# Ecology and stable isotope geochemistry of modern planktonic foraminifera in the Northeast Atlantic

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# Abstract

The understanding of the relationship between planktonic foraminifera and their surrounding environment, as well as each individual species' habitat and calcification behaviour are of fundamental importance to improve their use as a paleoceanographic tool. To this end, vertically stratified plankton tow hauls were used to study the vertical and horizontal distribution and stable isotope geochemistry of planktonic foraminifera in the eastern North Atlantic, a region that plays an important role in monitoring changes in the North Atlantic circulation and where the environmental conditions are particularly diverse. This work provides new insights into the vertical and horizontal distribution of individual species of planktonic foraminifera and the respective factors (temperature, chlorophyll, mixed layer depth, lunar/seasonal cycle) potentially controlling their distribution. New findings concerning the stable isotope signal recorded in the shells of four deep dwelling planktonic foraminifera species are also reported.

The vertical distribution of planktonic foraminifera varied among species, allowing us to identify different groups of species, such as species living typically above 100 m, species occurring commonly between the surface (50 m) and intermediate waters (100 m) and species living mostly below 100 m. In most cases, the vertical habitat also varied within species, but the variation was found to be predictable by a combination of environmental factors and ontogenetic migration. Horizontally, species distribution is linked to the surrounding environmental conditions, resulting in specific regional and seasonal faunal associations. Unlike the composition of sedimentary assemblages, plankton assemblages are predicted by multiple environmental parameters, indicating that the strong temperature signal in fossil assemblages is the result of seasonal and interannual accumulation and averaging.

The stable isotopic analysis of four deep-dwelling species confirmed that either larger size or presence of a secondary crust cause heavier isotopic signal. In three out of the four studied species, the oxygen isotopic signal could be better predicted by the Shackleton paleotemperature, whereas *Globorotalia scitula* signal is better described by the Kim and O'Neil paleotemperature equation.

Finally, we found inconsistencies between the living depth and the calcification depth of each species, revealing that the calcification depth does not correspond entirely to the habitat depth of a species.

# Zusammenfassung

Das Verständnis des Zusammenhangs zwischen planktischen Foraminiferen und ihrer Umgebung sowie das Habitat- und Verkalkungsverhalten jeder einzelnen Art sind von grundlegender Bedeutung, um ihre Verwendung als paläozeanographisches Instrument zu verbessern. Zu diesem Zweck wurden vertikal geschichtete Plankton Tow Hauls verwendet, um die vertikale und horizontale Verteilung und stabile Isotopengeochemie von planktischen Foraminiferen im östlichen Nordatlantik zu untersuchen, einer Region, die eine wichtige Rolle bei der Überwachung der Zirkulation des Nordatlantiks und der Umweltbedingungen spielt sind besonders vielfältig. Diese Arbeit liefert neue Einblicke in die vertikale und horizontale Verteilung einzelner Arten planktonischer Foraminiferen und die jeweiligen Faktoren (Temperatur, Chlorophyll, Mischschichttiefe, Mond / jahreszeitlicher Zyklus), die möglicherweise ihre Verteilung kontrollieren. Neue Erkenntnisse über das stabile Isotopensignal, das in den Schalen von vier Planepton-Foraminiferen-Arten in den tiefen Wäldern aufgenommen wurde, werden ebenfalls berichtet.

Die vertikale Verteilung der planktischen Foraminiferenarten unterscheidet sich von Art zu Art und erlaubt es, eine Gruppe von Arten zu identifizieren, die typischerweise über 100 m leben. Arten, die häufig zwischen der Oberfläche (50 m) und Zwischengewässern (100 m) vorkommen, leben unter ihnen 100 m. In den meisten Fällen variierte der vertikale Lebensraum innerhalb der Arten, aber die Variation erwies sich als vorhersagbar durch eine Kombination von Umweltfaktoren und ontogenetischer Migration. Horizontal ist die Artenverteilung an die Umweltbedingungen gebunden, was zu spezifischen regionalen und saisonalen Faunenverbänden führt. Anders als bei der Zusammensetzung von Sediment-Assemblagen werden Plankton-Assemblagen durch mehrere Umweltparameter vorhergesagt, was darauf hindeutet, dass das starke Temperatursignal in fossilen Gemeinschaften das Ergebnis saisonaler und interannualer Akkumulation und Mittelung ist. Die stabile Isotopenanalyse von vier tief lebenden Arten bestätigte, dass entweder eine größere Größe oder das Vorhandensein einer sekundären Kruste ein stärkeres Isotopensignal verursacht. In drei der vier untersuchten Arten konnte das Sauerstoffisotopensignal durch die Paläotemperatur von Shackleton besser

vorhergesagt werden, wohingegen Globorotalia scitula besser durch die Palotemperaturgleichung von Kim und O'Neil beschrieben wird. Schließlich wurden Inkonsistenzen zwischen der Lebenstiefe und der Verkalkungstiefe jeder Art gefunden, was zeigt, dass die Verkalkungstiefe nicht vollständig der Habitattiefe einer Art entspricht.

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# Chapter 1

## 1. Introduction

### 1.1 Microfossils as a tool in paleoceanography

One of the main objectives of paleoceanography is to understand the role of oceanic processes in global climatic and environmental change. This is achieved by reconstructing environmental conditions in the past, using methods that provide different levels of precision (Fischer and Wefer, 1999; Kennett, 1982). These methods are based on the extraction of measurable properties in geological archives that serve as indirect measures (proxies) of variables such as temperature, salinity, nutrients, carbon dioxide concentration, and productivity. The distribution of surface ocean temperature is one of the most useful variables for paleoceanographic reconstructions, providing important data on the state of the Earth's climate and ocean circulation, allowing direct comparison with paleoclimate modeling (Waelbroeck et al., 2008, 2005). Available proxies for temperature reconstructions include the faunal composition of microfossils of marine plankton, the oxygen isotopic composition and the magnesium or strontium to calcium ratio in biogenic carbonates precipitated in the ocean, and ratios of certain organic molecules produced by marine plankton (Fischer and Wefer, 1999). Microfossils are produced by those groups of marine plankton which possess resistant structures, such as skeletons or cysts made of calcite, aragonite, silica or organic biopolymers (Kennett, 1982). This feature provides an extraordinary preservation capacity of these microscopic organisms, making them one of the main constituents of marine sediments (Kennett, 1982). Siliceous microfossils include diatoms and radiolarians; aragonite microfossils include pteropods and some foraminifera; while calcite microfossils include benthic and planktonic foraminifera, ostracods and coccolithophorids (Kennett, 1982).

Some of the most commonly used proxies in paleoceanography are related to foraminifera. Planktonic foraminifera appeared initially in the Jurassic, experienced their first diversification in the Cretaceous, and ever since form a substantial constituent of the plankton (Hemleben et al., 1989; Kennett, 1982). In an ideal case, shells of dead planktonic foraminifera sink through the water column until settling down to the seafloor. Although dissolution of shells can occur on their way down to the seafloor, and even on the seafloor, it is estimated that one fourth of the initially produced planktonic foraminifera shells arrive at the seafloor and is preserved in the sediment (e.g. Berger, 1971; Milliman et al., 1999). At present, planktonic foraminifera contribute globally with 0.36 – 0.88 Gigatons*year$^{-1}$ of calcite to the surface sediments, corresponding to 32 – 80 % of the total marine sediments' calcite budget (Schiebel, 2002).

Murray (1897) was the first to recognize that the distribution of planktonic foraminifera species is related to surface temperature and Schott (1935) showed that the composition of their fossil assemblages could be used to trace surface-water properties. Following that, many discoveries concerning the biology and ecology of planktonic foraminifera have been made and the techniques to reconstruct ocean surface properties have greatly evolved, such as the use of transfer functions (Imbrie and Kipp, 1971) and stable isotope analysis (Emiliani, 1954). Further interpretations of the paleoproxies based on fossil foraminifera will highly benefit from a better understanding of their current ecology, growth and calcification. This can only be achieved through studies of living foraminifera, assuming that the knowledge on the environmental factors affecting the present planktonic foraminifera can be applied to interpret ancient assemblages from marine sediments.

## 1.2 Modern planktonic foraminifera

### 1.2.1 Biology of planktonic foraminifera

Planktonic foraminifera are unicellular eukaryotic organisms that belong to the protozoans, constituting a small percentage of the total living zooplankton (Hemleben et al., 1989; Johnson and Allen, 2012). These organisms are found in diverse oceanic environments, from tropical and subtropical waters to polar waters. They inhabit mainly the euphotic zone, since most of their food resources occur in the first 200 m of the water column, but can live down to several hundreds of meters (e. g. Hemleben et al., 1989). Along this depth gradient, individual species have been shown to possess individual depth habitat preferences (e. g. Bé and Hamlin, 1967; Fairbanks et al., 1980).

Moreover, it has been hypothesized that the habitat changes through life is a phenomenon called ontogenetic vertical migration (Kahn and Williams, 1981).

Planktonic foraminifera possess multilocular shells, where each chamber corresponds to a distinct growth period and the growth of the shell as a whole is thus considered discontinuous (Brummer et al., 1987; Hemleben et al., 1989). Most extant planktonic foraminifera calcify their shells in a bilamellar pattern, secreting a layer of calcite at each side of an organic sheet (Bé et al., 1979; Bé and Hemleben, 1970). The following chamber is built by extension of the protoplasm through the aperture, which delineates the shape of the new chamber and deposits a new primary organic sheet. This process is continuous through life and results in a succession of interconnecting chambers, which may be associated with a large change in the shape of the shell along the shell development (Brummer et al., 1987, 1986). There is evidence that additional calcite layers may be formed daily on top of the initial layer, as observed for *Orbulina universa* (Spero et al., 2015). The shells of planktonic foraminifera resulting from the sequential addition of chambers may be either planispiral or trochospiral, with large variations due to differences in the shape of the individual chambers. Surface ornaments of the shell include pustules, ridges and spines (Haq and Boersma, 1998). The contact with the exterior environment occurs through the pores by diffusion or through apertures by extensions of the protoplasm that form a complex reticulate network of pseudopodia external to the shell. The dense net formed by the pseudopods facilitates food capture and plays an essential role in chamber morphogenesis (Brummer et al., 1987; Hemleben et al., 1989). As the shell is built, it archives the chemical and physical conditions of the surrounding seawater, including temperature, salinity, isotopic composition of the sea water, nutrient content, and pH (e.g., Ravelo and Hillaire-Marcel, 2007).

Regarding diet, planktonic foraminifera are generally considered heterotrophic. Non-spinose species are considered mostly herbivorous but appear to also be able to capture zooplankton prey (Hemleben et al., 1989). In surface waters their diet include microscopic algae such as diatoms and dinoflagellates, whereas in deeper waters they seem to feed on debris and bacteria (Anderson et al., 1979; Hemleben et al., 1989; Itou et al., 2001; Spindler et al., 1978). For spinose species, the diet is more diversified, including a range of zooplankton such as copepods, amphipods, pteropods, tintinids, radiolarians, ostracods, crustacean and echinoderm larvae, polychaetes, and gastropods as observed in culture experiments (Fig. 1) and in individuals collected from the natural environment (Caron and Bé, 1984; Spindler et al., 1984). The food may include particles larger than the foraminifera, which are caught in the rhizopodial network supported by spines, where they are reduced to small fragments that are then transported to the endoplasm (cytoplasm inside the shell). To date, no selective predators of planktonic foraminifera are known, but foraminifera shells have been observed in filter-feeding planktontrophs such as pteropods, salps and other metazooplankton (Hemleben et al., 1989; Schiebel and Hemleben, 2005).

Some planktonic foraminifera species possess symbionts (Hemleben et al., 1989). Symbiont bearing species depend on light and are usually restricted to the euphotic part of the water column, whereas symbiont barren species can live in deeper waters, where light does not reach. Up to date, dinoflagellates, chrysophytes, cyanobacteria and pelogophytes have been found associated in a symbiotic relation with planktonic foraminifera (Bird et al., 2017; Gastrich, 1987). Algal symbionts exhibit a circadian migration pattern between the endoplasm and the rhizopodial network, following light intensity (Anderson and Be, 1976; Spero, 1987). Experimental data demonstrated that if grown in dark or without symbionts, planktonic foraminifera form smaller shells (Bé et al., 1982;). This indicates that species living in symbiotic associations that provide part or all of the food through photosynthesis possess an advantage particularly in oligotrophic waters where nutrients and food are limited (e.g., Jørgensen et al., 1985). In addition, the exchange of products (oxygen, carbon and nitrogen compounds) between the symbionts and the host supports the metabolic activity of the latter and

**Fig. 1** Image of living planktonic foraminifera *Orbulina universa* caught off Southern California. Surrounding the shell are the spines and rhizopodia that form a dense network that serves to trap and feed on the prey (artemia). Along the spines, it is possible to observe algal symbionts. The shell is approximately 0.5 mm across. (Photo by: H. Spero).

laboratory experiments have shown that symbionts may have a key role in calcification and chamber formation (Bé et al., 1982; Hemleben et al., 1989; Jørgensen et al., 1985; Rink et al., 1998).

The reproductive cycle has been determined only for a few species of planktonic foraminifera and within these, only sexual reproduction has been observed (Hemleben et al., 1989). Guaranteeing the success of the gametes' encounter in the vastness of the open ocean, with population densities ranging from <100 individuals/m$^3$ to >1000 individuals/m$^3$, is only possible using adaptive strategies (Schiebel and Hemleben, 2005). They include the release of a large number of gametes (hundreds of thousands), synchronization of reproduction in space (by limiting the vertical range to a smaller depth interval) and time (lunar, yearly cycle) (Jelle Bijma et al., 1990; Bijma and Hemleben, 1994; Erez et al., 1991; Spindler et al., 1979, 1978). Surface to intermediate water species such as *Hastigerina pelagica*, *Trilobatus sacculifer* and *Globigerina bulloides* appear to follow a lunar cycle and *Globigerinoides ruber* a half-lunar cycle (Bijma et al., 1990; Schiebel et al., 1997; Spindler et al., 1979). Deep-dwelling species like *Globorotalia truncatulinoides* and *Globorotalia hirsuta* seem to have a yearly reproductive cycle (Hemleben et al., 1989). Reproduction is usually accompanied by morphological changes of the shell such as the formation of an additional calcite layer (gametogenic calcification), the shedding or reabsorption of the spines, or the formation of a final chamber that is usually disfigured and displaced ("Kummerform") (Hemleben et al., 1989).

Planktonic foraminifera do not possess locomotive organelles, which make them vulnerable to be transported by water currents, turbulence and other hydrologic events, causing dispersion of the planktonic fauna locally (Johnson and Allen, 2012). Under the best of circumstances planktonic foraminifera are capable of regulating their vertical position in the water column, as it was observed for *Hastigerina digitata* during a 12-year-long observation (Hull et al., 2011). The exact mechanism that allows the adjustment of the buoyancy of these organisms is not fully understood, however it was verified that phytoplankton may use low-density metabolites and osmolytes to regulate their buoyancy in the water column (Boyd and Gradmann, 2002).

### 1.2.2 Taxonomy of planktonic foraminifera

Traditionally, the taxonomic classification of planktonic foraminifera is based entirely on morphologic characteristics of the adult forms of their shells. Since different species can be quite similar at the juvenile stage, while still lacking some diagnostic morphologic features, juveniles are challenging to identify. Among the morphological characteristics used for species identification are chamber shape and arrangement; wall texture and pore size; number, position and modifications of primary and secondary apertures; and coiling direction (Fig. 2). The groups that comprise individuals with bilamellar shells are: 1) spinose (Globigerinoidea); 2) non-spinose normal perforate or macroperforate (all Globorotaloidea); and 3) non-spinose microperforate (Heterohelicoidea) species. Commonly considered as a separate group is Hastigerinidae (4) that include species with monolamellar shells (Schiebel and Hemleben, 2017). Still, within each morphospecies a large morphologic variation exists, which has been commonly attributed to echophenotypic variations (Hecht, 1976; Malmgren and Kennett, 1972). More recently, molecular data provided new insights into the planktonic foraminifera taxonomy and besides confirming the classified morphospecies, it revealed that individual morphospecies usually contain different genetic types, referred to as cryptic species (Darling and Wade, 2008). The discovery of these cryptic species increased the diversity of planktonic foraminifera and consequently has significant implications on their use as a paleoceanographic tool. For example, some of the recognized cryptic species are not only genetically different but also possess contrasting ecology and distribution as it is the case for *Neogloquadrina pachyderma* and *Neogloboquadrina incompta* (Darling et al., 2006). On the other hand, *Trilobatus sacculifer* which includes different morphotypes and occurs globally in the tropics revealed a single genotype (André et al., 2012). The actual knowledge of planktonic foraminifera is based on approximately 50 morphospecies - within which around 20 are the most common in the oceans (Kennett, 1982; Schiebel and Hemleben, 2005) - and approximately 250 genotypes up to date (De Vargas et al., 2015; Morard et al., 2015). Previous studies have reported that different genotypes can diverge ecologically (Darling et al., 2000; de Vargas et al., 2001; De Vargas et al., 2002; Huber et al., 1997), implying that reconstructions were based on individuals

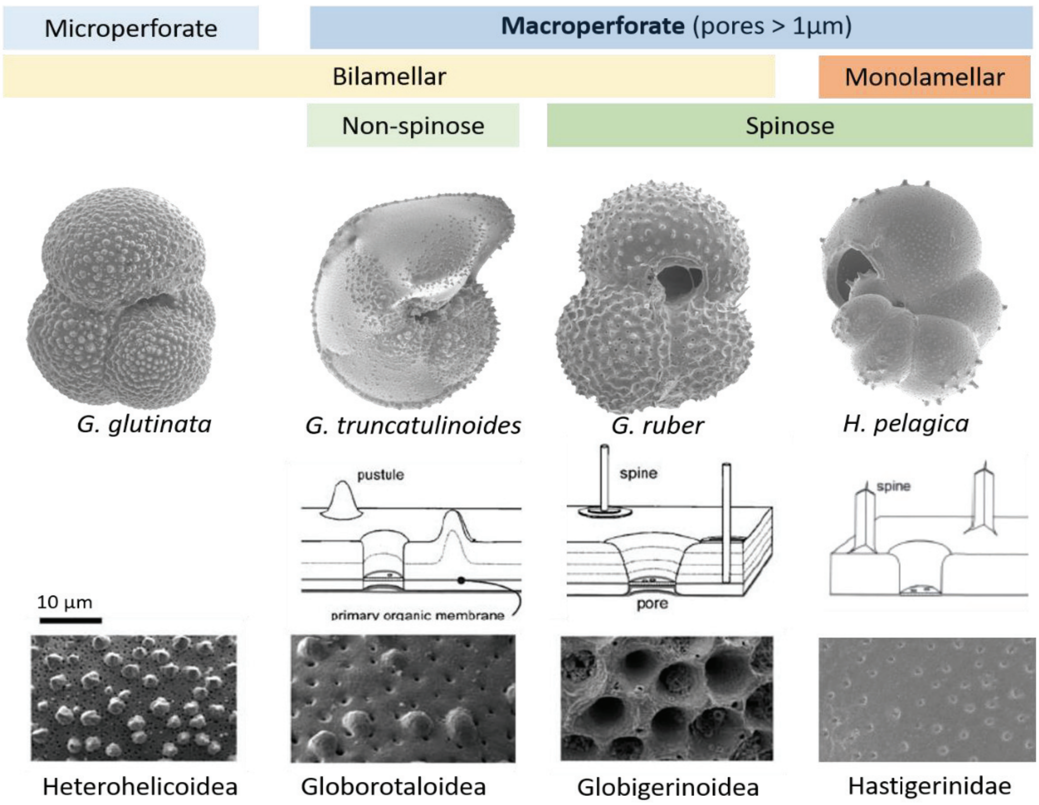

**Fig. 2 –** Scheme showing the four morphogroups of modern planktonic foraminifera. The groups' division is based on wall structure and shell ornamentation such as pores, pustules and spines. For each group, a typical specimen is represented. (Modified from Schiebel and Hemleben, 2005 and Kucera, 2007).

belonging to various genotypes with different ecological preferences. This would add a significant noise to paleoceanographic reconstructions (Darling et al., 2000).

Even though the biological definition of species is difficult to apply, since the majority of the species do not complete a full life cycle under laboratory culture conditions, the morphologic variability of some of the planktonic foraminifera species happen to coincide with distinct genotypes (André et al., 2014; De Vargas et al., 2002). Many of these genotypes show distinct patterns of geographic distribution being restricted to ocean basins or regions (Darling and Wade, 2008; Morard et al., 2011; Weiner et al., 2015). Others appear to be associated to sea surface temperature (Darling et al., 2000) or show distinct ecological preferences such as different trophic requirements (de Vargas et al., 2001; De Vargas et al., 2002). However challenging, combining the new evidence from the genotypes with the existing morphotypes provides an opportunity to redefine planktonic foraminifera classification. By being capable of recognizing cryptic species in the fossil record, the accuracy and reliability of planktonic foraminifera as a paleoceanographic tool could be greatly improved.

### 1.2.3 Ecology and distribution of planktonic foraminifera

Several environmental parameters affect the population dynamics of planktonic foraminifera both at species and assemblage level. The main factors that regulate population dynamics are the physical and chemical parameters of the water masses, abundance and type of nutrients and reproductive strategies of individual species (Hemleben et al., 1989). High flux rates of planktonic foraminifera shells follow pulses of primary productivity associated with seasonal hydrographic changes, with a lag of several days (Schiebel et al., 2001). This results in a succession of planktonic foraminifera species, starting with the opportunistic species after a pulse of primary productivity such as *Globigerina bulloides* and *Globigerinita glutinata* (Schiebel and Hemleben, 2005; Thiede, 1975). Afterwards, when the available food starts declining, these species' number decrease and the typical regional fauna is established (Schiebel and Hemleben, 2000). As a result, species' abundance changes throughout the year and the abundance peaks can occur at different times. This seasonal component is reflected in the variation of the oxygen isotope ratios of planktonic foraminifera. Thus,

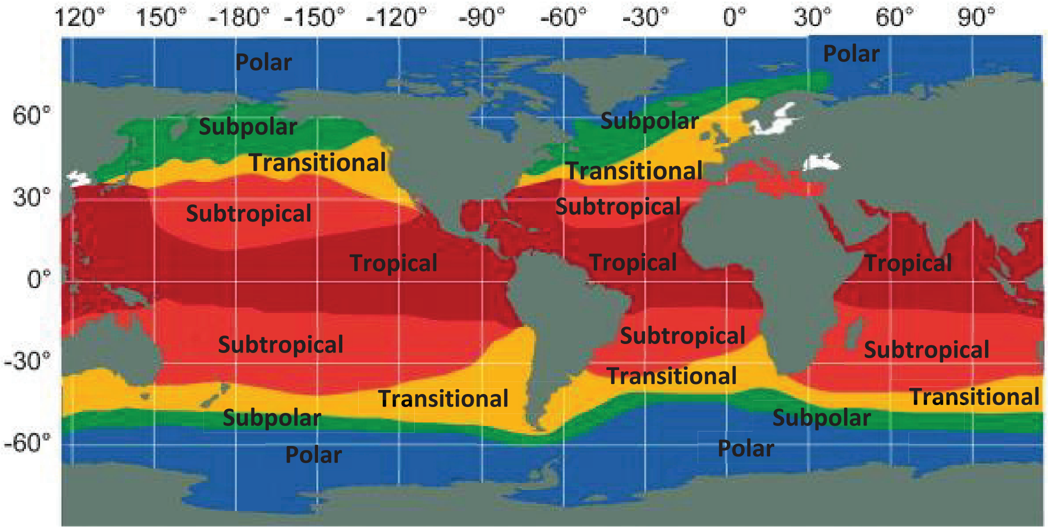

**Figure 3** - Planktonic foraminifera provinces in the modern ocean. The distribution of the province (Be, 1977; Vincent and Berger, 1981) follows sea-surface temperature gradients, reflecting the strong relationship between sea surface temperatures and species abundances.(From Kucera, 2007).

a record of the seasonal temperature variations of the ocean surface should remain preserved in the marine sediments, and could in theory be used to obtain information on past seasonal differences (Ganssen et al., 2011).

