foraminifera. The species that show a larger spread in σ_{ALD} inhabit the most variable habitat, as they also showed the largest spread in T_{ALD}. Among these species, *G. ruber* pink and *O. universa* appear to prefer a specific depth irrespective of the environmental conditions, whereas *T. quinqueloba* inhabits a variable depth habitat that is also not linked to a specific temperature or density. The observation of a tendency of most species to show lower σ_{ALD} is worth further investigation, optimally under oceanographic settings where density is less tightly linked to temperature, as it is the case in the studied region.

Having established that the depth habitat of many species is variable and that the variability cannot be solely attributed to tracking of a specific temperature or density layer, we proceeded by testing to what degree the variability in depth habitat is predictable (by other parameters). This analysis revealed that among the species that showed a variable habitat depth, the ALD variability contains a predictable component in 11 out of 17 species (Table 3). In this group, periodic changes (related to ontogeny) or variability in a small number of environmental variables often explain more than 50 % (up to 80 %) of the variance in the ALD.

5.4 Lunar and seasonal cycles in species habitat depth

Because of strong seasonal variations in mixed-layer properties such as the depth (MLD), temperature (TML) and chlorophyll *a* concentration (CML) in the studied area (Fig. 3), it is difficult to unambiguously distinguish changes in habitat depth due to environmental forcing from those resulting from a potential ontogenetic cycle. Although TML, MLD and CML are less variable at lunar/monthly frequency, we note that the data span several years and seasons. Consequently, ontogenetic periodicity in habitat depth (annual or lunar) could interfere, or be obscured, by changes in depth habitat in response to environmental forcing (e.g., Jonkers et al., 2015). That said, the periodic regression revealed several significant apparently cyclic patterns in ALD, which are worth analyzing (Fig. 9, Table 3).

The species that show an annual cycle in their depth habitat are *G. scitula*, *T. parkerae*, *N. incompta*, *G. truncatulinoides*, *G. glutinata* and *T. sacculifer* (Fig. 9). The periodic regression results for *G. hirsuta* also indicate a strong annual component in its ALD variability, but we note that this species was only found in sufficient numbers in the studied region in winter and spring (Fig. 9). This species clearly descends through the water column during this period, but we cannot comment on its behavior during the rest of the year and thus cannot attribute the observed pattern with certainty to an annual cycle. The remaining species with an annual ALD variability appear to descend in the water column from winter to spring, reaching the largest ALD in spring to summer (141 to 195 days of the year) and then their habitat shoals again towards the winter. Even though the number of observations from summer to autumn is low for *G. truncatulinoides*, this species also appears to follow the same cyclic pattern. Only *T. parkerae* shows a different pattern, reaching its greatest ALD later in the year. A probable explanation for the apparent seasonal shift in habitat depth could be food availability within and below the thermocline in summer, associated with the development of a deep chlorophyll maximum. For instance, the presence of *N. incompta* has previously been associated with upwelling/filament waters (Ufkes et al., 1998; Meggers et al., 2002) or food supply (Ortiz et al., 1995) which might explain the relationship between its ALD and the yearly cycle. Alternatively, species as *G. truncatulinoides* and *G. scitula* may follow an annual reproductive cycle, which would suggest that the observed periodicity in their ALD reflects an ontogenetic pattern (Hemleben et al., 1989; Schiebel and Hemleben, 2005). In the studied area the export flux and therefore reproduction of *G. truncatulinoides* and *G. scitula* occurs in a short period in winter and spring (Storz et al., 2009). Our data indicate an ALD shift from ∼ 30 m (winter) to 250 m (spring) for *G. truncatulinoides* and a deepening from 40–100 m (winter) to 300–350 m (spring/summer) observed for *G. scitula*. Although the data are certainly not conclusive, this may suggest that the population of these species dwell at depth before reproduction in winter/spring. The apparent annual cycle in the ALD of *T. parkerae* stands apart, as this species reaches the deepest habitat depth (250 m) at the end of the summer. There are no comparable observations on this species elsewhere and because of its low abundance at most stations in our study, determining the existence and exact shape of an annual cycle in ALD in this species requires more data.