Due to their physiology, feeding, behaviour and reproduction, planktonic foraminifera species exhibit a wide range of environmental preferences, which influence directly their temporal and spatial distributions and are recorded in their shell (Hemleben et al., 1989). On the one hand, the resulting distribution patterns provide important insights into the relationships between these organisms and their environment. On the other hand, it is fundamental to understand the drivers of the distribution, as a prerequisite for robust interpretation of paleoceanographic proxies. Spatially, the occurrence of planktonic foraminifera is distributed into five major faunal provinces: polar, subpolar, temperate, subtropical, and tropical (Fig. 3) (Bé and Tolderlund, 1971; Kucera, 2007). These faunal provinces typically follow sea-surface temperature (Bé and Tolderlund, 1971; Bijma et al., 1990). However, they do not necessarily correspond to the patterns exhibited by planktonic foraminifera in surface waters, as the relative abundance and flux peaks of different species are affected by changes in seasonal hydrographic conditions, such as upwelling and currents (Ottens, 1991). In addition, most planktonic foraminifera species are eurythermal, surviving under a wide temperature range of 15 – 25 °C (Bé and Tolderlund, 1971; Hilbrecht, 1997). Hence, other factors besides temperature determine the abundance of the various species, including the type and abundance of prey or nutrient demands, turbidity versus water transparency, luminosity or hydrodynamics of water bodies (Erez and Luz, 1983; Hemleben et al., 1989; Schiebel et al., 2001; Spindler et al., 1984). Polar regions are usually dominated by *Neogloboquadrina pachyderma,* whereas a higher diversity and larger sizes appear gradually towards the equator, with the most diverse assemblages inhabiting the subtropical waters (Fig. 3) (Bé and Tolderlund, 1971; Schmidt et al., 2004). This pattern has been explained by the higher number of ecologic niches available within the water column in the tropics compared to the polar regions. The sea-surface temperature rise from the polar regions to the tropics is coupled to an increase in stratification, which creates more ecologic niches and provides a higher diversity of species and the separation of potential competing species (Al-Sabouni et al., 2007; Schmidt et al., 2004).

According to their ecological needs, each planktonic foraminifera species prefers a typical depth habitat in the water column. Traditionally, the vertical distribution of planktonic foraminifera has been thought to be mainly affected by food availability (Fairbanks and Wiebe, 1980; Schiebel et al., 2001), with highest abundances coinciding with maximum chlorophyll concentrations (Fairbanks and Wiebe, 1980; Field, 2004; Schiebel et al., 2001). In addition, the habitat depth of planktonic foraminifera species is also influenced by the requirement of light in case of a symbiotic bearing species (e.g. Bé et al., 1982; Vincent and Berger, 1981; Weiner et al., 2012), vertical migration during species ontogeny (e.g. Bijma et al., 1990; Hemleben et al., 1989), vertical mixing (e.g. Friedrich et al., 2012) and upwelling (Schiebel et al., 1997; Thiede, 1975), and small to mesoscale hydrographic features such as fronts and eddies (Schiebel et al., 2002; Siccha et al., 2012; Steinhardt et al., 2015). Consequently, the habitat depth of individual species is known to vary regionally and seasonally. Vertical abundances give us information on the distribution of planktonic foraminifera species, their preferential habitat depth and the environmental conditions associated with their preference (e.g. Fairbanks et al., 1980; Field, 2004; Hemleben et al., 1989; Kuroyanagi and Kawahata, 2004; Schiebel et al., 2002). However, the influence of the specific environmental factors affecting each individual species of planktonic foraminifera is challenging to determine, since most of the surface water properties are strongly intercorrelated (Kucera, 2007).

## 1.3 Regional Setting: The Subtropical Eastern North Atlantic

The habitat of individual species of planktonic foraminifera is particularly varied in mid-latitude settings, where large seasonal shifts are combined with steep and variable vertical gradients in the water column (e.g. Schiebel and Hemleben, 2005). This is the case of our study area, which comprises the subtropical eastern North Atlantic, a region influenced by the subtropical gyre circulation, the Azores Current and seasonal upwelling (Fig. 4). The subtropical gyre circulation is composed of two different subsystems: the Canary and Iberian upwelling regions, divided by the Strait of Gibraltar (e.g., Barton et al., 1998). In the Strait of Gibraltar, a water mass exchange between the Mediterranean Outflow Water and North Atlantic Water occurs (Relvas et al., 2007). The entrainment of the North Atlantic Water into the Mediterranean

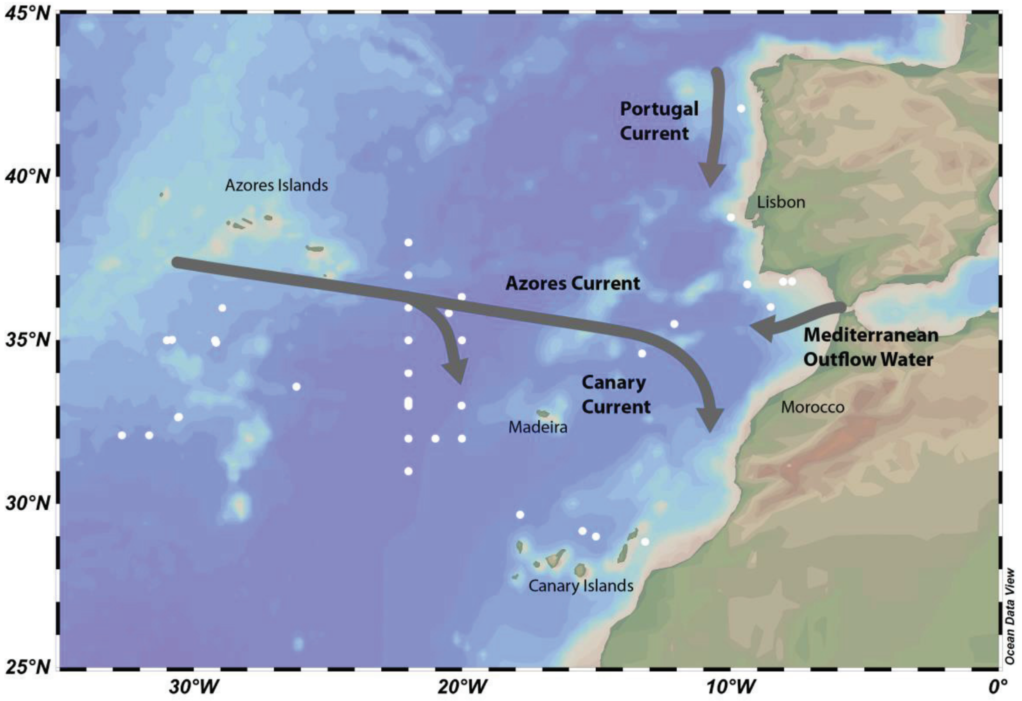

**Fig. 4** – Location of the stations (white dots) with vertical hauls of plankton nets used in this study and major oceanographic currents in the eastern North Atlantic (adapted from Voelker et al., 2015).

Outflow Water is thought to be essential for the establishment of the Azores Current (Jia, 2000; Özgökmen et al., 2001). The Azores Current initiates in the southern branch of the Gulf Stream (Sy, 1988), crosses the Mid Atlantic Ridge and extends eastward between 32° and 36° N (Gould, 1985; Klein and Siedler, 1989). This current can be as deep as 2000 m, with a width varying between 60 and 150 km (Alves et al., 2002; Gould, 1985) and flows all year-round with a variable seasonal transport (Alves et al., 2002). Strong mesoscale eddies and active meanders occur in the Azores Current (Alves et al., 2002; Fernández and Pingree, 1996; Gould, 1985). Southeast of the Azores Islands, the Azores Current divides into a northern ramification that flows towards the Portugal Current and a southern branch that joins the Canary Current (Barton, 2001; Sy, 1988). The Canary Current moves south-eastward from the African coast to the North Equatorial Current (Alves et al., 2002), links to the Caribbean Current and fuses with the Gulf Stream (Barton, 2001). The subtropical gyre’s northern limit is the Azores Current’s northern branch, which functions as a frontier between the warmer (18° C), saltier and oligotrophic waters of the Sargasso Sea and the colder, fresher and more productive waters of the northern and eastern North Atlantic (Gould, 1985). The associated thermohaline front is called the Azores Front and a 42 years-long study observed that the Azores Front's position varied between 30° and 37.5° N. Moreover, its movement appears to be related to the North Atlantic Oscillation (Fründt and Waniek, 2012). This front is associated with a strong change in temperature (~4° C) and in the water column structure, affecting the distribution of planktonic organisms including foraminifera (Alves et al., 2002; Schiebel et al 2002a, 2002b), and increasing pelagic biomass and production (Le Fevre, 1986). At mid-latitude regions an increase in the mixing depth of the surface waters, accompanied by recycling of nutrients and changes in light intensity, triggers primary productivity during spring and autumn. These primary productivity pulses cause different planktonic foraminifera species to respond (see 1.3), resulting in a faunal succession which is characteristic for each ecosystem (e.g., Schiebel et al., 2001). More productive than the seasonal bloom at the Azores Front are the coastal upwelling regions in our studied area. Along the western Iberian margin, upwelling typically occurs from April to October, when the northern winds become more intense and the surface layer becomes more stratified (Fiúza, 1983; McGregor et al., 2007; Peliz et al., 2007; Wooster et al., 1976). North of 25° N, off northwest Africa, upwelling occurs along with the seasonal variation of the northeast trade winds during summer and autumn (e.g. Barton et al., 1998).

Over the last decades, paleoreconstructions of the ocean circulation have postulated that the North Atlantic is of central importance in the thermohaline circulation (Curry and Oppo, 2005; Shackleton et al., 2000). It is thought that during extreme cold events, freshwater discharges in this region led to a weakening or shutdown of the thermohaline circulation, altering the whole ocean-climate system (Broecker, 1994; Cortijo et al., 1995). In this context, our study region is a benchmark for the understanding of abrupt climate change variability. However, despite decades of intense research (e.g. De Abreu et al., 2003; Meggers et al., 2002; Salgueiro et al., 2010; Shackleton et al., 2000), the understanding of planktonic foraminifera ecology in this region is not yet complete, especially in its eastern part. Thus, to improve the use of planktonic foraminifera as archives of past ocean conditions, the modern environmental preferences and habitats of individual species need to be understood. Mid-latitude areas are challenging for the development of foraminifera proxies (Chapman, 2010; De Abreu et al., 2003; Martrat et al., 2007; Salgueiro et al., 2010), but hold great promise in being able to reconstruct aspects of the surface-ocean structure, which are highly informative for the understanding of dynamic processes in the ocean.

## 1.4 Motivation and objectives

To increase the potential of planktonic foraminifera as a proxy in the interpretation and reconstruction of past ecosystems and the relation between past and modern environments, it is essential to improve the current knowledge on their biology and ecology. One way to do this is by analysing the populations and communities in their natural environment together with the environmental parameters. In this context, the main objective of this study is to contribute to a better understanding of the biology and ecology of modern planktonic foraminifera in the eastern part of the North Atlantic in order to ultimately facilitate better-constrained proxy calibrations for paleoclimate reconstructions. To this end, plankton-tow samples from stratified vertical hauls were used together with the environmental parameters measured at the time of collection to allow a direct comparison between the living planktonic foraminifera organisms and ambient environmental conditions. This PhD project aims more specifically to address the following questions:

1. What is the habitat depth of individual species of planktonic foraminifera species and what are the potential controlling factors (temperature, chlorophyll, mixed layer depth, seawater density, lunar and seasonal cycle) affecting its variation?

2. How is the regional distribution of planktonic foraminifera species affected by the environmental factors? How does species diversity change with temperature?

3. What is the calcification depth of each species? Does calcification depth coincide with maximum abundance depth?

## 1.5 Material and methods

### 1.5.1 Sampling strategy of planktonic foraminifera

As paleoceanographic studies become more advanced, the need to understand how the planktonic foraminifera fauna reflects the surrounding environment increases. Each planktonic foraminifera species has its own preference for temperature, water depth for calcification, food type, etc.; however, these preferences may vary in time and space (Hemleben et al., 1989). In this context, only studies at a regional scale of the ecological preferences of each individual species of planktonic foraminifera will serve to interpret paleocenographic data more accurately.

In recent years, laboratory cultures, observations from sediment traps and plankton tows provided a major contribution to a better understanding of planktonic foraminifera ecology. Each of these three commonly used methods in the study of planktonic foraminifera ecology have advantages and limitations. Laboratory cultures allow a continuous observation of planktonic foraminifera species under controlled environmental parameters. However, planktonic foraminifera do not complete their life cycle in laboratory cultures (Kucera, 2007; Schiebel and Hemleben, 2017), implying that this artificial environment is not representing the natural environment of the foraminifera and the observations may not be representative of their behavior in the ocean.

By allowing seasonal quantification of shell fluxes, sediment traps are the best means to study the seasonality in planktonic foraminifera species (Jonkers and Kucera, 2015; Storz et al., 2009; Žarić et al., 2005). However, since sediment traps only sample the export flux, they do not provide direct constraints on the vertical habitat of the sampled species. Sampling by stratified plankton tows, such as with a multiple opening-closing net device, is one of the only methods that allows a synchronous assessment of the relationship between environmental variables (temperature, salinity, nutrients, oxygen and light) and species abundance. It provides access to information on species abundances with depth, shell sizes and isotopic composition, in their natural environment, enabling a straightforward correlation between faunal assemblages and environmental parameters of the water column. In addition, it is the only method that can directly constrain the vertical depth habitat of each planktonic foraminifera species. Plankton nets do, however, have their limitation as the assemblages are not fully sampled, because individuals smaller than the net mesh are disregarded (Schiebel and Hemleben, 2017). Furthermore, this sampling method represents only a snapshot, in time and space, and the observations may be affected by spatial inhomogeneity (Siccha et al., 2012). Nevertheless, taking our objectives into consideration, this sampling type is the most appropriate method for our study.

In the present study we used samples from 13 oceanographic campaigns performed between 1995 and 2012 across different seasons and collected between 20º to 43°N and 8º to 40°W (Table 1; Fig. 1). The sampling was done using either a Hydro Bios Midi or Maxi multiple closing net (mesh size of 100 µm; opening of 50 x 50 cm) hauled upward in vertical position with a velocity of 0.5 ms$^{-1}$. Considering the local oceanographic settings and due to time constrains the sampling resolution scheme varied between 4 and 9 levels, sampling to maximum depth of 700 m, and in each case until at least a depth of 100 m. After sampling, the net content was preserved either with a saturated $HgCl_2$ solution or 4% formaldehyde buffered with hexamethylenetetramine ($C_6H_{12}N_4$) to a pH of 8.2 and stored in a refrigerating unit.

**Table 1.** Oceanographic campaigns during which plankton net samples were collected with corresponding year, respective season, person who did the species identification and thesis chapter where samples were used.

| Cruise | Year | Season | Taxonomy[a] | Chapters |
|---|---|---|---|---|
| Poseidon 212/1 | 1995 | Autumn | H. M. | 2, 3 |
| Victor Hensen 96/2 | 1996 | Winter | H. M. | 2, 3 |
| Poseidon 231/3 | 1997 | Summer | R. S. | 2 |
| Poseidon 237/3 | 1998 | Spring | H. M. | 2, 3 |
| Meteor 42/1 | 1998 | Summer | H. M. | 2, 3 |
| Meteor 42/3 | 1998 | Summer | R. S. | 2 |
| Poseidon 247/2 | 1999 | Winter | R. S. | 2 |
| Poseidon 334 | 2006 | Spring | A. R/ I. F. | 2, 3 |
| Poseidon 349 | 2007 | Spring | – | 4 |
| Poseidon 377 | 2008 | Autumn | A. R. | 2, 3 |
| Poseidon 383 | 2009 | Spring | A. R. | 2, 3, 4 |
| Poseidon 384 | 2009 | Spring | A. R. | 2, 3, 4 |
| Iberia-Forams | 2012 | Summer | A. R. | 2, 3. 4 |

[a]Taxonomy: H.M.= Helge Meggers; R.S.= Ralf Schiebel; I.F.= Igaratza Fraile; A.R.=Andreia Rebotim

### 1.5.2 Planktonic foraminifera processing

Planktonic foraminifera individuals were picked from the wet samples using the binocular microscope and left to air dry. All specimens from each sample were counted and identified to a species level by different persons (Table 1) in the fraction above either 100 or 125 µm following the taxonomy of Brummer and Kroon (1988), Hemleben et al. (1989) and Spezzaferri et al. (2015). In case of doubt, a scanning electron microscope (SEM) was used to confirm the identification. This was essential in the case of the smallest species such as *Tenuitella parkerae, Tenuitella fleisheri, Tenuitella iota, Dentigloborotalia anfracta* and *Turborotalita clarkei* whose SEM pictures are included in Chapter 3. Living specimens (cytoplasm bearing) were counted separately from dead specimens (partially or entirely free of cytoplasm), with exception of the samples of the POS 349 oceanographic campaign which were only used in Chapter 4 (Table 1). Since the morphological characteristics are not completely developed in the juvenile forms, the specimens of *Globigerinoides ruber – Globigerinoides elongatus* and *Globigerinella siphonifera - Globigerinella radians* were not distinguished and classified under the respective more common species name.

Abundance data (total or for each species) per cubic meter ($m^3$) were calculated by dividing the number of specimens counted in each plankton net sample by the volume of water filtered through the plankton net during the vertical haul across the respective depth interval (square shape opening*length of the depth interval).

Before each plankton net haul, water column properties such as temperature, chlorophyll and salinity were measured *in situ* using a CTD (conductivity-temperature-depth) device. During several cruises, the CTD was coupled to a water sampler rosette, which during the ascent was used to collect water samples (e.g., for stable isotope analyses). Stations where an *in situ* fluorescence profile was not available, chlorophyll *a* concentrations were extracted from NASA's satellite Ocean Color Web database (https://oceancolor.gsfc.nasa.gov) for the same day as the plankton net haul, or the 8-day or monthly composite depending on the nearest approximation to the date of collection and the closest coordinates to the station. For the oceanographic campaigns performed before July of 1997, no chlorophyll data was available where no CTD data was obtained. The data analysis done with the counted planktonic foraminifera species data and the used environmental parameters are described in detail within each manuscript.

### 1.5.2 Oxygen stable isotopes analysis

Cytoplasm-bearing shells of four planktonic foraminifera species (*Globorotalia truncatulinoides, Globorotalia hirsuta, Globorotalia inflata* and *Globorotalia scitula*) were picked from two size fractions (150 – 300 µm and >300 µm; referred to as small- and large-sized, respectively). If not in sufficient number, the different size fractions (>150 µm) or cytoplasm-bearing with cytoplasm-free specimens were merged from the same depth interval. In addition, encrusted and non-encrusted shells were also separated with exception of the samples of the POS 349 oceanographic campaign. For the stable isotope analysis, according to the species and size fraction, specimens were weighted to estimate the number of specimens needed (varying from 3 to 20 specimens). *G. truncatulinoides* and *G. hirsuta* shells are usually heavier and therefore fewer individuals are needed to perform oxygen isotope analysis while *G. inflata* and *G. scitula* shells are usually lighter and more specimens are required.

The stable oxygen isotopes analyses were carried out with a Finnigan MAT 251 isotope ratio mass spectrometer coupled to a Kiel I or Kiel III automated carbonate device at MARUM, University of Bremen. Oxygen isotopic ratios were expressed in the $\delta$-notation and calibrated to Vienna Pee Dee Belemnite (VPDB) scale using the NBS-19 standard. The analytical precision of an in-house carbonate standard (Solnhofen limestone) during the measurement period was ≤0.04 ‰ (1 s.d.).

Oxygen isotopic equilibrium values were calculated using temperature and salinity data obtained from the CTD measurements at the time of sample collection and the paleotemperature equations of Shackleton (1974) and Kim and O'Neil (1997). The conversion from VSMOW to VPDB was done by subtracting 0.2 ‰ from the $\delta^{18}O$ value(s) of the ambient seawater (e.g., Pearson, 2012) for the Shackleton (1974) equation and 0.27 ‰ (Hut, 1987) for the Kim and O'Neil (1997) equation, respectively. A regional $\delta^{18}O_w$ – salinity relationship was established using measurements done in the study area (25°N to 45°N and 5°W to 35°W) (Voelker et al., 2015) of the top 700 m of the water column, as this was the maximum depth used for the planktonic foraminifera sampling. Finally, we compared the oxygen isotope ratios with the vertical abundance of the measured planktonic foraminifera species.

## 1.6 Thesis outline and author contributions

This thesis is based on the results of three case studies presented in the form of manuscripts that are published (Chapter 2), submitted (Chapter 4) or under preparation to be published (Chapter 3) in international peer-reviewed scientific journals. A resume of each manuscript and the respective contribution is presented below.

### 1.6.1 Thesis outline

**Chapter 2**: **Factors controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic**

Andreia Rebotim, Antje H. L. Voelker, Lukas Jonkers, Joanna J. Waniek, Helge Meggers, Ralf Schiebel, Igaratza Fraile, Michael Schulz, Michal Kucera.

**Status:** Published in *Biogeosciences*, 2017, 14, 827 – 829.
https://doi.org/10.5194/bg-14-827-2017

The depth habitat of planktonic foraminifera species remains poorly constrained and existing conceptual models are not sufficiently tested by observational data. Here we present a synthesis of living planktonic foraminifera abundance data in the subtropical eastern North Atlantic from vertically resolved plankton tows. We use the data to test potential environmental factors influencing the species depth habitat and investigate yearly or lunar migration cycles. The results indicate that depth habitats differ among species and vary within species, but a substantial part of the variation is predictable. A better understanding of depth habitats has implications for the interpretation of geochemical signals in fossil foraminifera preserved in marine sediments when doing paleoceanographic reconstructions.

The study was designed by AR, AV, MS and MK. The samples were collected and prepared by AR, AV, JW, HM, RS and IF. The data analysis and interpretation was carried out by AR, MK and LJ. AR wrote the manuscript with feedback and additional lines of discussion provided by AV, LJ and MK.  The revision benefitted from feedback by AV, LJ, JW, RS, MS and MK.

### Chapter 3: Environmental factors controlling the spatial distribution of living planktonic foraminifera in the subtropical eastern North Atlantic

Andreia Rebotim, Antje H. L. Voelker, Joanna J. Waniek, Michael Siccha, Michael Schulz, Michal Kucera

**Status:** In preparation

To address how the regional distribution of planktonic foraminifera species is influenced by environmental factors, we compiled living planktonic foraminifera abundance data from different locations of the subtropical eastern North Atlantic. An analysis of the data reveals the presence of specific regional and seasonal faunal assemblages usually associated with multiple environmental parameters. These findings indicate that the temperature signal that appears to be the main determinant of composition of fossil assemblages is the product of seasonal and interannual accumulation of different living assemblages.

This study was designed by AR, AV, MS and MK. The data was acquired by AR. The data analysis and interpretation was carried out by AR, MS and MK. The manuscript was written by AR with contributions by AV and MK.

### Chapter 4: Calcification depth of deep-dwelling planktonic foraminifera from the eastern North Atlantic constrained by stable oxygen isotope signals of shells from stratified plankton tows

Andreia Rebotim, Antje H. L. Voelker, Lukas Jonkers, Joanna J. Waniek, Michael Schulz, Michal Kucera

**Status:** Submitted to *Journal of Micropaleontology*

Deep-dwelling species of planktonic foraminifera provide a unique opportunity to reconstruct subsurface conditions of the water column. However in order to use their full potential it is essential to understand how the isotopic signal is incorporated in their shell. Here we report $\delta^{18}O$ of shell calcite in four deep-dwelling *Globorotalia* species sampled in the eastern North Atlantic with vertical plankton tows. We assessed the size and crust effect in each of the species and compared the $\delta^{18}O$ values obtained by each species with predictions given by two paleotemperature equations. The results revealed different patterns of calcite addition with depth and isotopic equilibrium, highlighting the necessity to carry out extensive species-specific calibrations.

The study was designed by AR, AV, LJ, MS and MK. The samples were collected and prepared by AR. The data analysis and interpretation was carried out by AR, AV, LJ and MK. The manuscript was written by AR with feedback from LJ, AV and MK.

### 1.6.2 Description of own contributions

The material presented in this thesis and used in all the case studies comprises samples collected during different oceanographic campaigns (POS 349, POS 377, POS383, POS 384 and Iberia-Forams) between 2008 and 2012. Among these, I participated myself in the collection of samples on board the RV Poseidon (POS 377 and POS 383) and RV Garcia del Cid (Iberia-Forams). All the samples from the above mentioned oceanographic campaigns were processed (wet sieving, foraminifera wet picking, air drying) by me.

For chapter 2 and 3 all shells of planktonic foraminifera presented in the samples were isolated, separated by the presence of cytoplasm identified to a species level using a binocular microscope and counted. Taxonomic training and advice was provided by M. Kucera. In addition to this data, species abundance data from H. Meggers (POS 212/2, VH 96/2, POS 237/3 and M42/1), I. Fraile (POS 334) and R. Schiebel (M 42/3, POS 247/2, POS231/3) were compiled and organized by me and used in chapter 2 and/or 3. The oceanographic data from the respective cruises where the samples were collected were also compiled and arranged by me. The statistical analysis performed in chapters 2 and 3, were done by me with consultations from M. Kucera and M. Siccha. For chapter 3, I also compiled already published data from the same study area and with a similar collection methodology for comparison with the more recent data.

For the stable isotope analysis (chapter 4) I selected and picked foraminifera specimens from the samples (already processed) and weighted them. The regional seawater oxygen isotopic relationship estimation and the oxygen equilibrium values calculation was done by me under the advice of L. Jonkers and A. Voelker. The data organization and analysis were done with the consultation of L. Jonkers.

The first versions of the three manuscripts (chapters 2, 3 and 4) were written by me but were modified on the basis of comments by the listed co-authors and (in the case of chapter 2) the referees.

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# Chapter 2

## 2.1 First case study

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

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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-

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

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## 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-

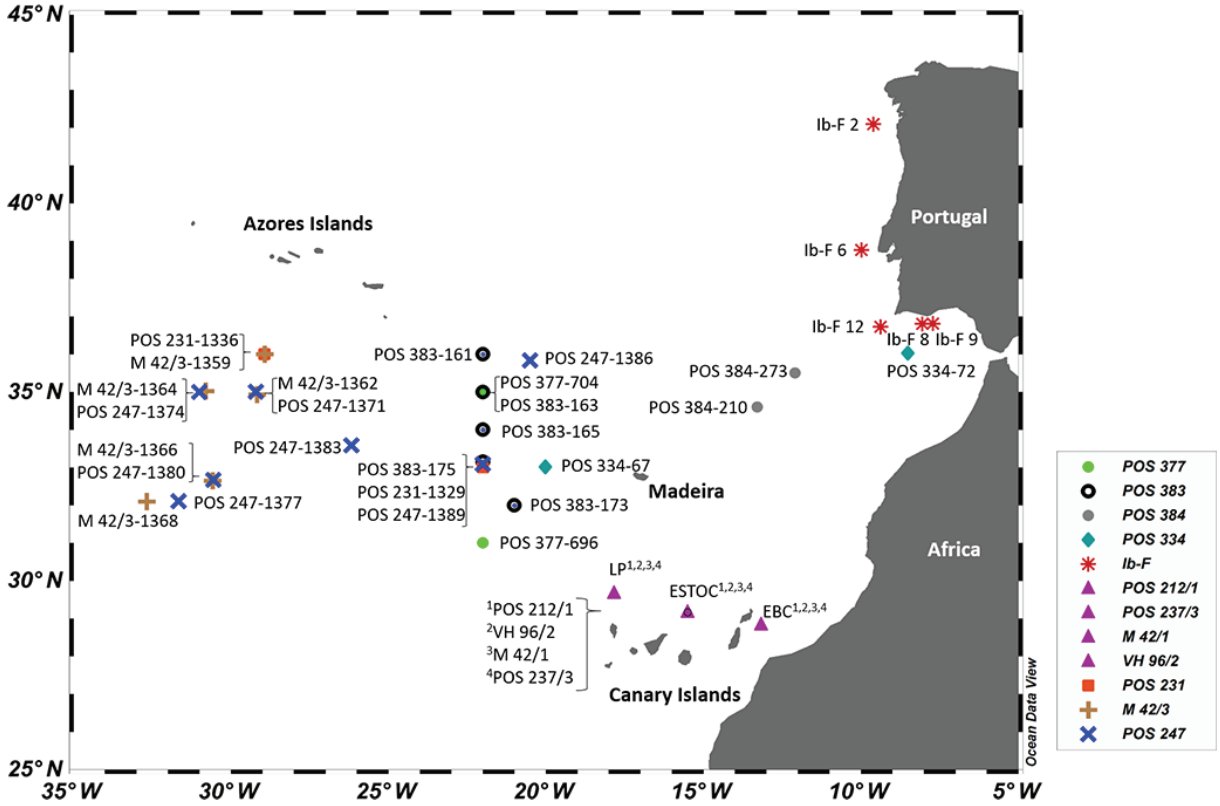


**Figure 1.** Plankton net stations in the eastern North Atlantic with vertically resolved planktonic foraminifera assemblage counts that were used in this study. The stations are coded by cruises. Superscript and brackets indicate repeated sampling at the same positions (for details see Table 1). Map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

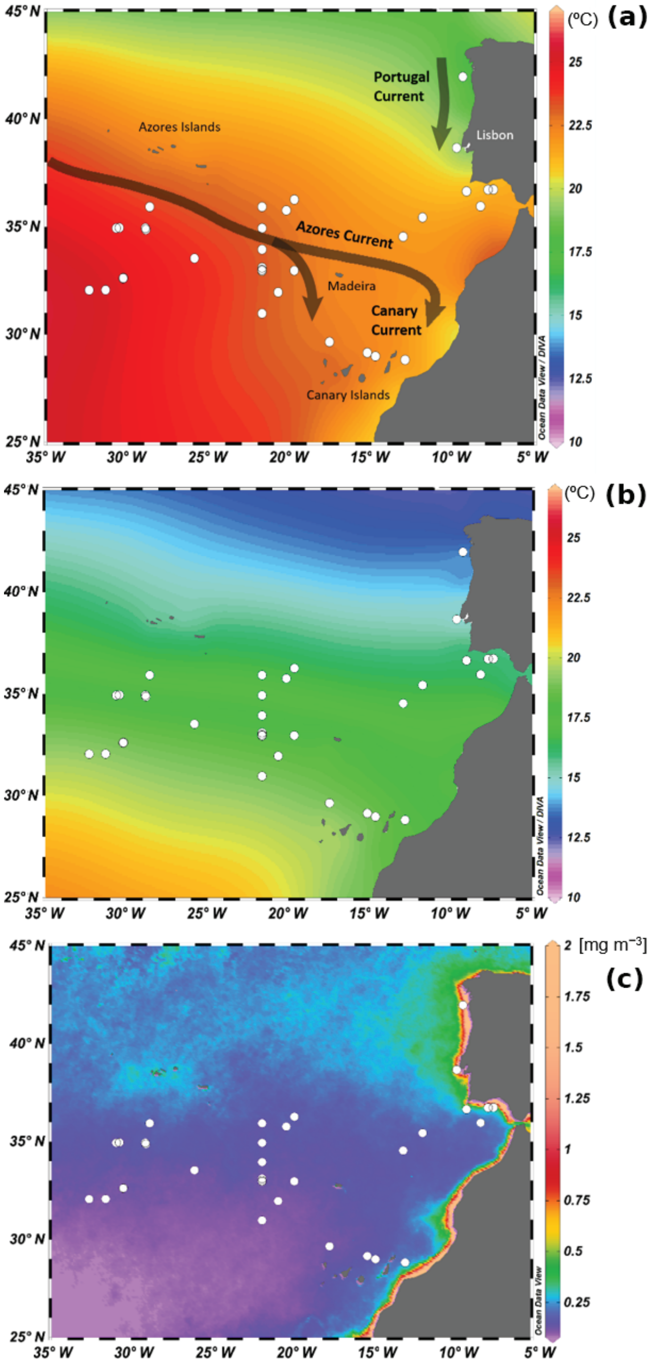


**Figure 2.** **(a)** Mean summer (July to September, from 1955 to 2012) SST (sea-surface temperature) (data from World Ocean Atlas 2013) with main surface currents shown by arrows, **(b)** mean winter (January to March, from 1955 to 2012) SST (data from World Ocean Atlas 2013) and **(c)** mean monthly 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 $0.5\,\mathrm{m\,s^{-1}}$. 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 100µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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 | > 125µm | 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]<br>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)<br>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 $\mathrm{m}^{-3}$):

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

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.

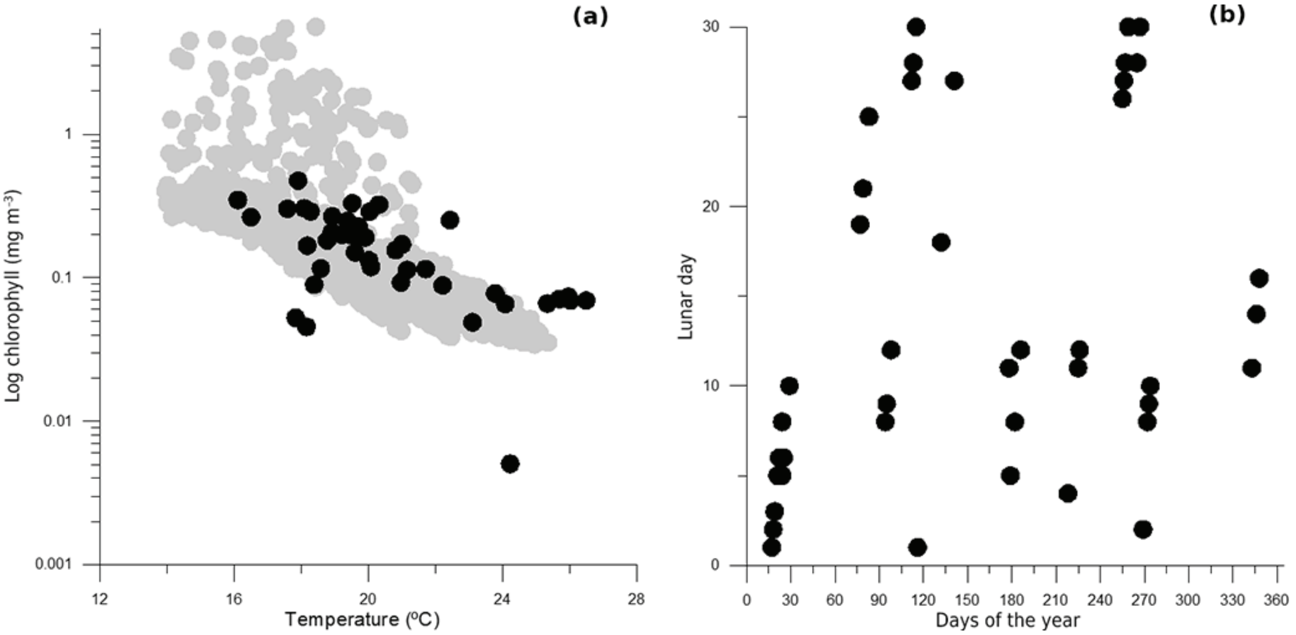


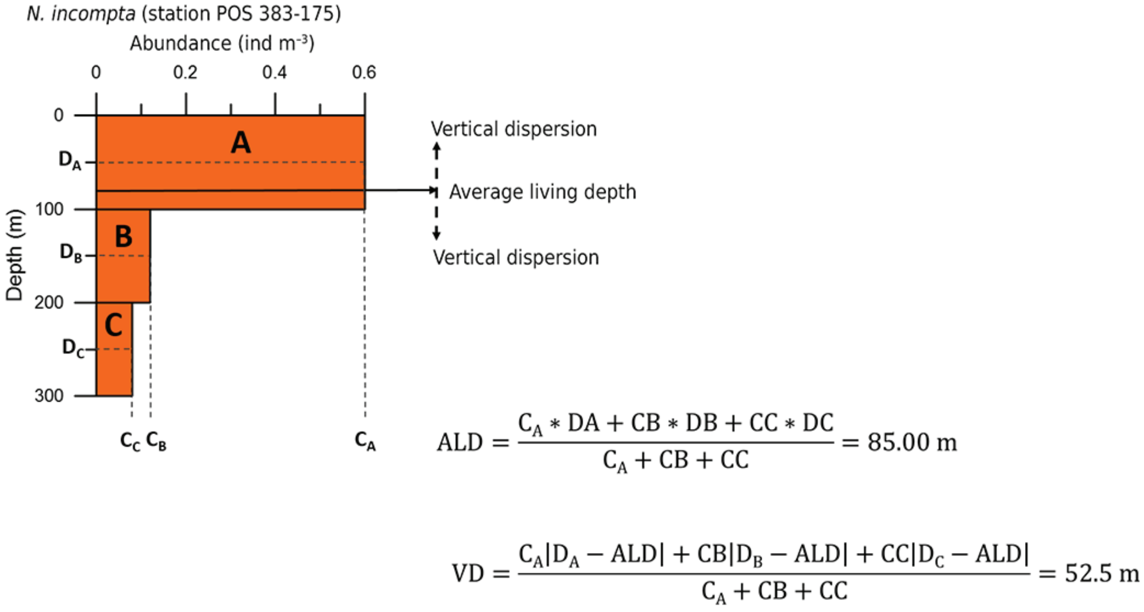
**Figure 3.** Coverage of the ecological space of planktonic foraminifera in the studied region by the sampled stations. **(a)** Gray symbols show the covariance between mean monthly SST (sea-surface temperature) (MIMOC: Monthly Isopycnal/Mixed-layer Ocean Climatology; Schmidtko et al., 2013) and chlorophyll (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).

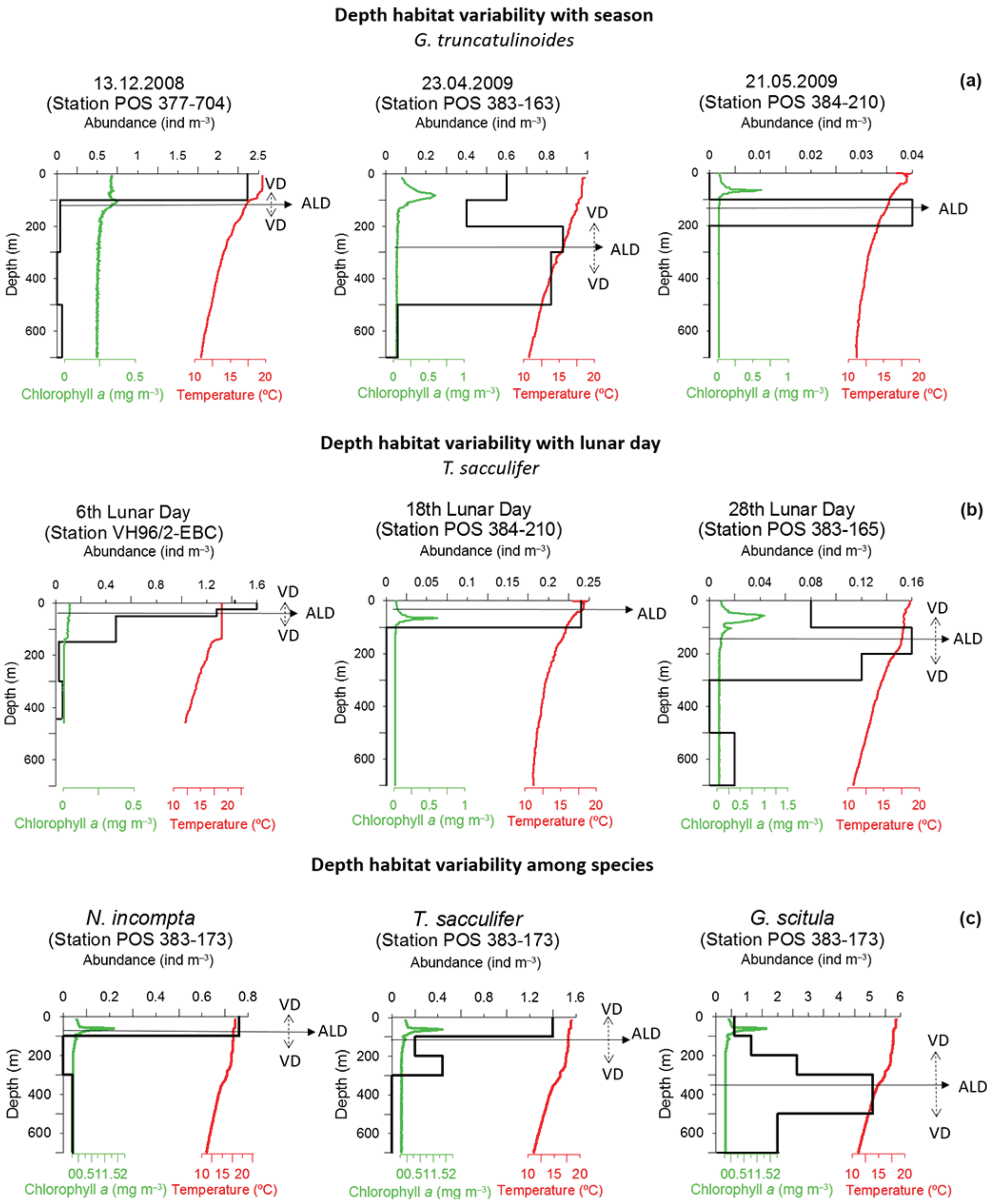


**Figure 5.** Examples of potential environmental parameters affecting vertical habitat of planktonic foraminifera in the studied region. **(a)** Vertical distribution of one species in the Azores region at different times of the year, showing apparent changes in ALD with season. Also plotted is the 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).

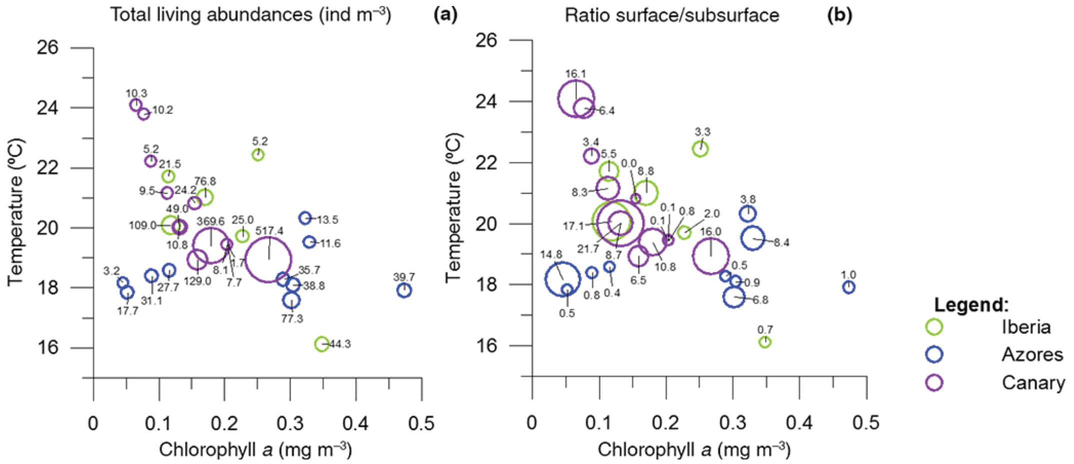


**Figure 6.** Total abundance given by circles size in the three regions from the study area of **(a)** living planktonic foraminifera and **(b)** the partitioning of the living population between surface and subsurface at the studied stations (Fig. 1) as a function of in situ mixed-layer interval mean 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-

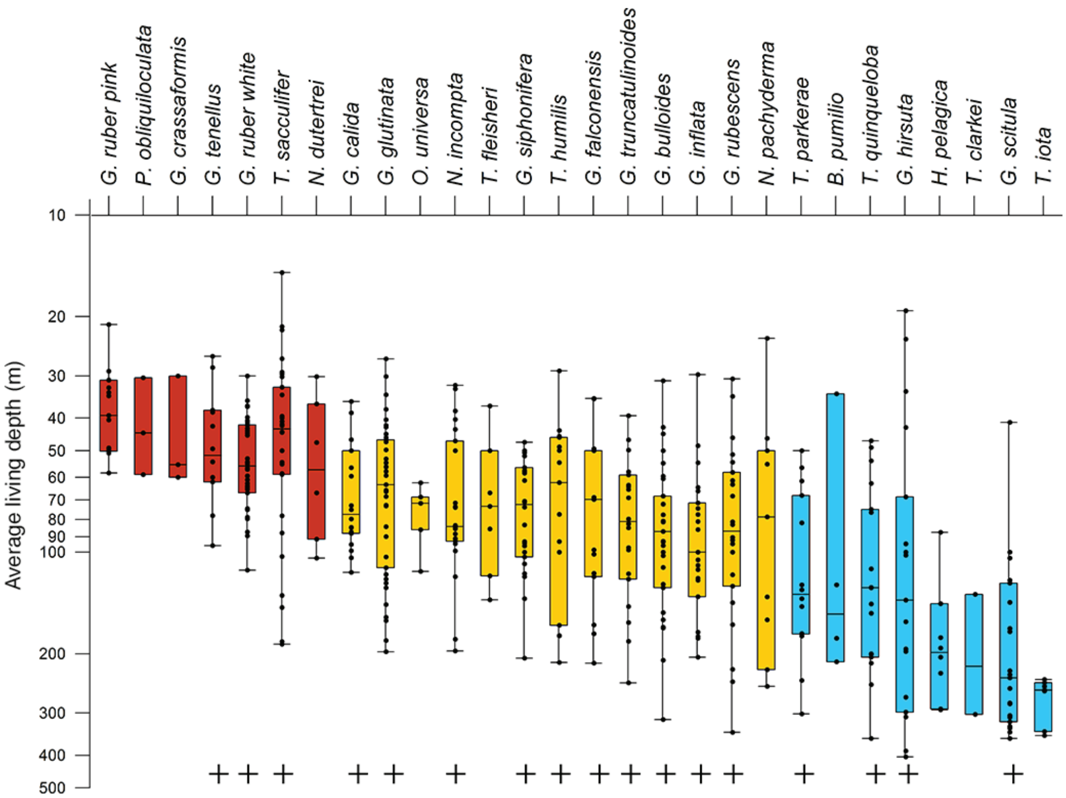


**Figure 7.** Average living depths of the 28 most abundant species of planktonic foraminifera obtained from analysis of 43 vertically resolved plankton hauls (Fig. 1, Table 1). Values are only shown for stations where at least five individuals of a given species have been counted. The box and whiskers 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

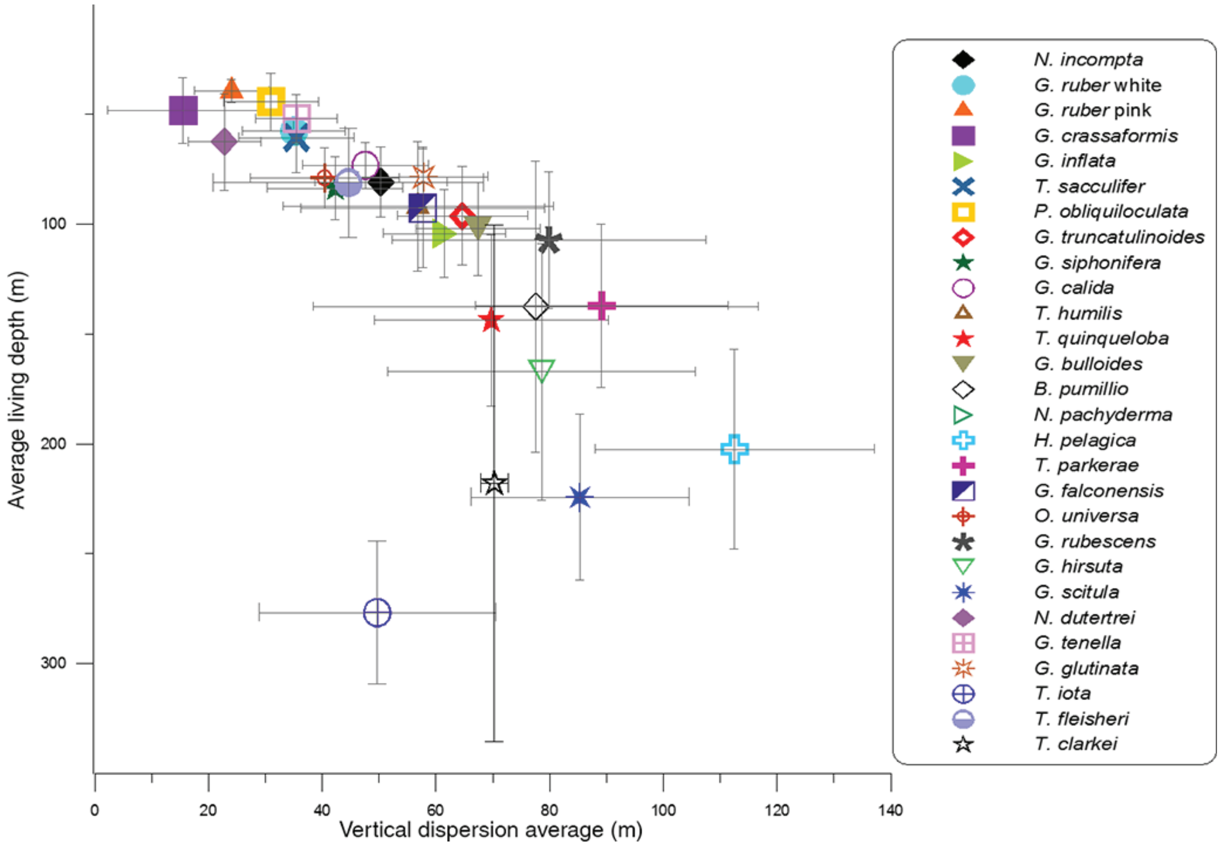


**Figure 8.** Relationship between the mean ALD and the mean vertical dispersion of the habitat of the 28 most abundant species of planktonic foraminifera analyzed in this study. Symbols are showing mean values, bars indicate 95 % confidence intervals and colored ellipses are used to highlight species 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