Besides the yearly cycle, the species *T. sacculifer*, *G. glutinata* and *G. truncatulinoides* also show an apparent habitat depth change following the synodic lunar cycle (Fig. 9). The tendency observed for the three species is similar; their ALD decreases reaching the shallowest depth between the 5th and 10th day of the cycle. Afterwards these species descend in

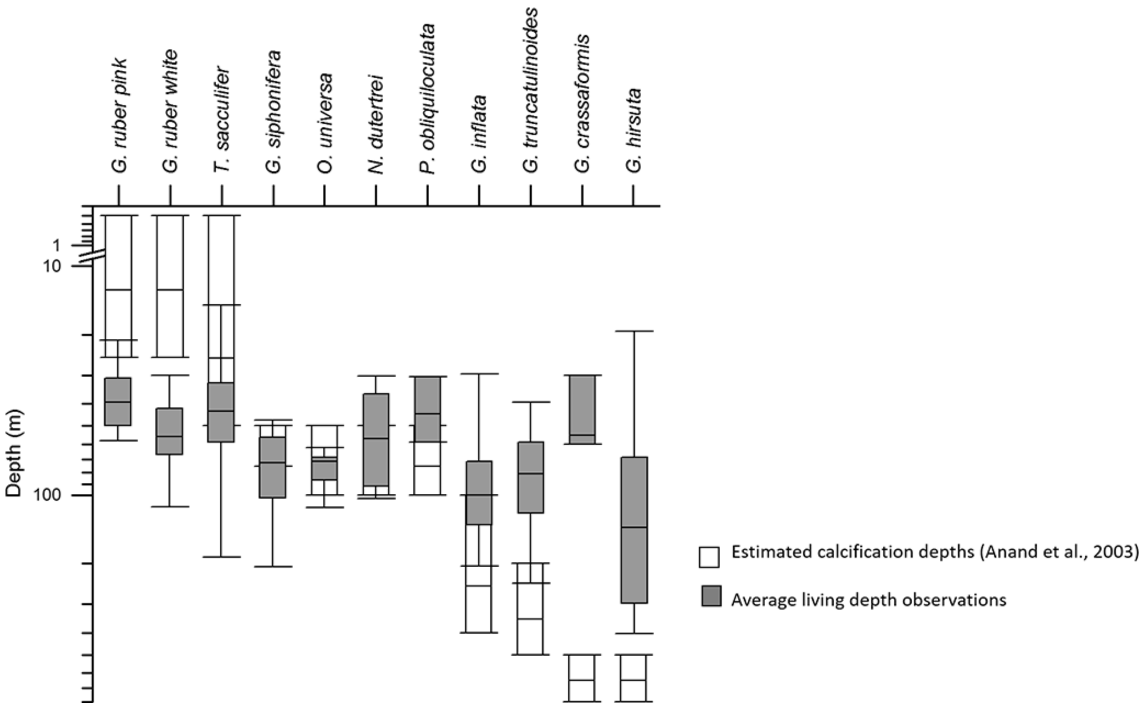


Figure 11. Estimated calcification depth based on $\delta^{18}O$ values of species of planktonic foraminifera from the Sargasso Sea and the calcite in equilibrium with seawater (white; Anand et al., 2003) and the average living depth based on observations of living specimens from vertically resolved plankton tows from the eastern North Atlantic (dark gray, Fig. 7).

the water column reaching maximum depth around the 24th lunar day. In *T. sacculifer*, the proportion of the variance in ALD explained by the lunar and annual cycle was similar (27 and 28 %, respectively). The influence of the lunar cycle on the reproduction in this species has been reported previously (Bijma et al., 1990a; Jonkers et al., 2015). The observed lunar cycle in the ALD of *T. sacculifer* is consistent with reported lunar synchronized reproduction (Erez et al., 1991; Bijma and Hemleben, 1994; Jonkers et al., 2015). The studies from the Gulf of Aqaba show that *T. sacculifer* descends in the water column prior to reproduction around full moon (Erez et al., 1991; Bijma and Hemleben, 1994). Our data from the northeastern Atlantic, however, indicate that *T. sacculifer* descends towards the new moon (Fig. 9). If reproduction in the northeastern Atlantic indeed takes place at maximum ALD around new moon, then these observations suggest that synchronized reproduction varies regionally in its phasing, as was also suggested by Venâncio et al. (2016). In the case of *G. glutinata*, Jonkers et al. (2015) demonstrated the existence of lunar cyclicity in the flux of this species. In our analysis, the ALD relationship of this species with the lunar cycle is stronger (explaining 30 % of the variance in ALD) than with the seasonal signal (explaining 18 %), providing support for synchronized reproduction of this species and associated migration through the water column. The amount of variance in the ALD of *G. truncatulinoides* explained by a yearly cycle is substantially higher (75 %) than that of a lunar cycle (48 %) and indeed for any of the environmental parameter alone (Table 3). The relationship of its ALD to the lunar cycle is thus likely an artefact due to interdependencies among the tested variables in the available data set.