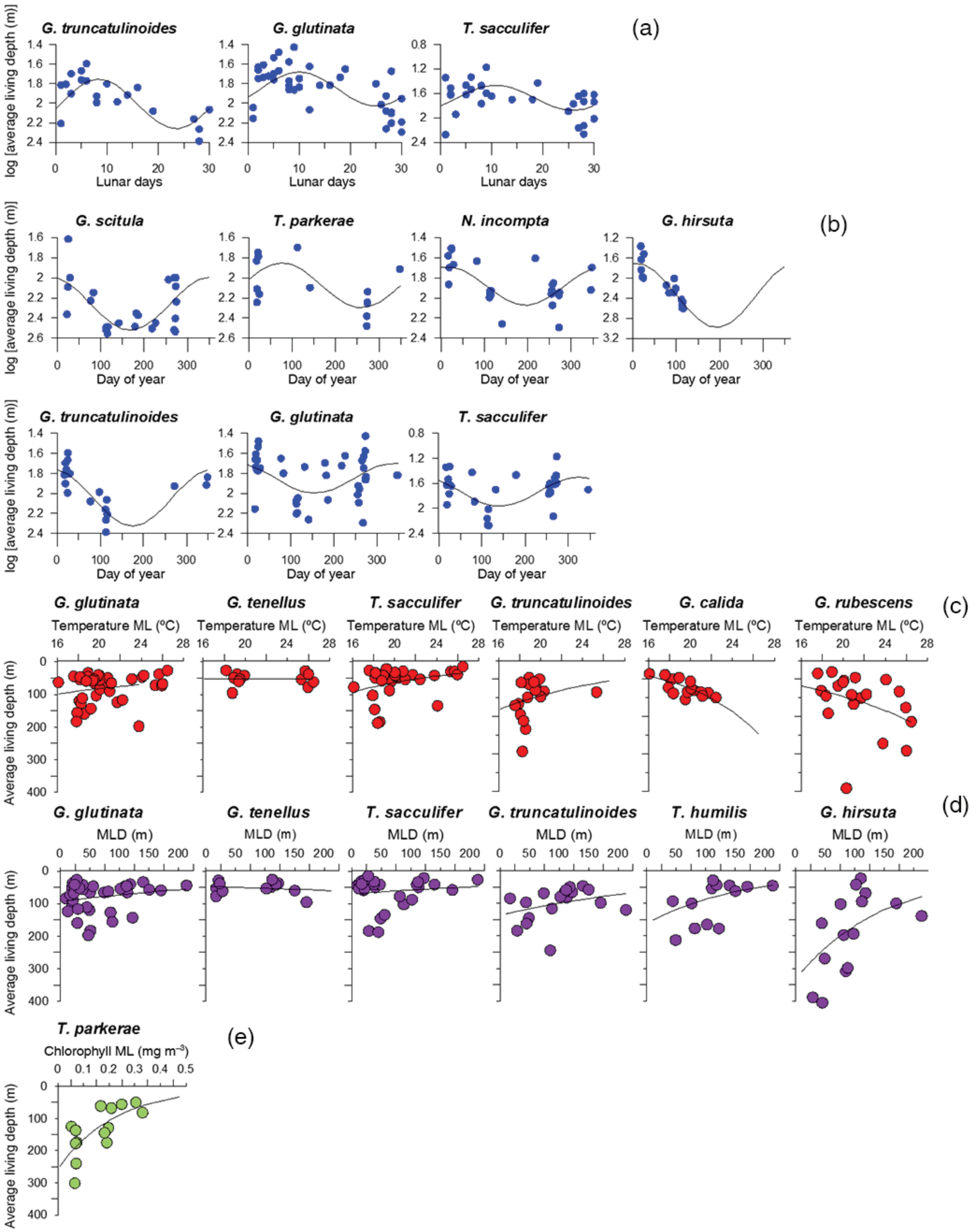


**Figure 9.** Comparison of modeled and observed ALD in species where ALD appears to be predictable ($p < 0.05$, Table 3) by **(a)** lunar cycle, **(b)** yearly cycle, **(c)** mean temperature in the mixed layer interval, **(d)** mixed layer depth and **(e)** mean chlorophyll $a$ concentration in the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

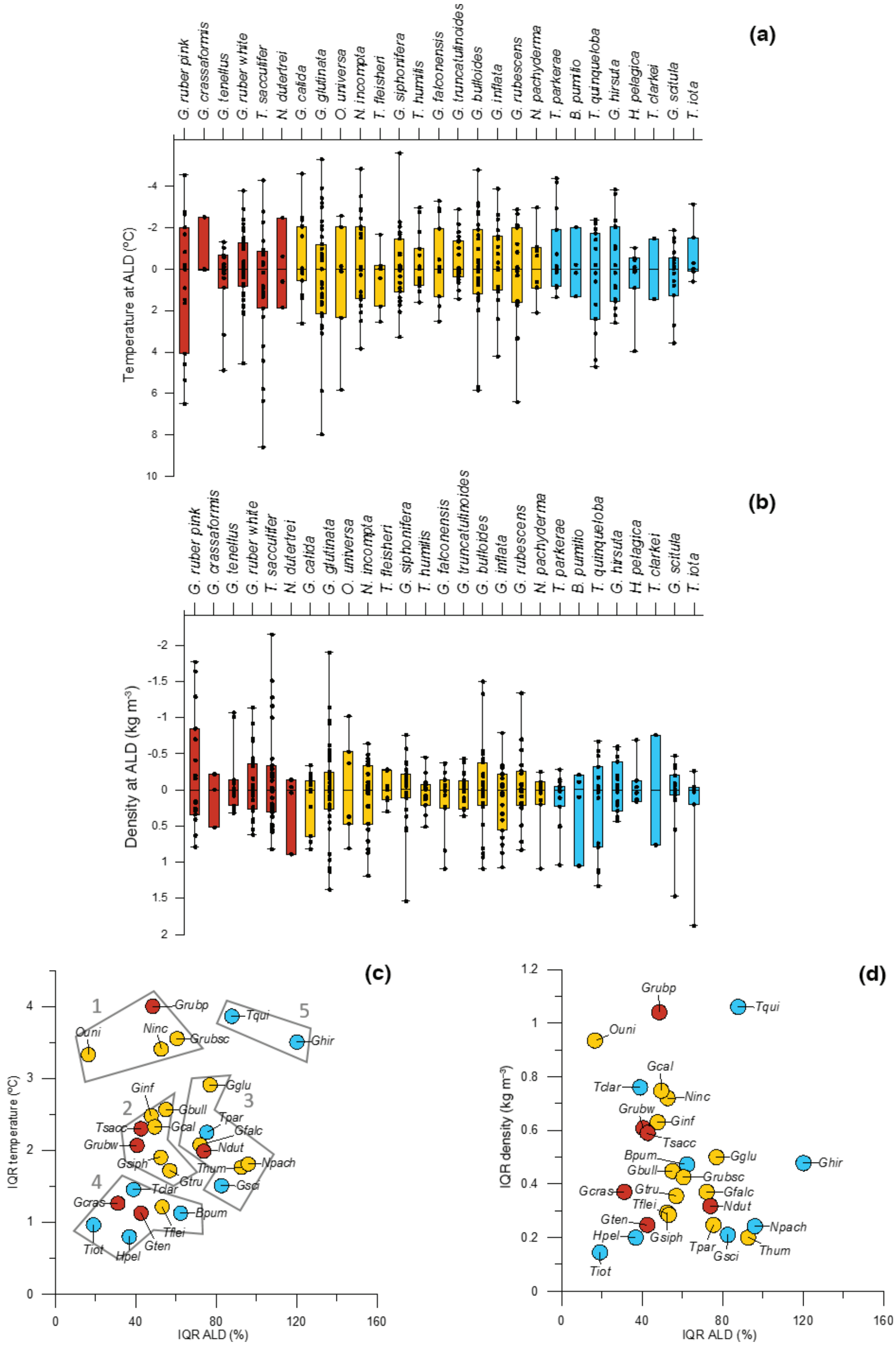


**Figure 10.** **(a)** Average temperature (°C) at ALD and **(b)** average seawater density (kg m$^{-3}$) at ALD for the 27 most abundant species normalized to the median value for each species and **(c)** relationship between the interquartile range of temperature (°C) at ALD (kg m$^{-3}$) and interquartile 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 $T_{\mathrm{ALD}}$ and narrow relative ALD range; 3 – species with intermediate $T_{\mathrm{ALD}}$ range and variable relative ALD; 4 – species with narrow $T_{\mathrm{ALD}}$ and narrow relative ALD; 5 – species with variable $T_{\mathrm{ALD}}$ 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 ($T_{\mathrm{ALD}}$) is considered:

1. Species showing a large spread in $T_{\mathrm{ALD}}$ 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 $T_{\mathrm{ALD}}$ 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 $T_{\mathrm{ALD}}$ 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 $T_{\mathrm{ALD}}$ 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 $T_{\mathrm{ALD}}$ 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 $\sigma_{\mathrm{ALD}}$ inhabit the most variable habitat, as they also showed the largest spread in $T_{\mathrm{ALD}}$. 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 $\sigma_{\mathrm{ALD}}$ 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

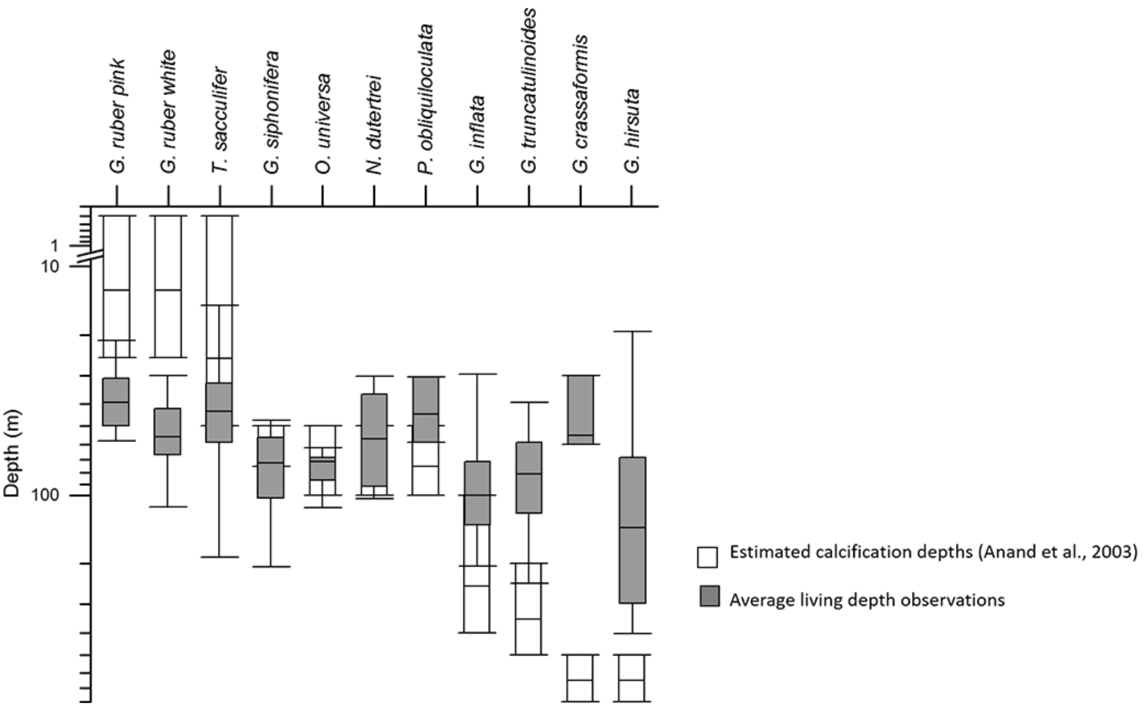


**Figure 11.** Estimated calcification depth based on $\delta^{18}$O values of species of planktonic foraminifera from the Sargasso Sea and the calcite in equilibrium with seawater (white; Anand et al., 2003) and the average living depth based on observations of living specimens from vertically resolved 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 counterintuitive. 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 $T_{\mathrm{ALD}}$ 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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## Supplementary material

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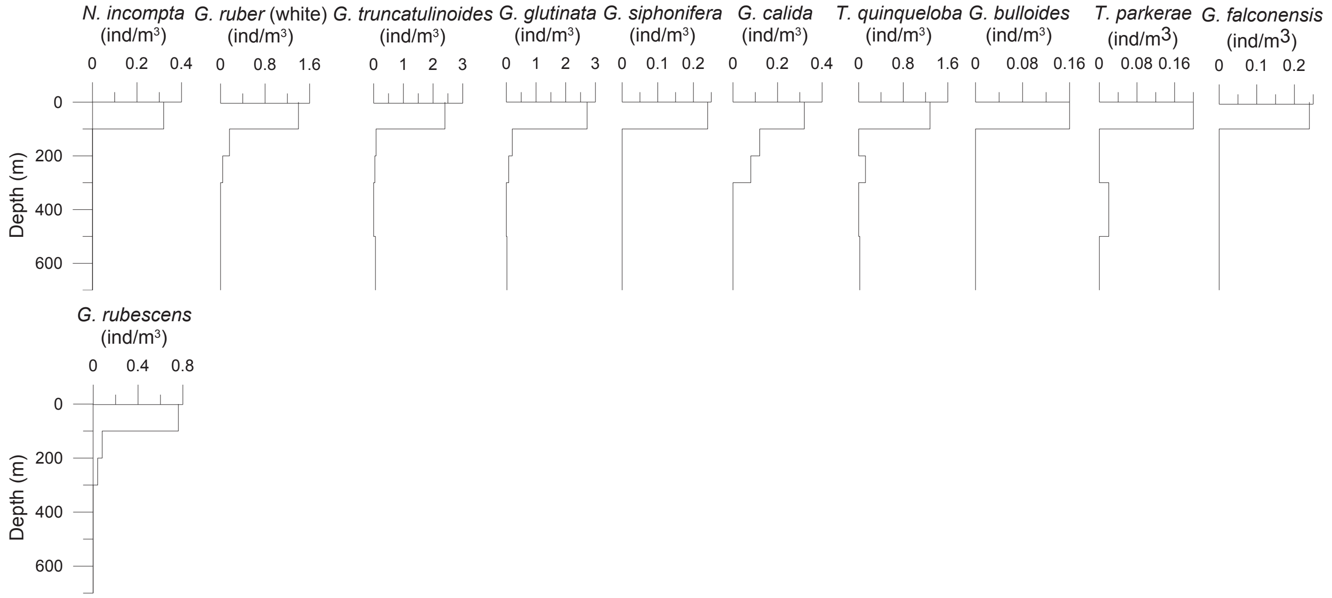
### Station 696

### Station 704



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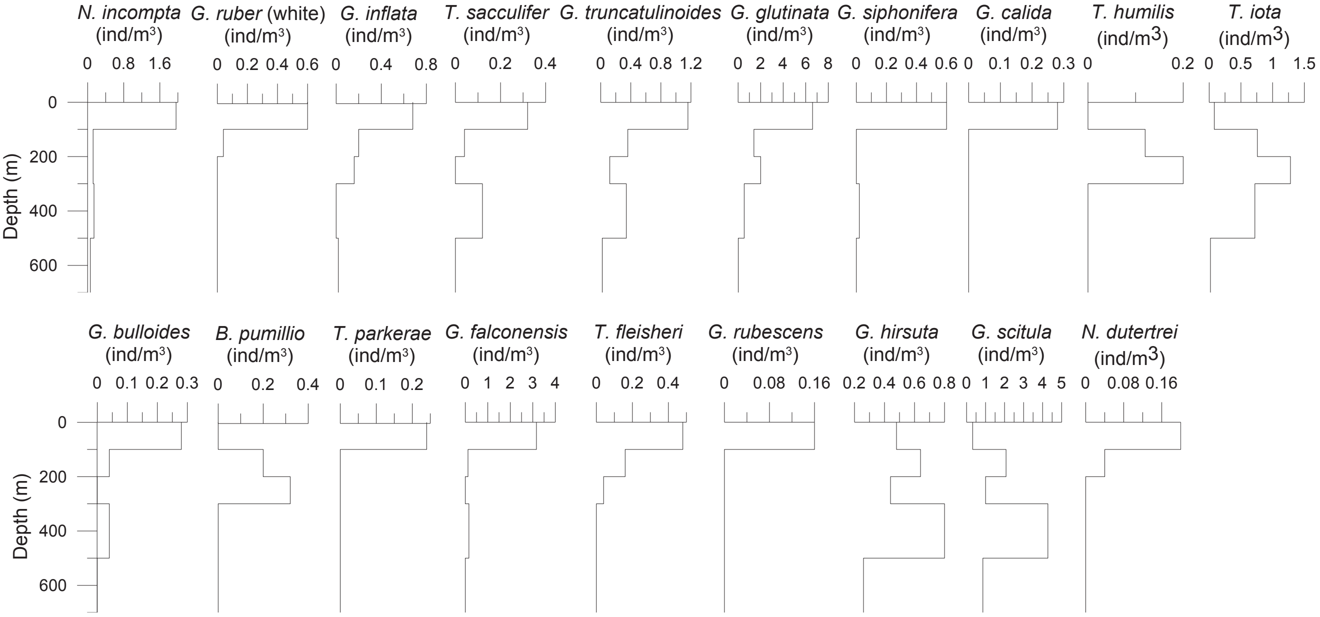

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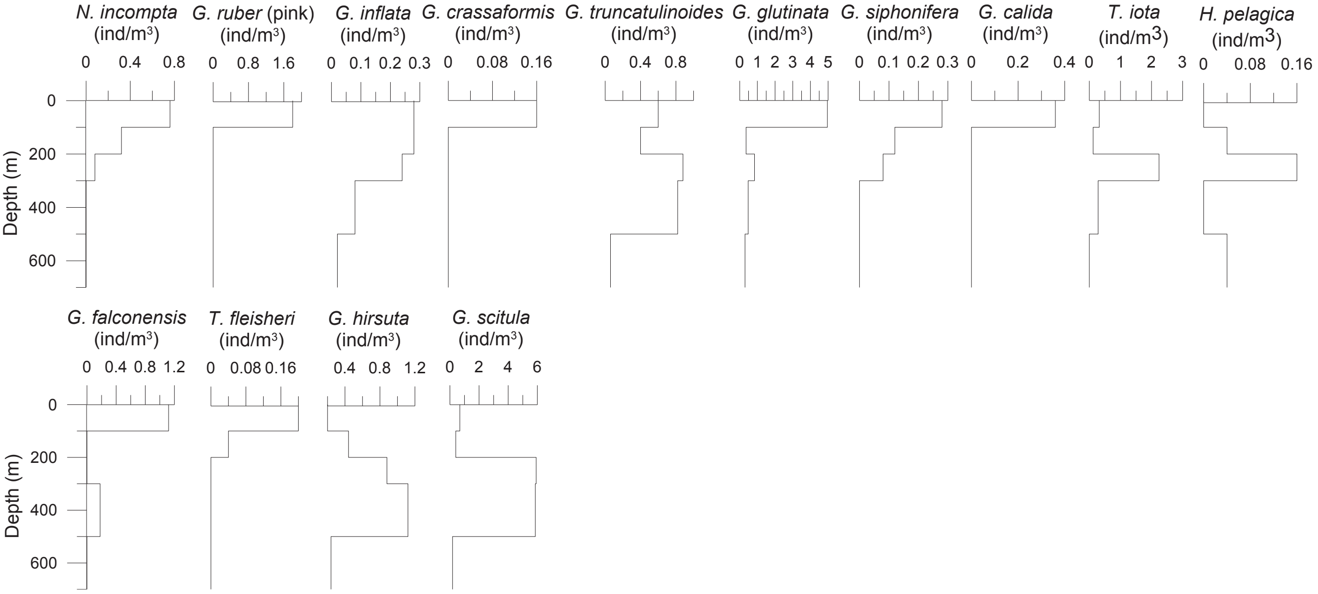

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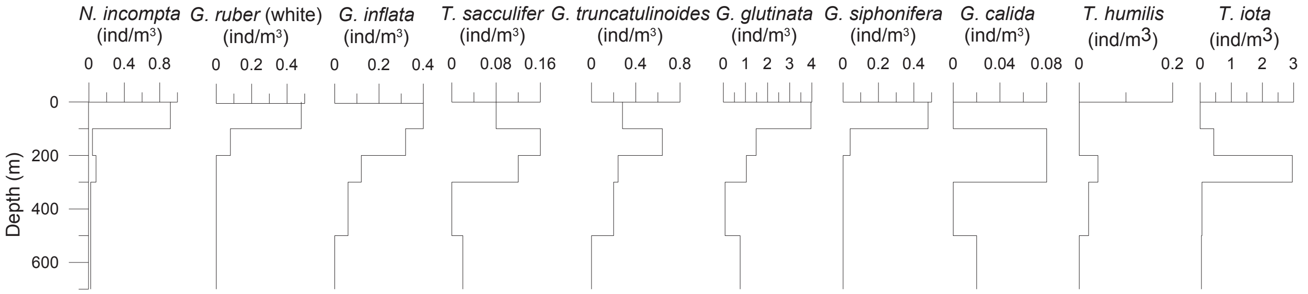

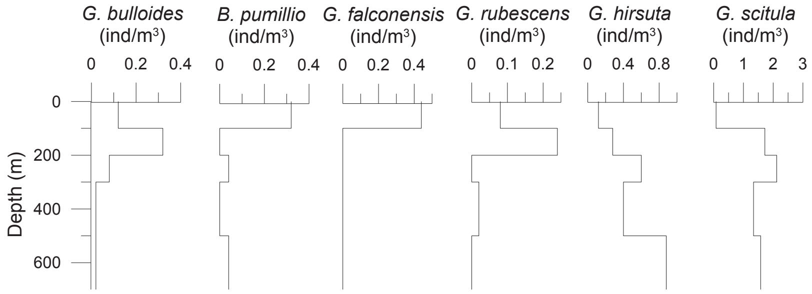

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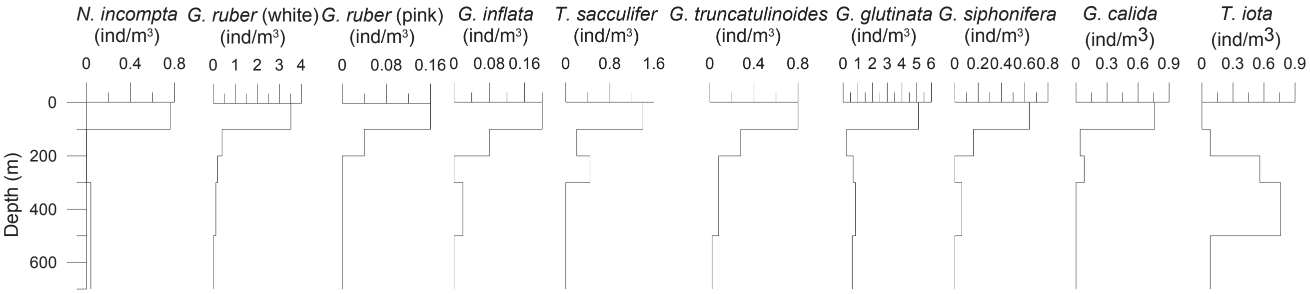

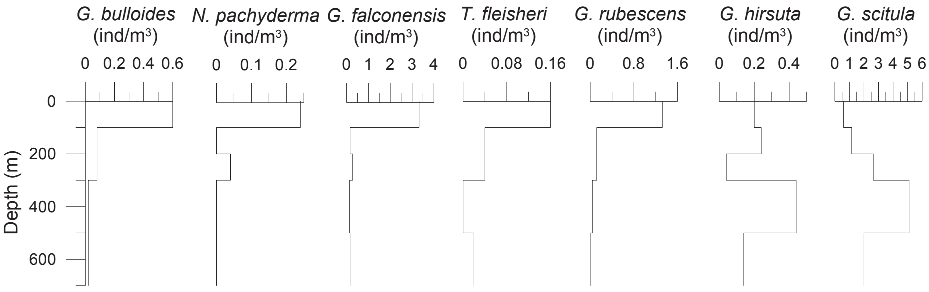

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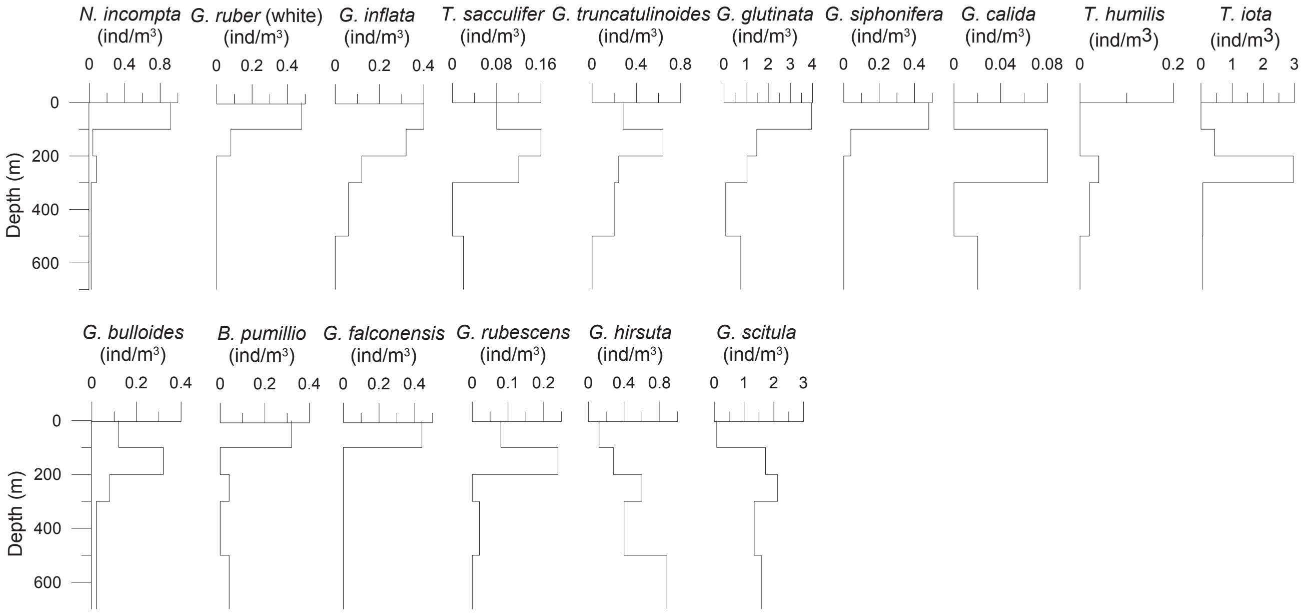

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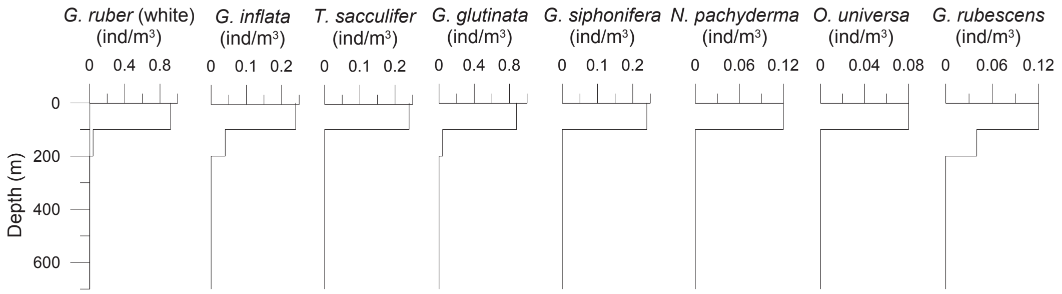

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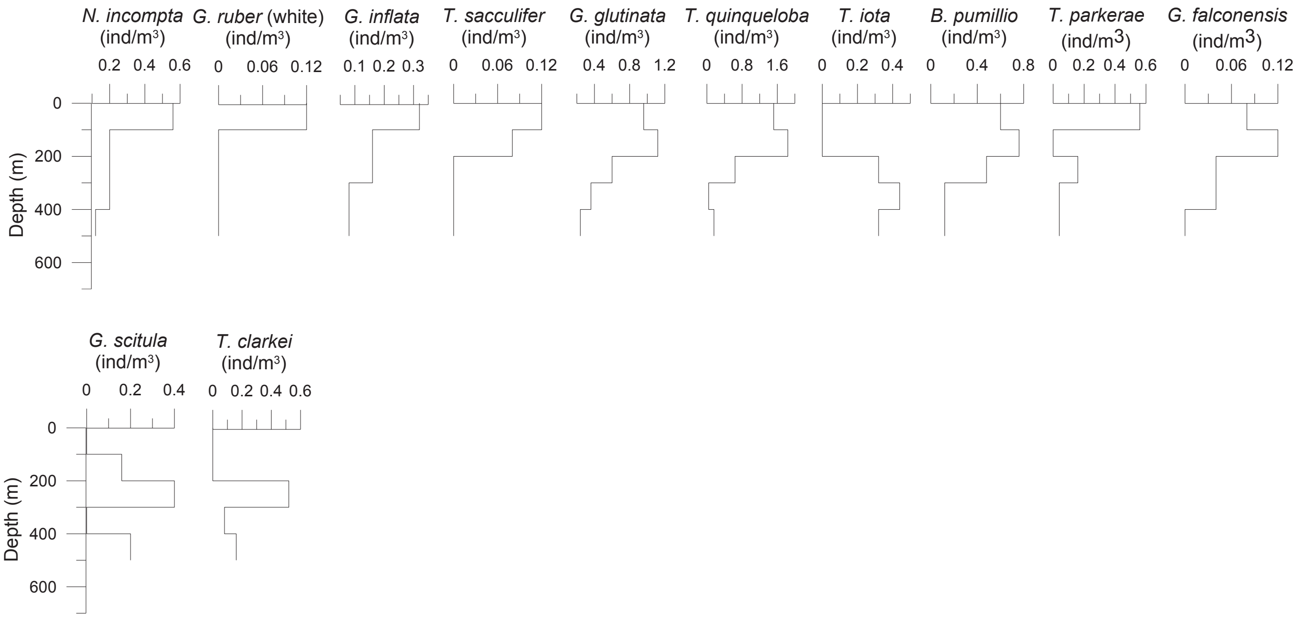

# Iberia-Forams

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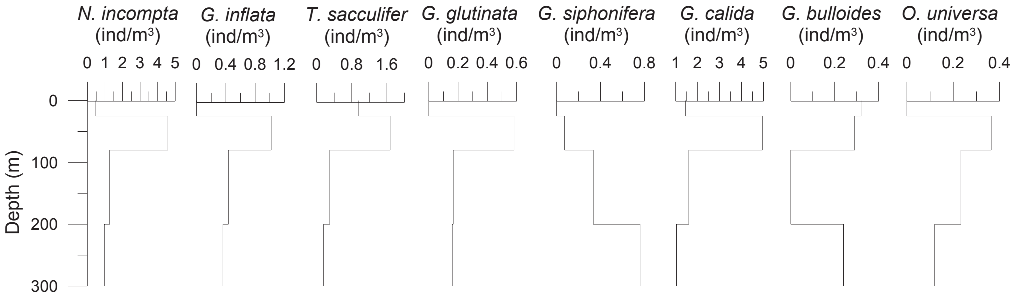

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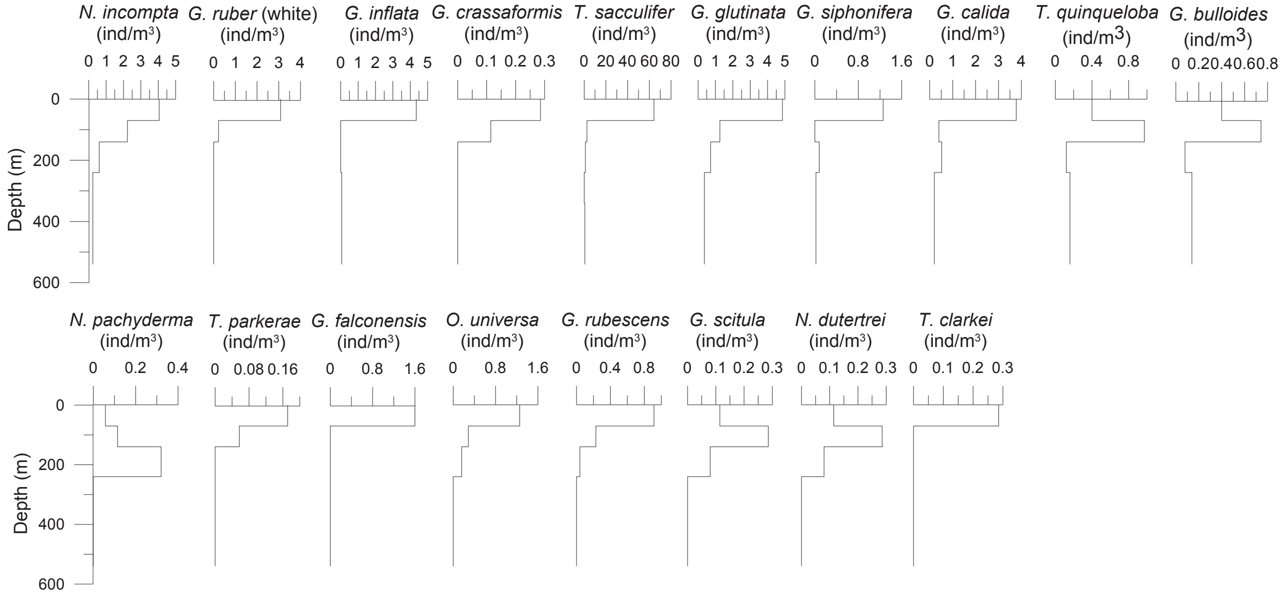

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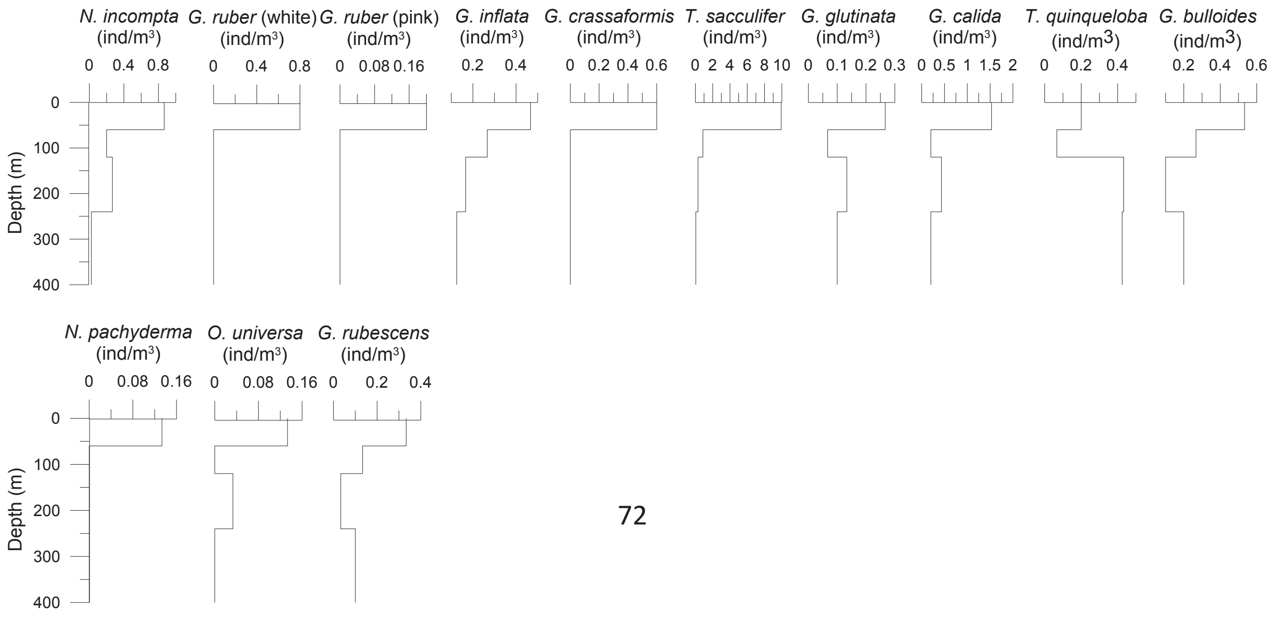

# Iberia-Forams

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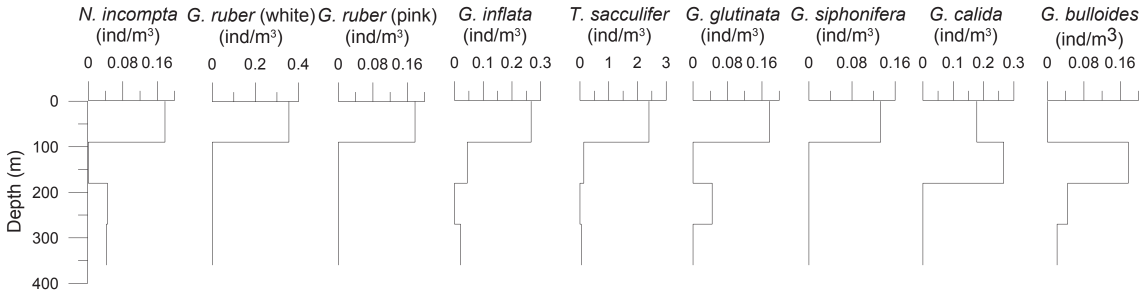

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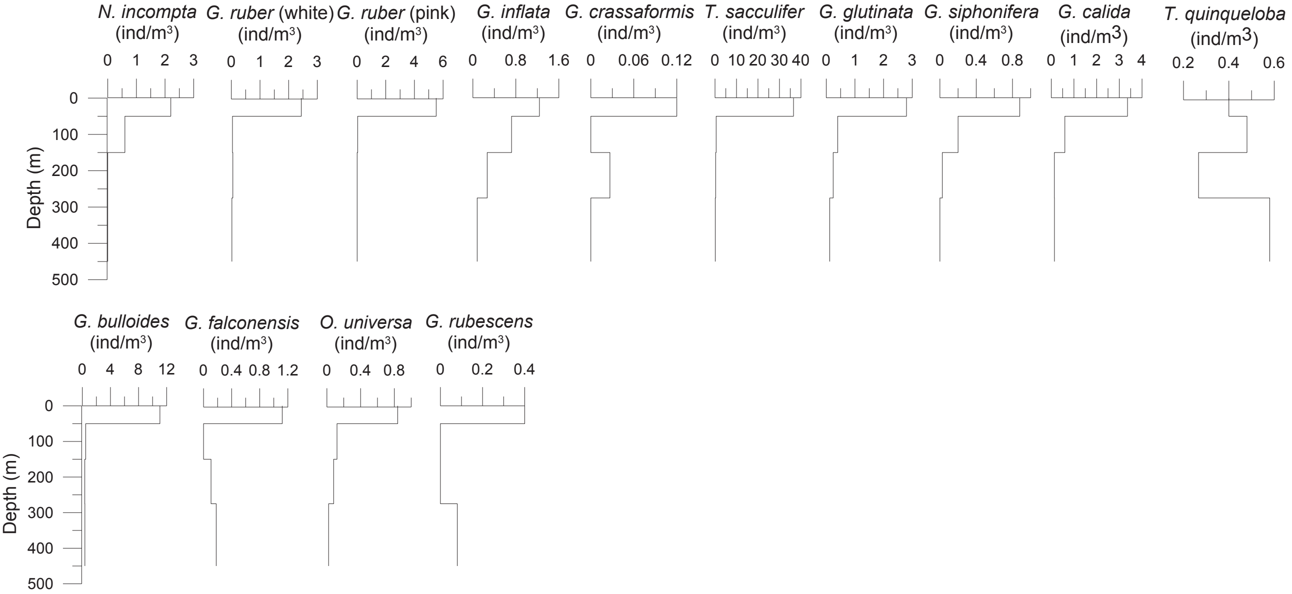

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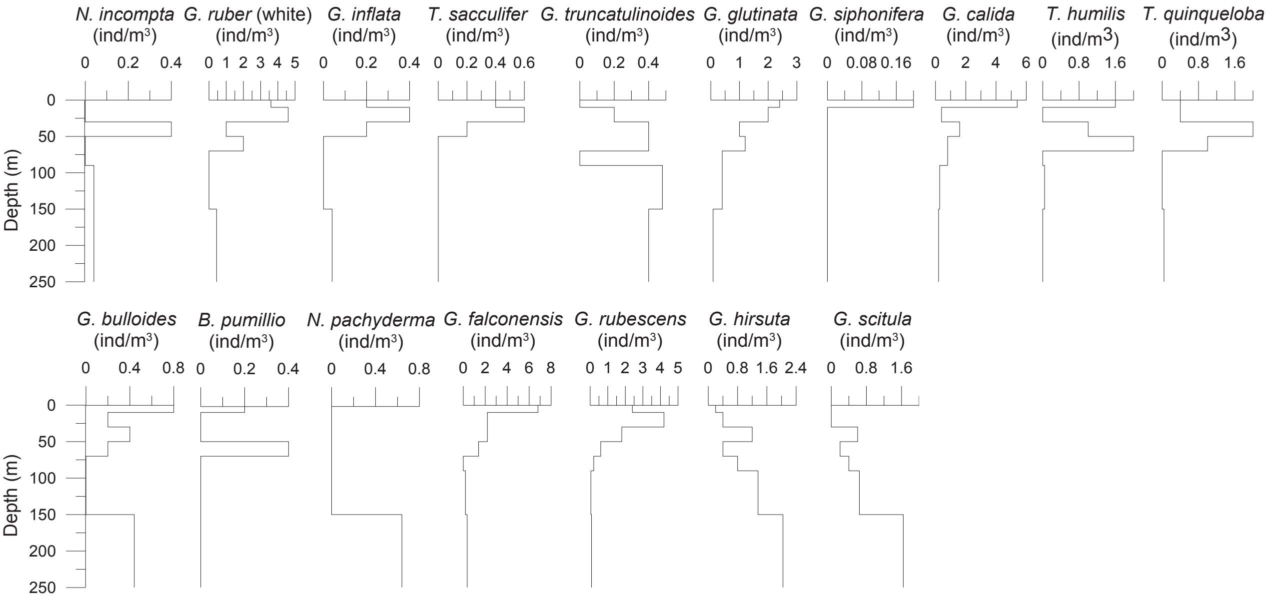

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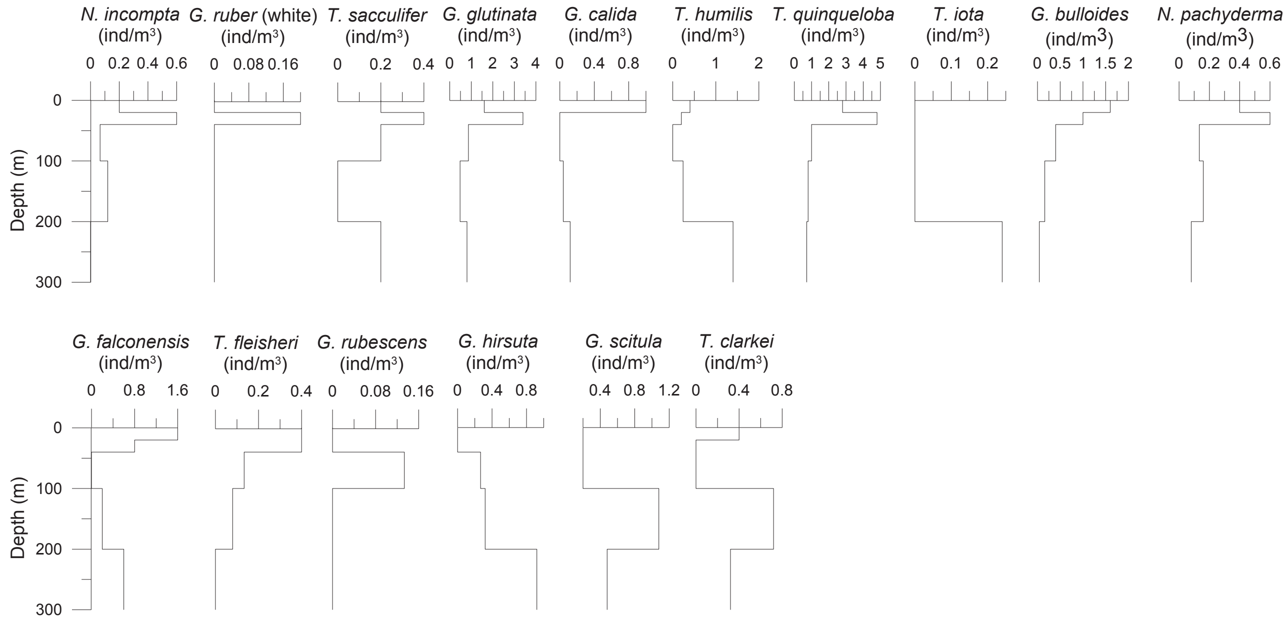
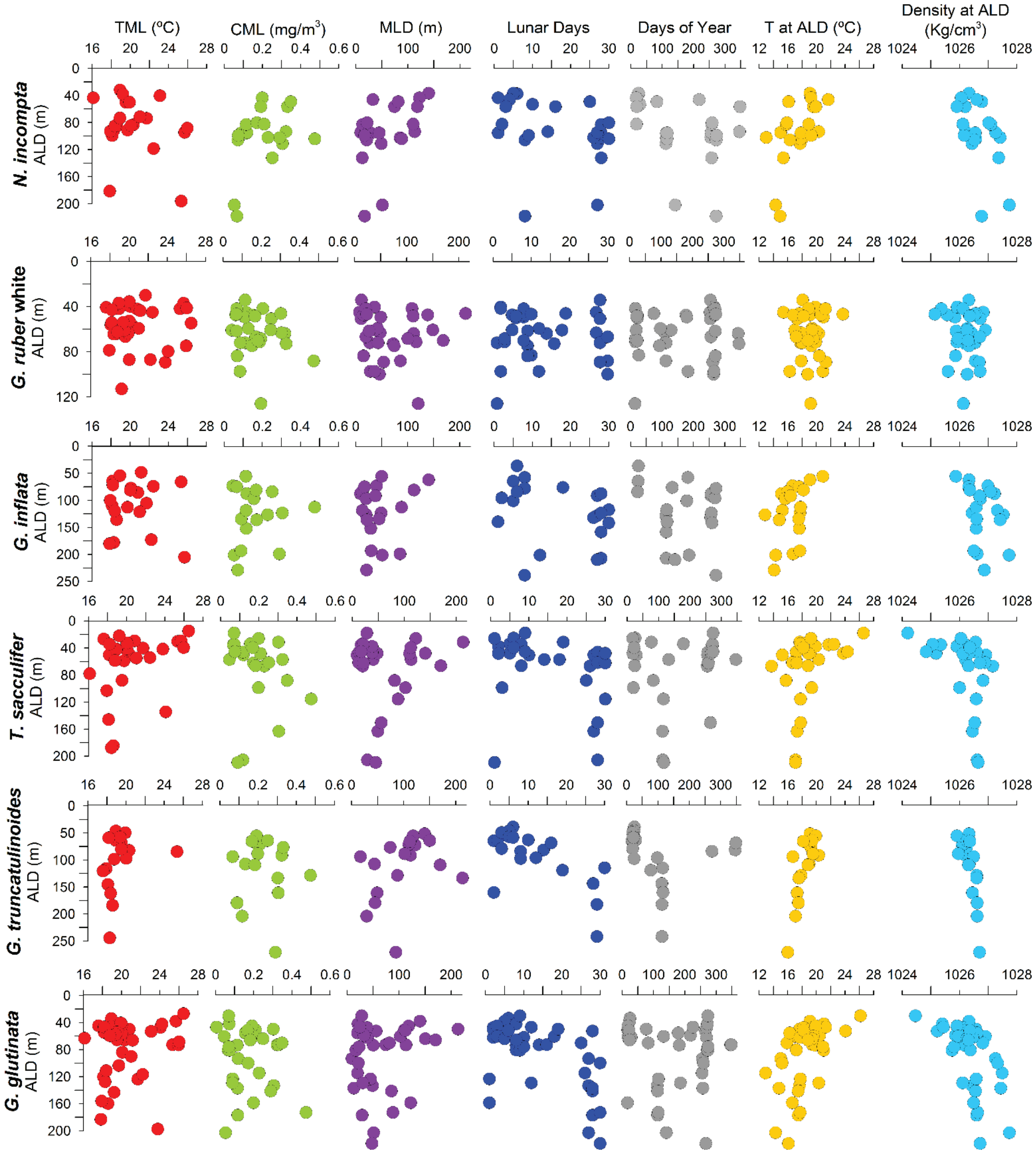
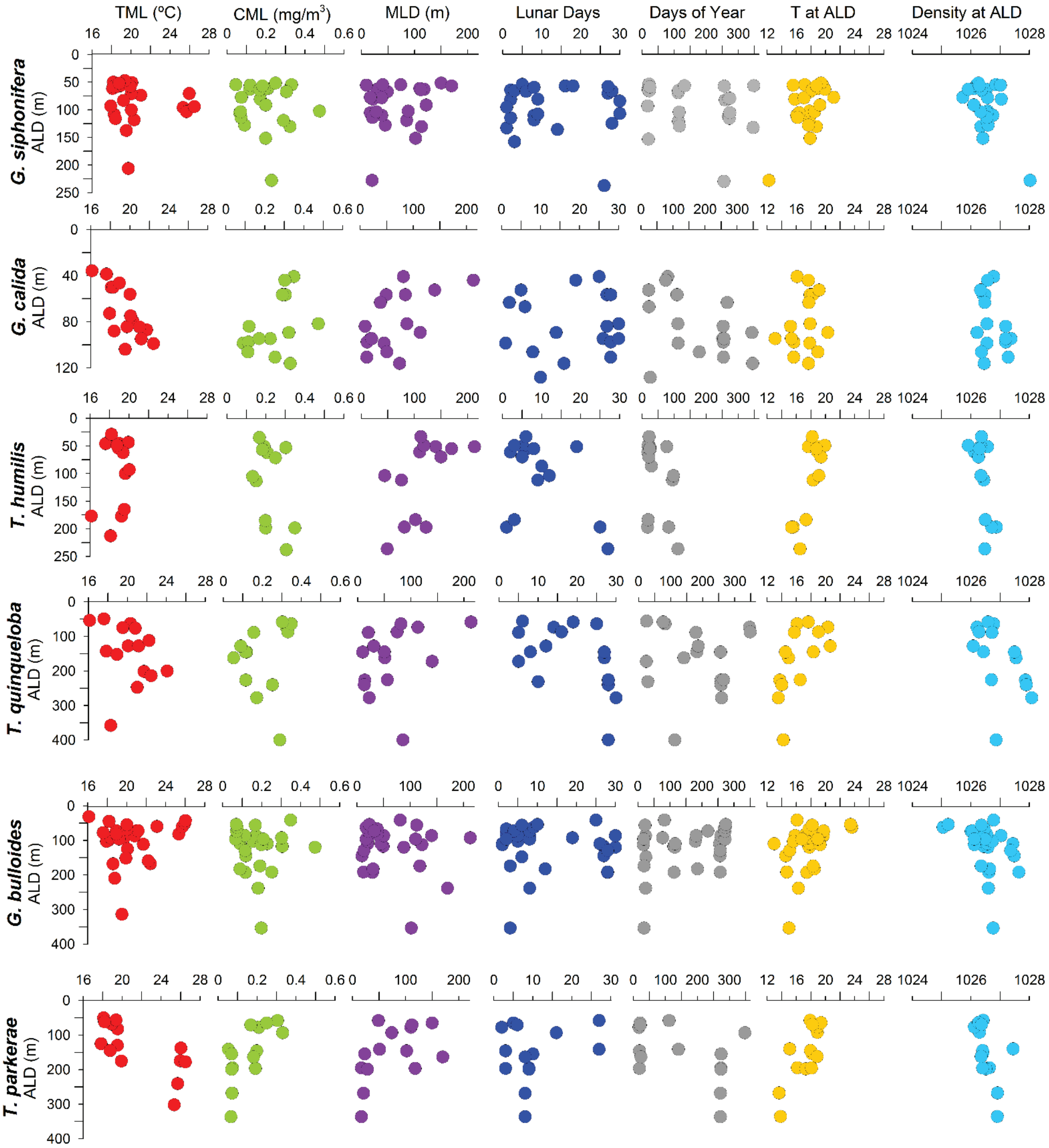