5.5 Environmental factors controlling vertical distribution

Besides showing a periodic pattern in their ALD, some species also reveal a statistically significant relationship between ALD and the tested environmental parameters (temperature in the ML, chlorophyll *a* in the ML and ML depth). These are *T. sacculifer*, *G. glutinata*, *G. truncatulinoides* and *G. hirsuta.* Others, such as *T. humilis*, *G. tenellus*, *G. rubescens*, and *G. calida*, do not show a periodic component in their ALD, but their ALD appears to be predictable by the tested environmental factors.

The ALDs of *G. glutinata*, *T. sacculifer*, *G. truncatulinoides*, *T. humilis* and *G. hirsuta* show a negative correlation with MLD (Fig. 9). For *G. truncatulinoides* and *G. hirsuta* the relationship between ALD and MLD explains a smaller proportion of the variance than the annual (but see discussion above for *G. hirsuta*) periodic regression model (Table 3), suggesting that the annual ontogenetic depth habitat change may reflect a seasonal change in MLD. For the other species, the relationship between ALD and MLD does not appear to result from a collinearity with annual (or monthly) cycles because no significant periodicity was detected in their ALDs. The direction of the observed relationship seems counter-intuitive. Theoretically, deeper mixing (greater MLD) should cause a deeper ALD, as the mixing should constantly redistribute the population of these species throughout the mixed layer. *G. glutinata* and *T. sacculifer* also exhibit a negative correlation between their ALD and TML, living closer to the surface where/when temperature is higher (Fig. 9). The observed shallowing of the ALD of these species with MLD and TML is therefore unlikely to be linked to light demands of these symbiont-bearing species, because light penetration increases with season and latitude, thus facilitating deeper habitats with increasing temperature. The habitat shoaling is also unlikely to result from a stronger stratification due to increasing TML. This is contradicted by the shoaling of the habitat with increasing MLD. The mechanism behind this apparently contradictory relationship between ALD and MLD and TML thus remains unresolved. We note however that it does not apply to *T. humilis*, which seems to respond only to MLD (Table 3). This species could have a preference for low-light conditions, which are expressed either below the surface under well stratified, summer or lower-latitude, oligotrophic conditions or closer to the surface when the water column is mixed and productivity is low or light level is lower in winter and/or at higher latitude. This case also demonstrates the difficulty to unambiguously attribute the ALD variation to one factor in a diversified setup like the one given here, spanning multiple years and localities.

The two remaining species that showed a significant relationship between ALD and TML, *G. calida* and *G. rubescens*, show the opposite relationship between ALD and TML. They appear to deepen their habitat as the temperature in the ML increases (Table 3). This relationship appears to exist irrespective of seasonality and productivity. While the data are rather noisy, in particular for *G. rubescens*, this relationship may reflect a narrower thermal niche in these species, with deeper habitats available only under warmer conditions. However, the range of T_{ALD} of these species (Fig. 10) is rather wide, suggesting that the relationship between ALD and TML could arise from collinearity between TML and an unknown temperature-related environmental parameter.

Of all the analyzed species, *G. tenellus* is the only one that showed a significant positive relationship between habitat depth and ML depth and a negative relationship between ALD and TML. However, the ALD range of this species is very small, preventing solid conclusions about the exact drivers of its depth habitat variability. The habitat depth of *T. parkerae* appears to be influenced by chlorophyll *a* in the ML (Table 3, Fig. 9). This relationship appears to explain more (60 %) of the ALD variance in this species than the seasonal cycle (50 %) and it is observed despite the fact that the optimum habitat of this species is mostly well below the surface (Fig. 7). The shallowing of the habitat with increasing productivity, irrespective of temperature of mixed layer depth, is difficult to interpret without a better knowledge of the ecology of this small and obscure species.