**Figure S1.** Abundance data for the most abundant species in each station. Only new data from Azores Current/Front and Iberian Margin are presented here.


TML (ºC)
CML (mg/m$^3$)
MLD (m)
Lunar Days
Days of Year
T at ALD (ºC)
Density at ALD (Kg/cm$^3$)
16 20 24 28
0 0.2 0.4 0.6
0 100 200
0 10 20 30
0 100 200 300
12 16 20 24 28
1024 1026 1028
N. incompta
ALD (m)
0 40 80 120 160 200
G. ruber white
ALD (m)
0 40 80 120
G. inflata
ALD (m)
0 50 100 150 200 250
T. sacculifer
ALD (m)
0 40 80 120 160 200
G. truncatulinoides
ALD (m)
0 50 100 150 200 250
G. glutinata
ALD (m)
0 40 80 120 160 200


TML (ºC)
CML (mg/m$^3$)
MLD (m)
Lunar Days
Days of Year
T at ALD
Density at ALD
16 20 24 28
0 0.2 0.4 0.6
0 100 200
0 10 20 30
0 100 200 300
12 16 20 24 28
1024 1026 1028
G. siphonifera
G. calida
T. humilis
T. quinqueloba
G. bulloides
T. parkerae
ALD (m)
0 50 100 150 200 250
0 40 80 120
0 100 200 300 400

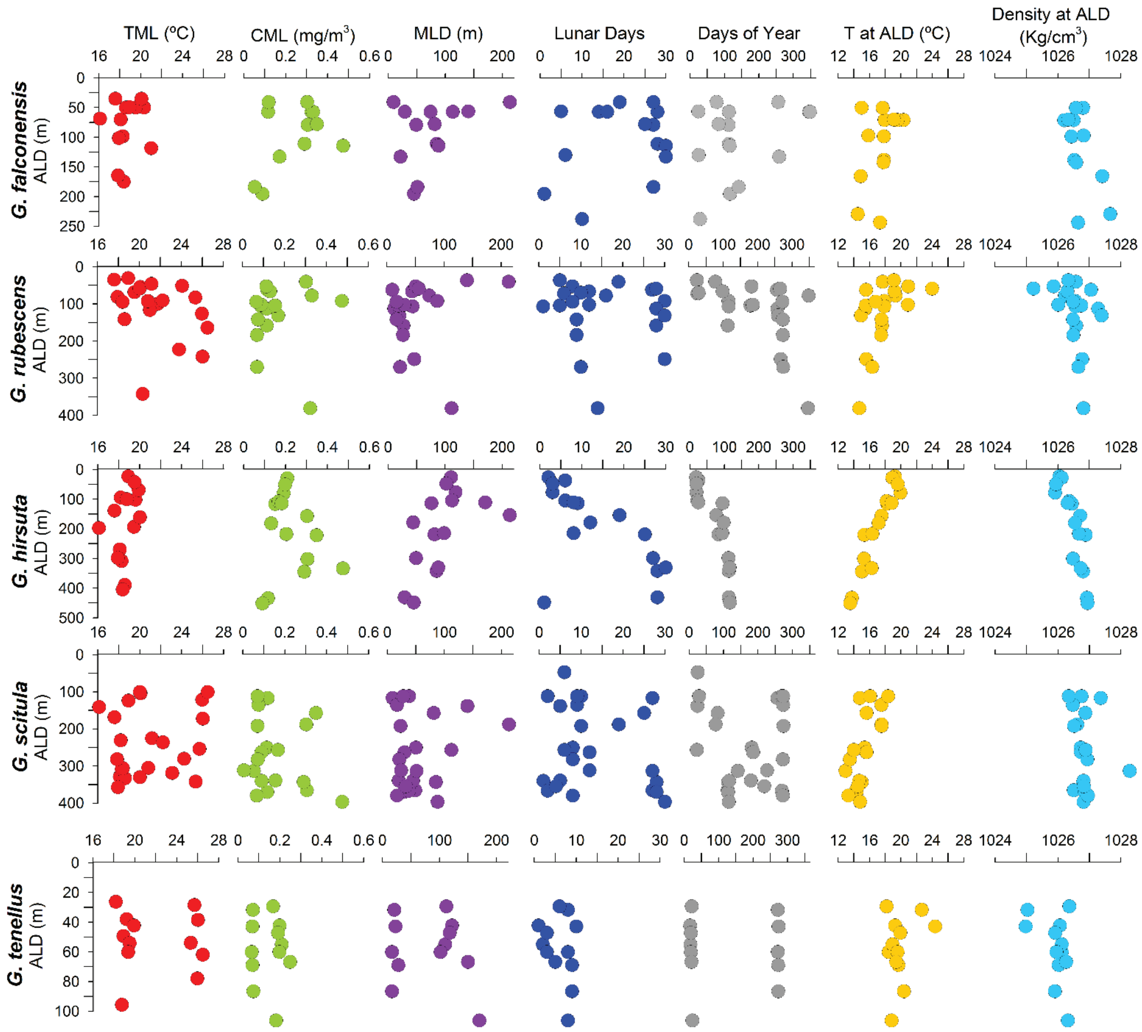


**Figure S2.** Observed ALD for the species with a variable habitat depth with the environmental parameters of the mix layer (temperature, chlorophyll *a* and mixed layer depth), lunar days, days of the year, temperature at ALD and seawater density at ALD.

# Chapter 3

## 3.1 Second case study

### Environmental factors controlling the spatial distribution of living planktonic foraminifera in the subtropical eastern North Atlantic

Andreia Rebotim, Antje H. L. Voelker, Joanna J. Waniek, Michael Siccha, Michael Schulz, Michal Kucera

**Status:** In preparation

# Environmental factors controlling the spatial distribution of living planktonic foraminifera in the subtropical eastern North Atlantic

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## Abstract

The application of planktonic foraminifera in paleoceanographic studies relies on the understanding of how the ecology of individual species is related to their environment. Here we present a compilation of planktonic foraminifera abundance in 31 plankton tows taken in the subtropical eastern North Atlantic between 1995 and 2012. The abundances of 21 living (cytoplasm-bearing) species allowed us to identify distinctive faunas, with the Iberian Margin and Canary Islands presenting a higher percentage of warm-water species and the Azores Front/Current region revealing higher abundance of deep-dwelling species. Correspondence analysis revealed that the stations can be grouped by geographic location, pointing to regionally stable faunal associations. A comparison with earlier observations reveals that the observed associations are coherent with previous plankton tow studies. *Globorotalia scitula* and *Globorotalia hirsuta* are related to the Azores Front/Current system whereas *Globigerinoides ruber* pink and *Globigerina bulloides* are associated with the Canary Islands (except for winter), and the Iberian Margin samples were characterized by a high number of *Trilobatus sacculifer*. To assess which environmental parameters affect individually each planktonic foraminifera species, a canonical correspondence analysis was carried out, using the mixed layer (ML) depth, temperature in the ML and chlorophyll *a* concentration in the ML as environmental variables. In the majority of the cases, the species seem to show a strong affinity to one of the tested environmental parameters. Some species, such as *G. ruber* pink showed an affinity to warmer temperature whereas *Neogloboquadrina pachyderma* exhibit the opposite behaviour. *Globorotalia truncatulinoides* seems to correlate with a deeper mixed layer whereas *Orbulina universa* appears to prefer a shallower mixed layer. *Globigerina falconensis* shows preference for a higher chlorophyll *a* concentration whereas *T. sacculifer* is

linked to low chlorophyll *a* concentrations. The lack of a strong singular relationship of the fauna to temperature is reflected in the lack of a diversity gradient with temperature, suggesting that temperature is not the main determinant of species diversity and composition in the studied region. This is in contrast to studies based on sedimentary assemblages of planktonic foraminifera, indicating that the ecological patterns in sedimentary assemblages are the result of seasonal superposition of distinct assemblages, masking the primary ecological relationships.

## 1. Introduction

Planktonic foraminifera are marine unicellular organisms inhabiting the upper water column of the world ocean. After the death of these organisms, their shells remain preserved in marine sediments, making planktonic foraminifera an important tool in the reconstruction of past ocean conditions and climate (e.g Hemleben et al., 1989).

The usefulness of planktonic foraminifera for paleoceanographic reconstructions relies on the understanding of species ecology and their relation with the biological, chemical and physical properties of the surrounding environment (e.g. Deuser et al., 1981; Ottens, 1991; Prell, 1985; Ufkes et al., 1998). Because of the complexity of these relationships and the complexity of the genetic diversity within morphologically identified species, it was shown to be of merit to consider the relationships between planktonic foraminifera faunas and the ambient environment on a regional scale (Hale and Pflaumann, 1999; Le and Shackleton, 1994). Commonly, such studies are based on species abundances preserved in core top sediment samples accumulating over decades to millennia (e.g. Salgueiro et al., 2008). Although this knowledge is valuable, this procedure makes a direct assessment of the response of the plankton to the interannual and seasonal hydrographic changes very difficult, since seasonal and depth habitat effects cannot be constrained in sediment samples (Chapman, 2010). Instead, only the use of direct plankton observations allows the establishment of realistic environmental calibrations (Volkmann and Mensch, 2001), providing an understanding of the dynamic interaction between individual organisms and populations with the abiotic and biotic components of the marine environment.

Studies based on sedimentary data suggest that temperature is the main environmental factor determining species composition (Morey et al., 2005) and these data consistently identify a strong latitudinal diversity gradient with species diversity increasing from the poles to the equator (Balsam and Flessa, 1978; Rosenzweig, 1995; Ruddiman, 1969; Stehli et al., 1969). In a detailed global compilation, Rutherford et al. (1999) showed that the diversity gradient of planktonic foraminifera peaks in subtropical gyres, but it remains unclear whether this pattern is due to a strict temperature-diversity forcing or whether it reflects other ecological processes. This is because the tropical-subtropical oceans are characterised by large gradients in productivity that are not strongly correlated to temperature, potentially revealing that temperature is not the only factor shaping planktonic foraminifera communities.

Because of the presence of strong environmental gradients, mid-latitude regions hold great promise to reconstruct aspects of the surface ocean structure which are highly informative for the understanding of dynamic processes in the ocean. Yet, despite decades of intense research (Chapman et al., 1996; De Abreu et al., 2003; Meggers et al., 2002; Salgueiro et al., 2008; Schiebel et al., 2002; Shackleton, 1974), the understanding of planktonic foraminifera ecology in the eastern North Atlantic is not yet complete. Thus, the aim of this paper is to contribute to these efforts by investigating which environmental factors are responsible for shaping the planktonic foraminifera community in a confined region in the NE Atlantic. In this region, large seasonal gradients in productivity occur and temperature variation is not strictly zonally. This will allows us to test specifically if temperature is the strongest determinant affecting species composition and diversity in this region.

## 2. Regional setting

The eastern North Atlantic is an area where large seasonal shifts are combined with steep and variable vertical gradients in the water column, especially at higher latitudes (Kase and Siedler, 1982). Limiting the north of the subtropical gyre is the Azores Current, which has its origin in the southern branch of the Gulf Stream (Sy, 1988) and crosses the Mid-Atlantic Ridge at 32 – 36° N as it flows eastward (Gould, 1985; Klein and Siedler, 1989). Jia (2000) and Özgökmen et al. (2001) proposed that the Mediterranean outflow through the Strait of Gibraltar is a complementary factor for the Azores Current formation. Although present throughout the year, the Azores Current’s transport varies seasonally (Alves et al., 2002). The Azores Current’s width can change between 60 and 150 km and throughout most of the year it has a maximum depth of 1000 m (Alves et al., 2002; Gould, 1985). Furthermore, it has been shown that the Azores Current can form strong mesoscale eddies and active meanders across the Atlantic (Alves et al., 2002; Fernández and Pingree, 1996; Gould, 1985).

Southeast of the Azores Islands, the Azores Current divides into a northern branch that merges with the Portugal Current and a southern ramification that feeds the Canary Current

(Barton, 2001; Sy, 1988). The latter recirculates in the Canary Basin, where it has a major influence (Barton, 2001).

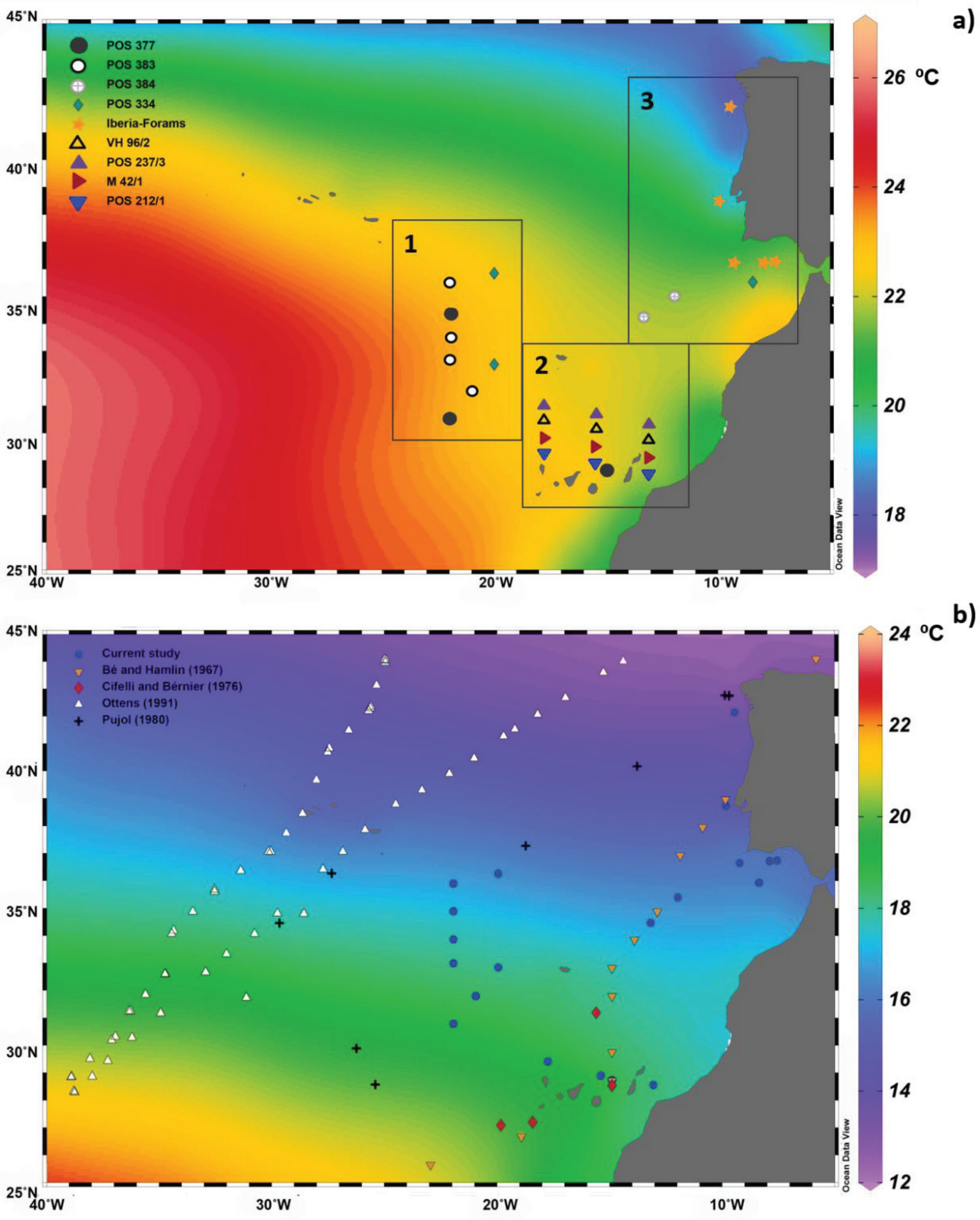

**Figure 1. a)** Positions of plankton net stations in the eastern North Atlantic where data were collected using the same protocol. These include 29 stations with vertically resolved sampling across the entire water column from Rebotim et al. (2016) and 2 additional stations where only the top 100 m were sampled. Station symbols are coded by cruises and rectangles comprise stations from 1- Azores region; 2- Canary Islands; 3- Iberian Margin, **b)** Position of plankton net samples with assemblage information obtained during previous studies using different protocol (green triangles: Ottens (1991), black crosses: Pujol (1980), red diamonds: Cifelli and Bérnier (1976), inverted orange triangles: Bé and Hamlin (1967). Blue dots represent the stations from a).

North of the Azores Current is a thermohaline front – the Azores Front, which separates the warmer (18ºC), saltier and oligotrophic water mass of the Sargasso Sea from the colder, fresher and more eutrophic water mass of the North Atlantic (Gould, 1985; Storz et al., 2009). These two different water masses cause a strong change in temperature (~4° C) and water column structure, which impacts among other things the distribution of planktonic organisms including planktonic foraminifera (Alves et al., 2002; Schiebel et al., 2002). Between 1996 and 2007, the Azores Front has moved between 30° N and 37.5° N, with its positioning being associated to the North Atlantic Oscillation (Fründt and Waniek, 2012).

In the Eastern North Atlantic the spring bloom is initiated in fall by the deepening of the mixed layer and entrainment of nutrients that result in three different production regimes according to their latitudinal position. A more productive region found in the north (> 41° N), a transition zone standing between 36 and 41° N and an oligotrophic area at the south (< 36° N). These regions are associated with different spring blooms intensities, timings and winter mixed layer depths: 1) in the northernmost part, the winter mixed layer depths are deep (200 – 300 m) and the spring bloom is more intense, with the occurrence of a small fall bloom; 2) in the midlatitude area the mixed layer depth lies between the two regions (150 m) and the spring bloom has an intermediate intensity, starting in fall with an entrainment bloom, continues its development in winter and peaks in spring with the occurrence of a restratification bloom; 3) finally, the southernmost area is characterized by the shallowest mixed layer depth (100 m) and a single weak spring bloom that occurs from fall to February (Lévy et al., 2005).

In addition to the typical northeast Atlantic spring bloom, our study area comprises one of the most productive upwelling systems, which are located in the western Iberian and the northwest African coasts (Santos et al., 2005). In the western Iberian Margin, the upwelling occurs from April to October as soon as the north winds start being favourable (Fiúza, 1983; Peliz et al., 2007; Wooster et al., 1976). In the northwest African coast, the strongest upwelling take place during summer and fall, as a result of the seasonal northeast trade winds, with the formation of filaments that spread some hundreds of kilometres off the coast (Barton et al., 1998).

### 3. Materials and Methods

For the analysis of factors controlling species abundances in the studied region, data from 29 stations with counts resolving the entire water column (from the surface to at least 275 m) were taken from Rebotim et al. (2017). We have excluded counts from stations where only a part of the fauna were quantified. In addition, data from two new stations resolving the surface layer (0 – 100 m) are presented (Fig. 1a). The counts from these new stations were carried out using the same procedures as described in Rebotim et al. (2017). Planktonic foraminifera are known to live below 100 m, but highest densities are typically found in the surface layer (Berger, 1969). Therefore, these additional samples could be used to assess distribution patterns in the surface layer only and were excluded in analyses where the total assemblage including deep dwelling fauna was considered. In addition, all available planktonic foraminifera data from earlier studies in the same region was synthesized, comprising the studies by Bé and Hamlin (1967), Cifelli and Bénier (1976), Pujol (1980) and Ottens (1991) (Table 1; Figure 1b). These studies were carried out using different methods, mesh sizes, taxonomic resolution and depth ranges, but they provide an important benchmark for the temporal and spatial stability of the observed patterns. The details of all considered stations are shown in Table 1 and Figure 1b.

**Table 1.** Data source, specification of the sampling method, size of the counted specimens, vertical resolution of the collection and taxonomic considerations.

| **Data source** | Collection method | Count size (µm) | Vertical resolution | Taxonomic considerations |
|---|---|---|---|---|
| Ottens (1991) | Pump | > 125 | 0 – 5 m* | *G. aequilateralis = G. siphonifera*<br>*N. incompta* and *N. pachyderma* were distinguished |
| Pujol (1980) | Net | >50 | 0 – 25 m*<br>0 – 50 m*<br>0 – 100 m*<br>0 – 200 m* | *G. eggeri = N. dutertrei* juvenile<br>*G. ruber* alba = *G. ruber* white<br>*N. pachyderma* dextral = *N. incompta*<br>*G. trilobus = T. sacculifer* |
| Cifelli and Bérnier (1976) | Net | > 158 | 0 – 100/200 m* | *T. iota* and *G. anfracta* were counted<br>*N. incompta* and *N. pachyderma* were distinguished<br>*G. trilobus = T. sacculifer* |
| Bé and Hamlin (1967) | Net | > 200 | 0 – 10 m*<br>0 – 300 m* | *G. aequilateralis = G. siphonifera*<br>*N. incompta* and *N. pachyderma* were not distinguished |
| Current study | Multiple Closing Opening Net | > 63 | 0 – 100 m**<br>0 – 700 m** | *N. pachyderma* and *N. incompta* were distinguished<br>Small species *(T. iota, T. parkerae, T. clarkei, B. pumillio, T. fleisheri* and *G. anfracta)* were counted |

*Without resolved sampling intervals **With resolved intervals between these depths

*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 for all stations. These data were used (Table 2) to determine the base of the mixed layer (ML) depth, the depth where *in situ* temperature decreased by more than 0.5°C compared to the surface. The value obtained for the ML depth was used to calculate the mean temperature in the ML and the chlorophyll *a* concentration in the ML. For stations, where *in situ* fluorescence data were not available (Table 2), this measure was approximated from satellite values at the ocean surface at the same day whenever available or using the 8-day or monthly mean, using the best existent approximation to the date of collection and the closest available coordinates from NASA's Ocean Color Web database (http://oceancolor.gsfc.nasa.gov/cms/) (Table 2).

**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 et al., 1997[a]<br>Ocean Color Database[b] | Ocean Color Data[c] |
| Poseidon 237/3 | Knoll et al., 1998 | Ocean Color Data[d] |
| Meteor 42/1 | Pfannkuche et al., 1998 | Ocean Color Data[d] |
| Poseidon 334 | Schulz et al., 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<br>Ocean Color Data[d] |
| Poseidon 384 | Christiansen et al., 2009 | Christiansen et al. (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

To explore the variation of planktonic foraminifera communities across different geographic areas, in a way that we could visualize differences or consistencies in the species spatial distribution, a correspondence analysis (CA) was used, first including only the fauna of the top 150 m of the water column and then including fauna of the entire water column, including the subsurface, deep-dwelling assemblage components (Rebotim et al., 2017). A Canonical Correspondence Analysis (CCA) was used to determine which environmental variables explain the highest amount of variation in the spatial distribution of the planktonic foraminifera species present in our dataset. The environmental variables tested in the CCA were chlorophyll *a* concentration in the ML, the temperature in the ML and the ML thickness. For the purpose of the analysis, the species concentrations were log-transformed. In both analyses, species with less than 5 ind/m$^3$ in the total of stations analysed were excluded as well as the smaller species namely *B. pumillio*, *T. parkerae*, *T. iota, T. fleisheri* and *T. clarkei*, since the samples were taken using different mesh sizes (either above 100 µm or 125 µm). As a result, the concentrations of 21 species out of the 36 counted taxa could be used in the analyses. To assess how species diversity varies with temperature, we determined species richness rarefied to 200 individuals, as well as the Shannon-Wiener and the Equitability indices, for the total fauna at all stations, where at least 200 specimens were counted in total. The results were then plotted against the temperature in the ML. The diversity indices, rarefaction and correspondence analysis were carried out in the software PAST version (Hammer et al., 2001), the CCA was carried out in software Canoco 4.5 (Leps and Smilauer, 2003).

## 4. Results

The faunas from 31 stations compiled for this study present a good coverage of three distinct geographical areas from the subtropical eastern North Atlantic, namely the Canary Islands region, the Azores Front in the open ocean near Madeira and the western Iberian Margin, and the respective environmental conditions. Altogether, 34 species were encountered in the samples for these regions. Among these, 26 are imaged and discussed in the Appendix. The abundance data of 21 species were used to investigate the variation of the planktonic foraminifera communities across the different regional settings and to attempt finding relationships between the different species and the environmental factors.

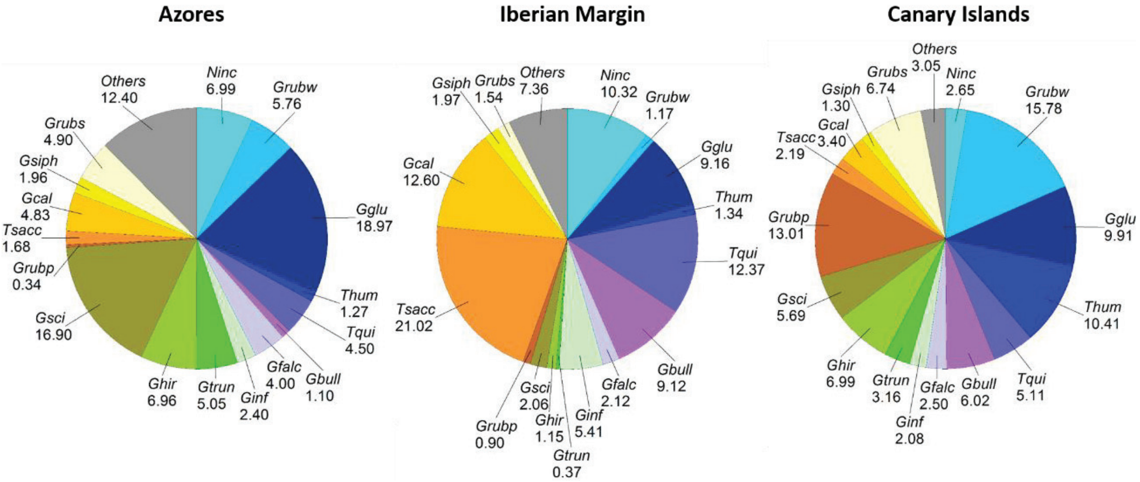

**Figure 2**. Mean relative abundance of planktonic foraminifera species in plankton samples from the three regions defined in Figure 1. Only samples covering the entire water column are considered. Warm water species are shown in yellow to red, cold-water to temperate species are shown in blue and violet and deep dwelling species are shown in shades of green. Others refer to species whose mean abundance was below 5 % across all samples. Species names are abbreviated with full names given in the Taxonomic appendix.

### 4.1 Regional fauna composition

Figure 2 shows that the species composition is more similar in the Canary Islands and Iberian Margin regions than in the Azores Front/Current region. In the first two, the higher occurrence of warm to temperate species such as *G. ruber* and *T. sacculifer* is observed, whereas in the Azores Front/Current region the subsurface species such as *G. hirsuta* and *G. scitula* (following Rebotim et al., 2017) are present in higher numbers. Around the Canary Islands the most frequent species are *G. ruber* white (15.78 %) and pink (13.01 %), followed by *T. humilis* (10.41 %). At the Iberian Margin, *T. sacculifer* is the dominant species with 21.02 %. In the Azores Front/Current region, the most abundant species are *G. glutinata* (18.97 %) and *G. scitula* (16.90 %).

### 4.2 Relative and absolute abundances variations with temperature

The first analysis of the data presented in Figure 2 is affected by the presence of samples from different seasons in the three areas considered. To obtain a more direct picture of species ecology, we assessed how the relative and absolute abundance of the species varies with the temperature in the ML (Fig. 3). Within the colder-water species (e.g. Schiebel and Hemleben, 2017) relative and absolute abundances of *N. incompta* and *G. bulloides* show a low correlation with temperature ($R^2 \leq 0.01$) while *T. quinqueloba* shows the strongest negative correlation with temperature ($R^2=0.12$). The warm to temperate species *G. ruber* white, *G. glutinata* and *G. calida* correlate weakly with the temperature , while *T. sacculifer*'s relative abundance shows the higher correlation among these species ($R^2=0.12$). The deep-dwelling species, *G. hirsuta* exhibits a small positive correlation with the temperature in the ML between 18 and 20° C. Above this temperature, however, the relative abundance decrease.

### 4.3 Species associations

The correspondence analysis of species concentrations both in the surface layer and for the total fauna (Fig. 4) reveal the presence of regionally consistent faunas that are arranged along one major gradient (first CA explains 35.41 % of the variance in surface layer analysis and 34.49% in the total analysis). The position of individual samples in the space of the first two correspondence axes (Fig. 4a) reveals that each quadrant of the graph is practically assigned to a different region except for the three stations that appear in the 3rd quadrant. The 1st quadrant contains stations from the Canary Islands region, with characteristic species *G. ruber* pink, *G. bulloides*, *G. siphonifera,* and *G. inflata*. Correlated to the Azores Front/Current

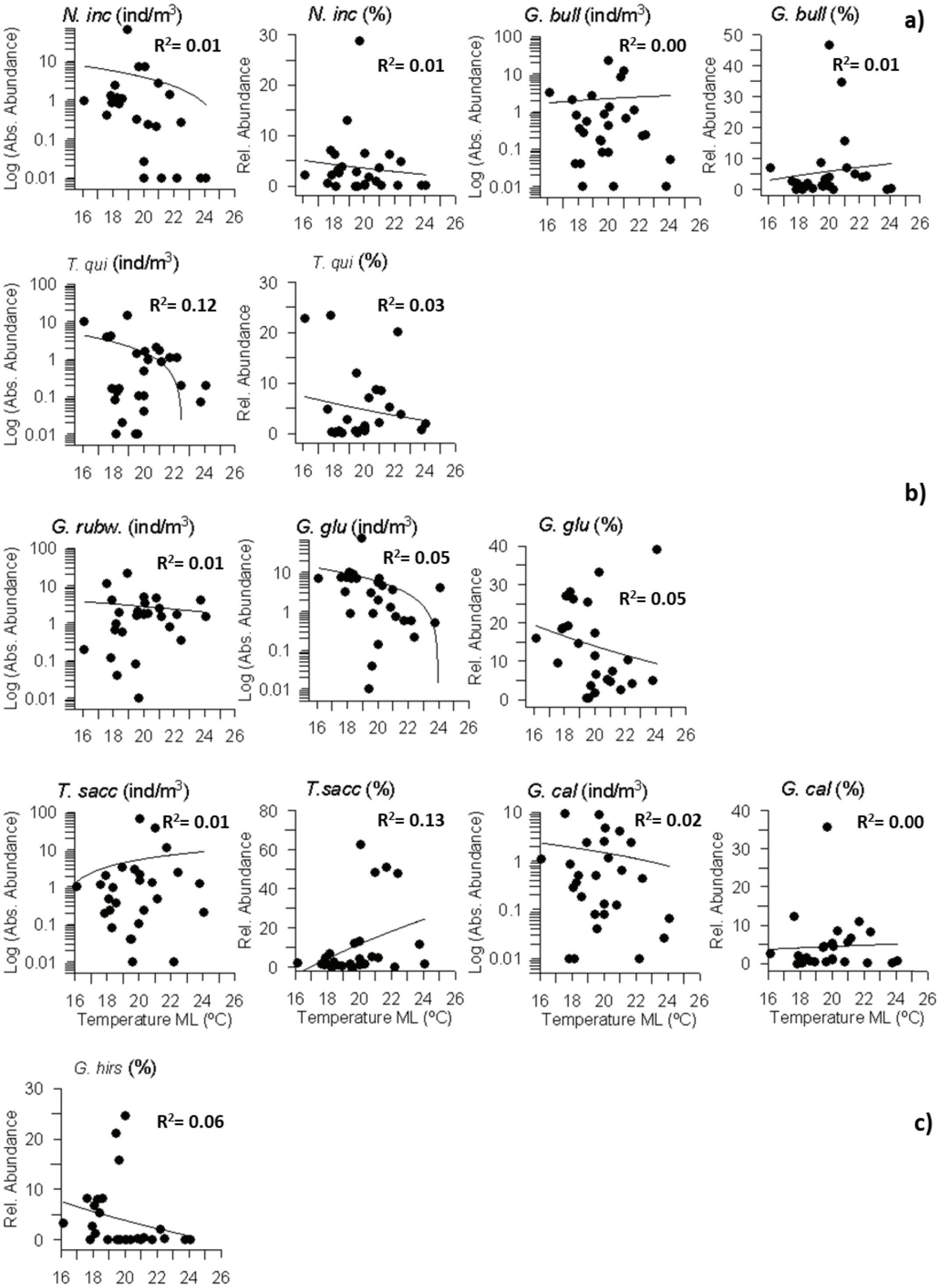

**Figure 3**. Absolute (ind/m$^3$) and relative (%) abundances from samples covering the entire water column against temperature in the ML depth of the most common individual species within the samples shown by groups: a) Cold-water species, b) Warm to temperate water species, and c) Deep-dwelling species. Only species where the correlation was significant (p>0.05) are shown.

stations are the species *G. hirsuta, G. scitula, T. quinqueloba, G. falconensis, G. truncatulinoides,* and *G. glutinata*. The three winter stations from the Canary Islands, which appear as an isolated group in the 3rd quadrant, seem to be distinguished by *G. rubescens, N. incompta, N. dutertrei, T. humilis,* and *P. obliquiloculata.* In the 4th quadrant, spatially isolated from the remaining stations, are the Iberian Margin stations except for the northernmost station (Ib-F 2); those samples are characterised by *G. calida* and *T. sacculifer*. Only the species *G. ruber* white and *N. pachyderma* do not seem to be typical of any region and plot in between the stations from the three regions. A similar pattern is showed in the analysis for the entire water column (0 – 800 m) with the exception of stations belonging to the POS 383 cruise in the Azores Front/Current region, which are separated due to the presence of *G. scitula* and *G. hirsuta.* These species are more abundant below 70 - 100 m (Rebotim et al., 2016; Schiebel et al., 2001) and their higher abundance in these stations together with station POS 334-72 indicates that the encountered faunas had a higher proportion of subsurface species.

To visualise how the unconstrained ordination of the samples and species may be related to environmental variability, the values of the three considered environmental parameters were projected into the space of the first two correspondence axes (Fig. 4). Taking into account the chlorophyll *a* concentration in the ML depth at each station (Fig.4b), the general tendency seems to be an increase from the right to the left, except for 5 stations (POS 383-165, POS 383-175, POS 237/3-LP, M 42/1-LP, and POS 384-273) that are positioned on the graph's left side but have low values of chlorophyll *a* concentration. The same trend is seen in the ML depth, showing an increase from the right to the left except for the same stations that have a shallow ML depth (Fig. 4c). For the temperature in the ML depth (Fig.4d), the opposite correlation, i.e. an overall increase from the left to right is observed, except for the same stations in which the temperature is lower. According to the stations' distribution, species more related to a higher chlorophyll *a* concentration, a deeper ML depth and lower temperature are *G. glutinata, T. quinqueloba, G, falconensis, G. truncatulinoides, T. humilis, P. obliquiloculata, N. dutertrei, G. rubescens,* and *N. incompta*, whereas species associated with a lower chlorophyll *a* concentration, shallow ML depth and higher temperature in the ML are *G. bulloides, G. ruber* pink*, G. siphonifera, G. sacculifer, G. calida,* and *G. inflata*.

### 4.4 Environmental parameters controlling geographic distribution

A CCA was used to assess more directly, which environmental factors might be influencing the distribution of the different species (Fig. 5). In this context, the environmental factor with most impact on the planktonic foraminifera species distribution is the ML depth, followed by

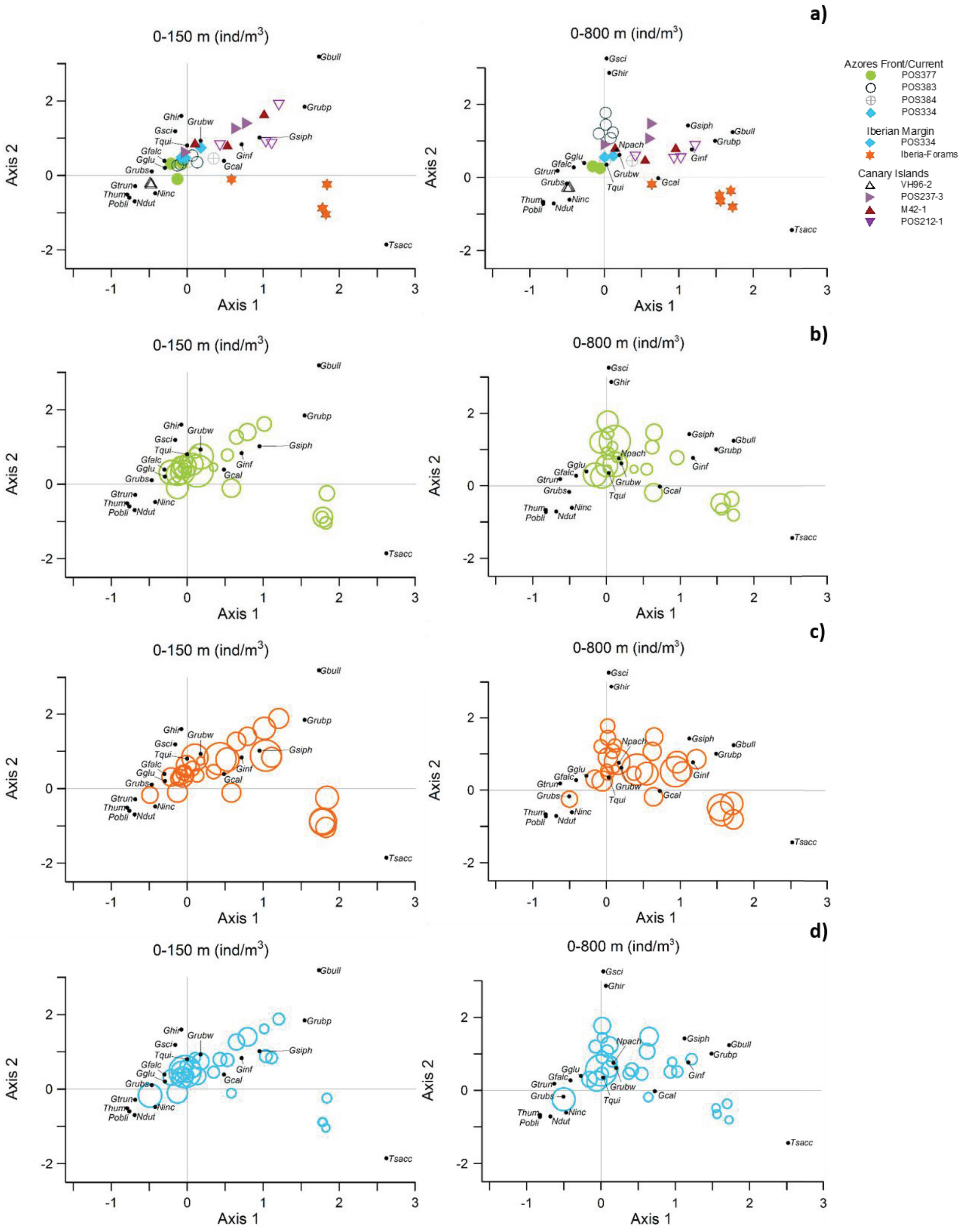

**Figure 4.** Correspondence analysis of absolute abundances (ind/m$^3$) of the planktonic foraminifera species (black dots) from 0-150 m (surface assemblages) and from 0-800 m (total assemblages) in the studied stations: **a)** Stations from the same cruise are shown with the same symbol, and the three different regions are represented with the same symbol shape; **b)** For each station the chlorophyll *a* in the ML is shown, with a higher bubble size being directly linked to a higher concentration; **c)** For each studied station the temperature in the ML is plotted as bubbles, with a bigger bubble size representing a higher temperature in the ML, and vice-versa; **d)** For each studied station the MLD is shown as bubbles, with the increase of the bubble size being directly linked to the increase in the MLD.

temperature, and chlorophyll *a* concentration. The ML depth appears to correlate positively with *G. truncatulinoides, G. falconensis* and *T. humilis* and negatively with *O. universa* and *G. inflata.* On the other hand, temperature in the ML correlates positively with *G. ruber* pink, *G. crassaformis* and *G. bulloides* and negatively with *N. pachyderma, G. scitula, G. hirsuta,* and *G. glutinata*. Regarding chlorophyll *a* concentration in the ML, *G. falconensis, G. hirsuta* and *G. truncatulinoides*, correlate positively and *G. crassaformis, G. bulloides* and *G. ruber* pink negatively with this parameter.

When projecting the average composition of stations from the three main regions, the CCA allows a definition of distinctive planktonic foraminifera species composition for each region:

1) Canary Islands - *T. quinqueloba, G. ruber* white, *N. dutertrei, G. rubescens, T. humilis, G. calida;*

2) Azores Front/Current - *G. truncatulinoides, G. falconensis, G. hirsuta, N. pachyderma, G. scitula, G. glutinata, N. incompta;*

3) Iberia Margin - *G. siphonifera, H. pelagica, G. inflata, O. Universa, T. sacculifer, G. bulloides, G. crassaformis, G. ruber* pink.

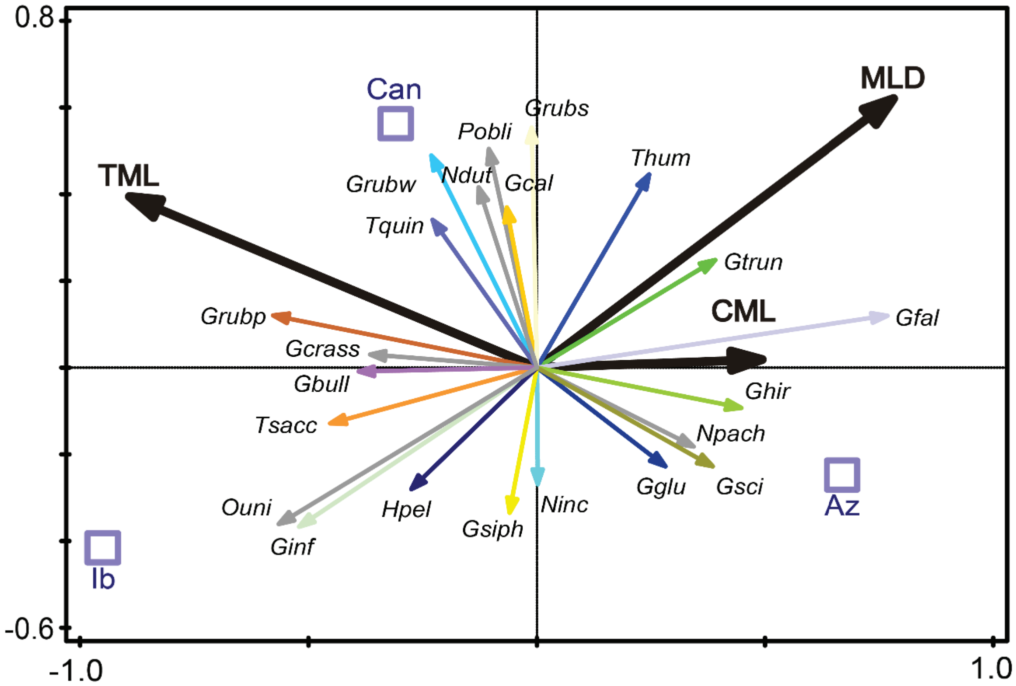

**Figure 5.** Ordination diagram of Correspondence Canonical Analysis (CCA) of the absolute abundance of 22 planktonic foraminifera species (coloured arrows) distributed within the three regions (Az = Azores Islands; Ib = Iberian Margin; Can = Canary Islands) and three environmental parameters (black arrows) from *in situ* measurements: temperature in the mixed layer depth (TML), chlorophyll *a* concentration in the mixed layer depth and mixed layer depth (MLD). Only samples that include the entire water column (0-800 m) were included. Warm water species are shown in yellow to red, cold-water to temperate species are shown in blue and violet, deep dwelling species are shown in shades of green and species whose mean total abundance was below 5 % are coloured in grey.