Species that showed variable ALDs, but did not show a statistically significant relation with either the yearly or lunar cycle or the tested environmental parameters include *G. falconensis*, *G. bulloides*, *G. siphonifera*, *G. inflata*, *G. ruber* white and *T. quinqueloba* (Table 3; Fig. S2). *G. bulloides* show a relatively large range of ALDs and an affinity for the deeper part of the surface layer (Fig. 7). These observations, together with its light independency due to the lack of symbionts, facilitate the occupation of a broader vertical niche. *G. bulloides* is generally associated with high primary productivity (Thiede, 1975; Mohiuddin et al., 2005; Hemleben et al., 1989; Ganssen and Kroon, 2000). However, since we do not have vertically resolved chlorophyll *a* concentration data for each station and our sites do not cover the full range of productivity conditions in the area (Fig. 3), we cannot evaluate the influence of chlorophyll *a* concentration in the water column on the ALD of these species. *G. siphonifera* and *G. inflata* show a similar vertical habitat (Fig. 7). However, these species were usually observed in low numbers, possibly indicating that they occur at the extreme end of their ecological niches in the study area or maybe reflecting different genotypes in the case of *G. siphonifera* (Bijma et al., 1998; Weiner et al., 2014), which may render their ALD difficult to predict. The lack of statistically significant predictability of the ALD of *G. ruber* white is likely related to the presence of multiple genotypes with distinct environmental preferences within our samples. The two main lineages of this species exhibit different geochemical signatures, which are interpreted as resulting from different depth habitats (Steinke et al., 2005; Wang, 2000; Numberger et al., 2009). These lineages are morphologically separable in adult specimens but their characteristic features are not well developed among pre-adult specimens that dominate plankton assemblages (Aurahs et al., 2009). Separation was therefore not possible in our study. Cryptic diversity could also have contributed to the apparent unpredictable ALD of *G. bulloides* and especially the large and somewhat bimodal ALD distribution in *T. quinqueloba*. Both species are characterized by the presence of multiple genotypes arranged in two deeply branching lineages, whose geographic range overlaps in the studied region (Darling and Wade, 2008).

5.6 Comparing habitat depth with calcification depth

The predictability of the depth habitat of many species investigated here provides the opportunity to (re-)interpret paleoceanographic signals based on the chemistry of their shells. However, to do so, we also must consider the difference between habitat depth and calcification depth. Calcification depth is inferred from the stable isotope or trace element composition of the foraminifera shells. It refers to the apparent depth where the conditions correspond to the average geochemical signal locked into the shell (Emiliani, 1954).

Because of exponential growth, calcification depth is heavily weighted towards conditions when the last few chambers of the shell were formed. In species that form a layer of secondary calcite, this weighting is further intensified towards the conditions at the very end of their life cycle. In addition, symbiont photosynthesis, respiration, carbonate-ion concentrations and salinity, may further affect the estimated calcification depth (Nürnberg et al., 1996; Rohling and Cooke, 1999; Martínez-Botí et al., 2011; Eggins 2004).

Comparing the habitat depth observed in the current study with calcification depth estimates from the Sargasso Sea (Anand et al., 2003) – the nearest regional analogue to the studied region with well-constrained calcification depth data for the same species – reveals differential patterns (Fig. 11). The calcification depths estimated for *G. ruber* pink, *G. ruber* white and *T. sacculifer* are shallower than our ALD observations. This appears puzzling and must reflect differences in the water column structure such as a thinner mixed layer depth in the Sargasso Sea or it might be caused by an overestimation of ALD caused by a flux of dead specimens, which still beard cytoplasm and that were counted as alive.

In the cases of *G. siphonifera*, *O. universa*, *N. dutertrei* and *P. obliquiloculata*, the estimated calcification depths overlap with our ALDs. Previous studies have reported that prior to gametogenesis *T. sacculifer* (Bé, 1980; Duplessy et al., 1981), *O. universa* (Deuser et al., 1981) and *N. dutertrei* (Duckworth, 1977; Jonkers et al., 2012) descend in the water column and a secondary calcite crust is added. This phenomenon should result in a deeper calcification depth than the ALD, which is not apparent from the data, suggesting that either the difference between the primary and secondary calcite is small, or differences in the vertical temperature gradient between the areas obscure the signal. Additional uncertainty in estimating calcification depth may result from the presence of cryptic species such as *O. universa* and *G. siphonifera* (de Vargas et al., 1999; Morard et al., 2009; Weiner et al., 2014), where different genotypes appear to be associated with different isotopic signatures (Bijma et al., 1998; Marshall et al., 2015). In addition, the symbionts of the deeper living *G. siphonifera* type II have a higher concentration of light harvesting pigments than in type I, implying a higher photosynthetic rate for type II in relation to type I (Bijma et al., 1998).

Regarding *G. inflata*, *G. truncatulinoides*, *G. crassaformis* and *G. hirsuta* the estimated calcification depth is much deeper than the ALD where these species were found. The contrast most likely exceeds what could result from differences in the water column structure and probably reflects the addition of secondary calcite at depth or the incompleteness of the life cycle (Nürnberg et al., 1996; Martínez-Botí et al., 2011).

Previous studies have shown that initial calcification of *G. truncatulinoides* occurs near the surface and a heavy secondary crust is added between 400 and 700 m depth at the end of its life cycle (Bé and Lott, 1964; Mulitza et al., 1997). Similar behavior has been suggested for other Globorotaliids such as *G. inflata* (Wilke et al., 2006; Chiessi et al., 2007), *G. hirsuta* (Orr, 1967) and *G. crassaformis* (Regenberg et al., 2009). However, ALDs of these species rarely exceed 200 m and the maximum ALD observed is 450 m (Fig. 7), indicating that the majority of the population of foraminifera in the pelagic mid-latitude ocean lives – and calcifies – relatively shallow. Therefore, even though the ontogenetic migration and secondary calcite addition in the subsurface is a probable explanation for the deeper calcification than habitat depths, the depths where this calcite is added may be overestimated. Clearly, the new insights on the predictability of habitat depth aid the interpretation of foraminifera proxy records, but the discrepancies between habitat and calcification depth in some of the species highlight the need to better understand the causes and effects of secondary calcification.

6 Conclusions

To investigate the vertical habitat and its variability in planktonic foraminifera from the eastern North Atlantic region, the abundance of 34 species was determined in vertically resolved plankton tows collected at 43 stations between 1995 and 2012. The resulting observations collectively form a coherent framework allowing quantitative assessment of factors affecting habitat depth and its variability:

- Total standing stocks of planktonic foraminifera seem to be affected mostly by chlorophyll *a* concentration and temperature whereas the partitioning of the abundances of planktonic foraminifera shallower and deeper than 100 m was associated with seasonal upwelling or winter deep mixing.

- None of the species was evenly distributed throughout the water column and we use average living depth (ALD) to investigate depth habitat variability. Some species, such as *G. ruber* pink and *T. iota*, showed a constant narrow habitat depth, suggesting that depth habitat variability will not affect their sedimentary signal. However, most species showed a variable ALD, indicating that depth habitat variability within species cannot be ignored in the interpretation of paleoceanographic records.

- Among the species that showed a variable ALD, this variability could in the majority of the cases be predicted by the presence of an ontogenetic yearly or synodic lunar cycle and/or a relationship with mixed layer depth, temperature or chlorophyll *a* concentration.

- Globorotalid species such as *G. truncatulinoides* and *G. scitula* showed a yearly cycle in their ALD, living in the uppermost part of the water column in the winter and reaching the greatest depths during spring/summer.

- The ALD of *T. sacculifer* and *G. glutinata* appears to show a lunar cycle, which is in agreement with previous studies.

- Apart from the presence of a yearly or lunar cycle, properties of the mixed layer could serve as useful predictors of habitat depth. The most common relationship is shoaling of the habitat depth with the deepening of the MLD. *G. glutinata*, *G. tenellus*, *T. sacculifer* and *G. truncatulinoides* show a shoaling of their habitat with increasing temperature, whereas only *G. calida* and *G. rubescens* follow the opposite pattern. Chlorophyll *a* concentration in the ML appears to be a useful predictor for the depth habitat of *T. parkerae* only.

- Further, we observe that temperature and seawater density at the depth of the ALD were not equally variable among the studied species, and their variability showed no consistent relationship with depth habitat.

Overall, individual species seem to adjust their habitat in response to different environmental and ontogenetic factors (e.g., temperature, chlorophyll *a*, water column structure, seasonality, lunar cycle) exhibiting species-specific mean habitat depths as well as species-specific changes in habitat depth.

7 Data availability

Data is available through parent link https://doi.pangaea.de/10.1594/PANGAEA.872477.

The Supplement related to this article is available online at doi:10.5194/bg-14-827-2017-supplement.

Competing interests. The authors declare that they have no conflict of interest.

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