### 4.5 Comparison with previous plankton tow data from the eastern North Atlantic

A compilation of previously existing plankton tow studies from the eastern North Atlantic was carried out to determine how representative our sampling is for the region during a longer period of time and across a larger area (Fig. 7 and Fig. 8). First, a joint CA was carried out for our surface data (from 0 to 150 m) and the data from Ottens (1991) based on surface pumps (0 – 5 m) and plankton tows from Pujol (1980) from 0 to 200 m (Fig. 7). Although Pujol's data include 50 m more than our surface data, we consider that his data are more comparable to the surface layer observations. Since all datasets contain the temperatures *in situ* for each station, it is possible to compare not only the species assemblages but also how it maps on temperature. In terms of faunal composition, our data plot within the same space occupied by data from Ottens (1991) and Pujol (1980), and follow the same gradient, although the Ottens (1991) data covers a larger geographical area extending further to the north and to the south than our study area. Since the Cifelli and Bénier (1976) study comprises plankton tows from 100 to 200 m and Bé and Hamlin (1967) includes plankton tows from 0 to 300 m, we found the data more appropriate for a comparison with our data for the entire water column, including the subsurface fauna (Fig. 8). This comparison reveals again the presence of common gradients, with the literature data covering a broader range.

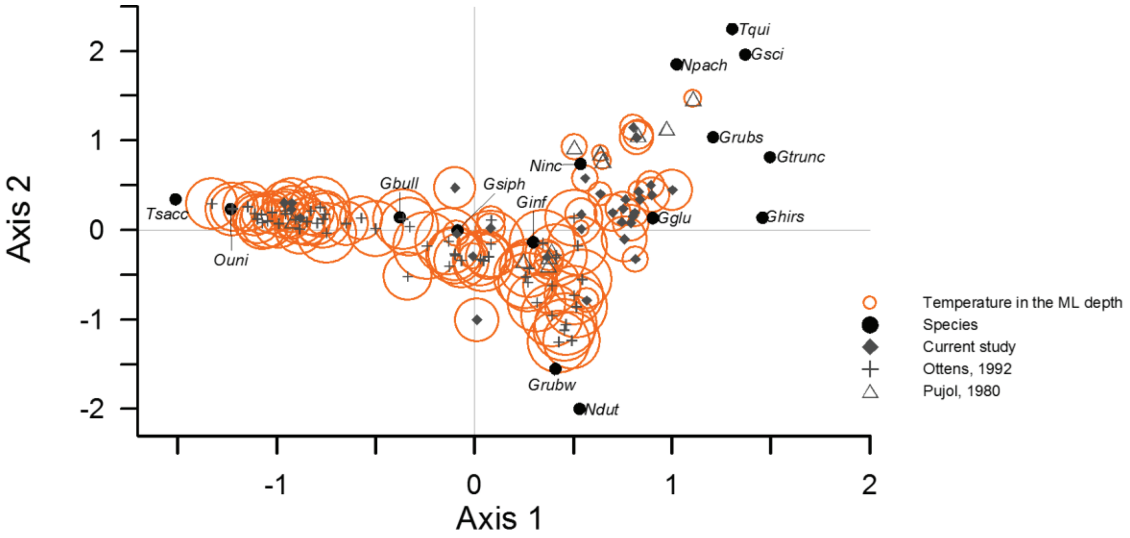

**Figure 6.** Correspondence analysis of surface abundance in percentage of different planktonic foraminifera species, including our data, data from Ottens (1991) and data from Pujol (1980) from the eastern North Atlantic. The black dots represent each species. The size of the bubbles represent the temperature of the mixed layer depth at each station, i.e. the greater the size the higher the temperature in the mixed layer depth.

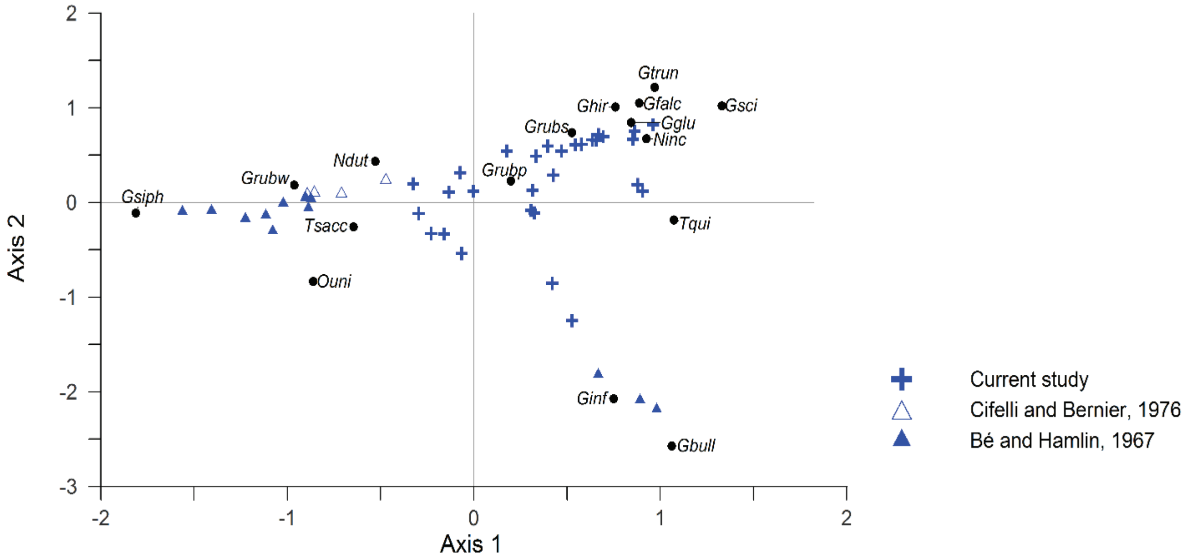

**Figure 7.** Correlation analysis between the abundance percentages in the deep tows of common planktonic foraminifera species in the eastern North Atlantic with the data from the current study presented as crosses, data from Cifelli and Bérnier (1976) as empty triangles and data from Bé and Hamlin (1967) as filled triangles. Black dots and name abbreviations mark the respective species. Only species with common occurrence in the three different datasets were included.

### 4.6 Diversity with temperature

Independently of the stations' location, there is a general decrease of the species richness with temperature in the ML depth (Fig. 8). In the Azores Front/Current region there is initially a decrease from 20 to 14 species with the increase of temperature (18° to 20°C). The Iberian Margin species richness has a decrease tendency (19 to 16) along with the rising temperature (16° to 22° C). The Canary Islands stations recorded the lowest species richness (10). In this region, we also observe a decrease in the species richness (16 to 10) with rising temperature. Both, the Shannon-Wiener diversity and Equitability indices show a low correlation of respectively, 0.05 and 0.02, to chlorophyll *a* concentration. The correlation between temperature in the ML and the Equitability index is also small ($R^2$=0.06). When plotting the Ottens (1991) and Pujol (1980) data along with our stations, the stations are dispersed in the plot and no correlation appears to exist between the Shannon-Wiener diversity index and the increase of temperature in the ML. This is contrary to the negative correlation observed when plotting only our samples, but we also observe that the values for our samples lie entirely within the cloud of samples circumscribed by the surface pump data by Ottens (1991).

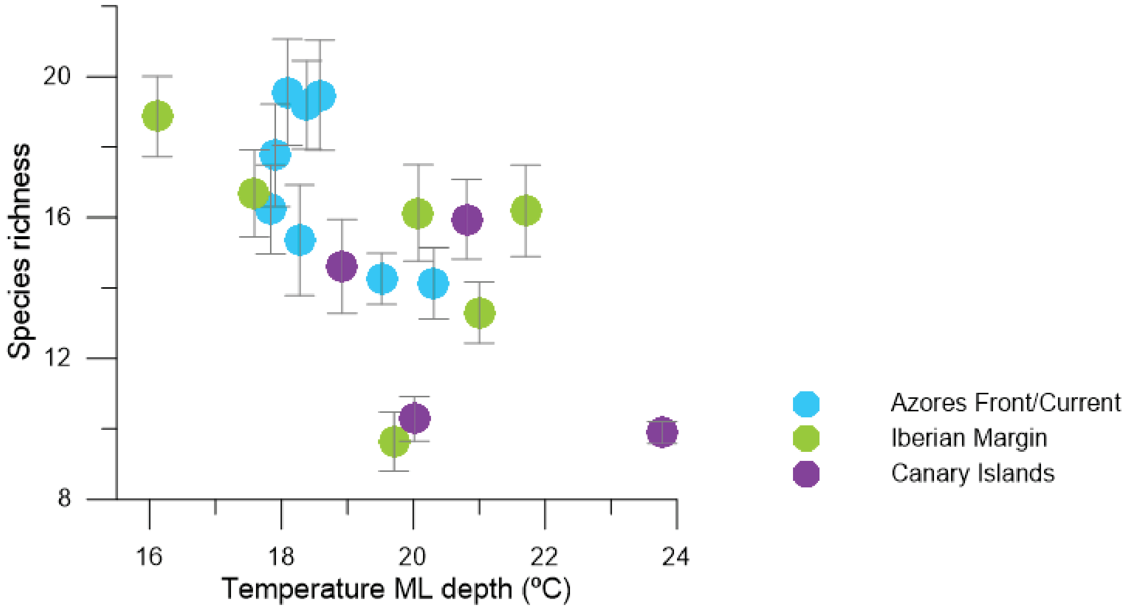

**Figure 8.** Variation of the species richness of planktonic foraminifera in the studied stations colour coded for the different regions with a total abundance >200 specimens against the temperature in the ML depth obtained from *in situ* data from each station. Only stations covering the entire water column (0 – 800 m) were included. The error bars error bars represent the standard error associated to each species richness.

## 5. Discussion

### 5.1 Planktonic foraminifera fauna distribution

#### 5.1.1 Canary Islands (winter)

The winter Canary stations exhibit the highest planktonic foraminifera abundances among all samples, and showed a distinct faunal composition, representing an end-member of the encountered gradient (Fig. 4). According to Neuer et al. (2002), the sampling was coincident with the winter bloom caused by deep mixing, thus providing nutrients to the surface and causing a phytoplankton maximum which would result in increased food availability. The species that appear more associated with the winter Canary stations are *G. truncatulinoides, T. humilis, P. obliquiloculata, N. dutertrei, N. incompta,* and *G. rubescens,* showing also the highest abundances among all samples (Fig. 2 and 4). The chlorophyll *a* concentration in the ML depth is not available for the VH 96-2 cruise and therefore it is not possible to check this environmental parameter, however we do have the temperature in the ML depth (18.19ºC) and the ML depth (140 m) for one of the stations (EBC) confirming a deep mixed layer and a colder temperature at the time of the cruise, in comparison to the data that we have for the remaining seasons. *G. truncatulinoides* is thought to have a yearly cycle, ascending to the sea surface during winter to reproduce and descending to deeper waters during summer (Lohmann, 1995; Schiebel and Hemleben, 2005; Wilke et al., 2009), which would explain the very high concentration of 49 ind/m$^3$ and 375 ind/m$^3$, respectively, in the region of the Canary Islands in winter, first described by Meggers et al. (2002) using the same samples. Although two abundance peaks in winter and spring were reported for *G. truncatulinoides* in a Sargasso Sea study (Deuser and Ross, 1989), our results only show one peak during winter with a significant higher concentration in comparison to the other seasons. A very high abundance of *G. truncatulinoides* was also observed in the Azores Current region in the winter of 1999, with *T. humilis* being abundant as well (Schiebel et al., 2002; Storz et al., 2009). These species appear to occupy a similar ecological niche as first suggested by Schiebel et al. (2002). In addition, *G. truncatulinoides* feeds preferentially on phytoplankton (Spindler et al., 1984) and appears to occur at the margin of subtropical gyres such as the Sargasso Sea and the Azores Current (Hemleben et al., 1989; Schiebel et al., 2002), and supported by our data for the gyre boundary marked by the Canary Current.

Likewise, *P. obliquiloculata* and *N. dutertrei* have been reported to occur more abundantly in winter and spring in the Sargasso Sea (Deuser and Ross, 1989). However, as before, only one abundance peak occurs in winter for both species (*P. obliquiloculata* – 49 ind/m$^3$; *N. dutertrei* – 12 ind/m$^3$) when compared to the other seasons. *P. obliquiloculata* seems to be more related to productive water masses (Hilbrecht, 1996), whereas *N. dutertrei* is thought to mark the post-upwelling period (Thunell and Sautter, 1992), which would explain the maximum concentrations of these species at these stations.

Another species with high abundances in the winter Canary Islands stations was *N. incompta.* This species occurs in subpolar and transitional water masses, having a wide temperature range (Darling et al., 2006; Hemleben et al., 1989) and is associated with productive zones (e.g. Ortiz et al., 1995; Salgueiro et al., 2008), showing high abundances in the North Atlantic, Benguela upwelling system, parts of the South Atlantic and equatorial upwelling in the Pacific Ocean (Fraile et al., 2008). In addition, it is also frequent throughout the year off northwest Africa but with lower concentrations (Fraile et al., 2008), which is not in agreement with our results, since this was the location where we obtained the highest (148 ind/m$^3$ – winter) and the lowest (<1 ind/m$^3$ – remaining seasons) concentration of *N. incompta*. The maximum concentration obtained is much higher than in the remaining geographic locations, though it was also abundant in the Azores (66 ind/m$^3$) and Iberian Margin stations (20 ind/m$^3$).

*G. rubescens* was a further species that had maximum abundances in the winter Canary stations. This species is thought to inhabit a similar ecologic niche as *G. ruber* pink (Deuser et al., 1981), which is considered a summer species that occurs in warm waters (e.g. Bé and Hamlin, 1967). Our data indicate that although *G. ruber* pink and *G. rubescens* show some morphological similarities (Schiebel and Hemleben, 2017), their depth habitat, temperature preferences, occurrence peak and perhaps the inhabiting hydrographic conditions are quite distinct.

### 5.1.2 Canary Islands (spring, summer and autumn)

For the remaining stations from the Canary Islands, placed in the 1st quadrant of the graph, the species that show a higher correlation with these stations and occur with the highest concentrations among all the studied stations are *G. ruber* pink and *G. bulloides*. *G. ruber* pink is a warm water species (Bé and Hamlin, 1967; Hemleben et al., 1989) and is indicative of summer conditions (e.g. Ganssen and Kroon, 2000), which agrees with the fact that this species was found more abundantly in the Canary Islands (except in winter) and Iberian Margin stations, which recorded the highest temperature in the ML depth, ranging from 19 to 24ºC (Fig. 4c). On the other hand, *G. bulloides* is usually associated with upwelling or productive conditions (Bé and Tolderlund, 1971; Ganssen and Kroon, 2000; Hemleben et al., 1989; Salgueiro et al., 2008) and boundary currents (Be, 1977), tolerating a wide temperature range (Storz et al., 2009). According to (Wooster et al., 1976), upwelling takes place north of 25ºN on the African coast during summer and early fall, which is coincident with the highest concentrations obtained for *G. bulloides* in the EBC station, reported first by Abrantes et al. (2002) and Wilke et al. (2009) based on the same samples. Although the EBC station is not directly affected by upwelling, it is a near shore station and thus reached by a filament of nutritive and cooler waters forming off Cape Yubi during summer and fall (Parrilla et al., 1999). For the EBC station we only have the chlorophyll *a* concentration in the ML depth for the spring and it indeed registered the highest concentration compared to the LP and ESTOC stations. Furthermore, up to date, 7 different genotypes have been identified for *G. bulloides*, with one of the genotypes (Type Ib) characteristic for the Canary Islands (Darling and Wade, 2008), most likely corresponding to the type that we see in our samples.

### 5.1.3 Iberian Margin

The species that appear most associated with the Iberian Margin, except for station Ib-F 2, was *T. sacculifer,* which outnumbered by far the concentration of the other species (124 ind/m$^3$); this being the reason for the distant position of the Iberia - Forams stations in relation to the remaining studied stations (Fig. 4a). *T. sacculifer* is described as preferring warmer temperatures, being a subtropical to tropical species (Bé, 1977; Zaric et al., 2005; Kucera, 2007; Storz et al., 2009), which agrees with the fact that these stations had the highest temperature in the ML (19.70 – 22.43ºC). Ufkes et al. (1998) have reported high concentrations of *T. sacculifer* in the boundary of two different water masses (Equatorial Atlantic and the Congo river), which could be the case since the Mediterranean Outflow water enters into the North Atlantic through the Strait of Gibraltar leading to a mix of two very different water masses along the southern Iberian margin. Ib-F 2 appears outside of the others Iberian stations, possibly because it is the northernmost (42ºN) station, presenting one of highest chlorophyll *a* concentration in the ML depth (also observed for station Ib-F 9) and the coldest temperature in the ML depth. However, the Iberia Margin samples represent a snapshot of a summer situation that might not have been a typical summer on that year.

### 5.1.4 Azores Front/ Current

The species associated with the Azores region were *G. hirsuta* and *G. scitula* showing the highest concentrations of 29 ind/m$^3$ and 68 ind/m$^3$, respectively (Fig. 4a). High abundances of *G. scitula* have been associated to the Azores Front whereas both species account for a main part of the deep-dwelling fauna north of the front (Schiebel et al., 2002). According to (Hemleben et al., 1989), non-spinose species such as *G. scitula* and *G. hirsuta* feeding on particulate organic matter, thus living mostly in subsurface waters, which would explain the separation of these species from the other species in the graph. Also, showing the maximum abundances in the Azores region were *G. siphonifera* (7.4 ind/m$^3$) and *G. calida* (29 ind/m$^3$) (Fig. 2). Besides being abundant in the Azores region, *G. siphonifera* occurred in the Canary Islands and Iberian Margin regions with concentrations ranging from 2.5 to 4 ind/m$^3$, whereas *G. calida* had abundances of 22 ind/m$^3$ in the Iberian Margin stations. Both species are associated with warmer waters (Eguchi et al., 2003; Kucera, 2007; Meggers et al., 2002). In addition, *G. siphonifera* is known to prefer oligotrophic water masses (Be, 1977; Fraile et al., 2008; Storz et al., 2009) and is related to upwelling regions and boundary currents (Be, 1977). This is in agreement with our results with the Canary Islands and Iberian Margin stations having the highest temperature in the ML depth and both being upwelling regions (Santos et al., 2005) with oligotrophic water masses offshore. *G. calida* is found in the tropics, subtropics and temperate regions (e.g. Be, 1977; Huber et al., 1997; Kucera, 2007).

*G. inflata* also showed the highest concentration for the Azores region (14.5 ind/m$^3$). This species was also frequent on the Iberian Margin with 7.8 ind/m$^3$. Based on core-top sediments located along the Iberian Margin, Salgueiro et al. (2008) found this species associated with the eastern branch of the Azores Current and to the Portugal Current. In a study performed by Ufkes et al. (1998), *G. inflata* was one of the species dominating the Angola-Benguela Front and therefore its occurrence may be correlated with the existence of a mixing zone between two different waters masses, such as the Azores Front. In the Sargasso Sea, *G. inflata* highest fluxes were observed in late winter (Deuser and Ross, 1989) whereas in the NE Atlantic it was more abundant in spring and summer (Chapman, 2010). Off Cape Cod in Massachusetts, this species occurred throughout the year (Keigwin et al., 2005). Although we only have samples from the winter and spring seasons, the concentration of *G. inflata* was higher in spring than in winter, which is similar to what was suggested by Chapman (2010).

### 5.1.5 Ubiquitous species

Some of the species that are positioned between stations from different regions recorded abundances with high values for more than one of the regions such is the case of *G. ruber* white, *G. glutinata*, *G. falconensis,* and *T. quinqueloba* (Fig. 4a). *G. ruber* white had the highest concentrations in the winter Canary stations (41 ind/m$^3$) and Azores (38 ind/m$^3$), though it was also frequent in the Canary stations during the remaining seasons of the year with a range of 14-18 ind/m$^3$. During several years, this species was thought to inhabit warm waters (e.g. Hemleben et al., 1989) and reflecting summer surface conditions (Ganssen and Kroon, 2000). However, this species occurs from subtropical-tropical waters to transitional waters, tolerating temperatures from 9.7 - 15ºC to 31ºC (Darling and Wade, 2008; Žarić et al., 2006), which would explain its occurrence throughout the studied area. *G. ruber* comprises multiple genotypes with different seasonal and geographic distribution that belong to two different lineages (Aurahs et al., 2009; Darling and Wade, 2008). According to Aurahs et al. (2009), one of the existing types – type IIa – occurs in the Canary Islands and shows a constant abundance throughout the year, with no peak during the warm season. Similarly, in a sediment trap study located north of the Canary Islands, *G. ruber* white was common through the year with maximum concentrations during winter (Storz et al., 2009). Both studies are comparable with our abundance results obtained for this species. In addition, the other genotype described in our region – type Ia – has been previously observed in the Azores Current, which might correspond to the type present in our samples from the Azores region. Although these two lineages are morphologically different in the adult stage, the plankton tows assemblages are dominated by pre-adult specimens, in which the main morphologic features are not well developed (Aurahs et al., 2009), making their separation impossible in the current study.

Also not associated to any of the three regions was the species *T. quinqueloba* (Fig. 4a). Indeed, the abundance of this species for the Azores, winter Canary and Iberian Margin stations is 19, 23 and 15 ind/m$^3$, respectively, with lower concentrations for the remaining Canary stations. The fact that it is very difficult to find any correlation between the abundance of this species and environmental parameters could indicate the presence of multiple ecologically distinct genetic types (Darling and Wade, 2008).

*G. glutinata* and *G. falconensis* occurred with highest concentrations in the Azores (101.18 ind/m$^3$ and 39.14 ind/m$^3$, respectively) and winter Canary stations (149.48 ind/m$^3$; 54.89 ind/m$^3$, respectively). According to Storz et al. (2009), the highest flux of these species was in winter and spring. *G. falconensis*, has also been previously associated with winter conditions and minimum annual temperatures (Xu et al., 2005). Both studies agree well with the highest abundances obtained for the Canary Islands stations in winter. However, regarding the Azores region, the sampling was done mostly in spring, being poorly represented during winter and not represented in the rest of the year, therefore more sampling would be needed to fill this seasonal gap.

### 5.2 Environmental factors controlling geographic distribution

Overall, the ordination of the species in the CCA shows that there is very little redundancy among the species with regard to their ecological preferences, partitioning the space evenly and responding differently to the environmental parameters. Exhibiting a strong correlation with a deep ML are *G. truncatulinoides, T. humilis* and *G. falconensis*. The first two species are thought to change their position in the water column seasonally (Hemleben et al., 1989; Rebotim et al., 2017), which is coincident with abundance changes through the year. Since the ML depth also changes during the year in our study area, being shallower and more stratified in summer and deeper and well mixed in winter (Waniek et al., 2005), these species might be affected by seasonal alterations of the ML depth both in its habitat and abundance. *G. falconensis* is considered a mixed-layer species (Kipp, 1976), related to a deep mixed layer as observed in the NE Arabian Sea (Schulz et al., 2002) and in the NE Atlantic (Storz et al., 2009).

Related to a shallow ML depth are *H. pelagica, O. universa* and *G. inflata.* In the eastern South Atlantic, Ufkes et al. (1998) made the same observation for *O. universa* and *G. inflata*.

The latter also showed a weak correlation with chlorophyll *a* concentration in the ML, which is not in total agreement with its previous association with upwelling/filament waters (Meggers et al., 2002; Thiede, 1975) and chlorophyll concentrations (Storz et al., 2009). In agreement with our results is Salgueiro et al. (2008), who found this species related to the eastern branch of the Azores Current and to the Portugal Current, with higher relative abundances in the boundary with the upwelling front but in oligotrophic waters.

The species that appear to be more affected by a higher concentration of chlorophyll *a* in the ML depth were *G. falconensis, G. glutinata, G. truncatulinoides, G. hirsuta, N. pachyderma,* and *G. scitula*. *G. falconensis* and *G. glutinata* are described as inhabiting productive water masses (Chapman, 2010; Peeters and Brummer, 2002; Schiebel and Hemleben, 2000), with the first being associated with an early upwelling stage (Mohiuddin et al., 2005; Storz et al., 2009) and the second occurring in a late stage of a bloom and at the margin of productive zones (Hilbrecht, 1996), feeding mainly on diatoms (Spindler et al., 1984). *N. pachyderma* has also been related to high chlorophyll *a* concentrations (Kuroyanagi and Kawahata, 2004; Ufkes et al., 1998). In addition, Chapman (2010) reported an increase of *G. scitula* and *G. hirsuta* during the spring bloom in the NE Atlantic, probably because both species inhabit subsurface waters and feed on the organic matter settling through the water column, being dependent on the productivity at the surface. The same might be the case for *G. truncatulinoides,* which is a surface to subsurface species (Rebotim et al., 2017; Schiebel et al., 2002), and therefore might also feed on settling organic matter.

Unexpectedly, *G. bulloides* shows a negative correlation with chlorophyll *a* concentration and ML depth. In contrast, this species is usually associated with productive areas (e.g. Thiede, 1975) and tropical upwelling systems (Watkins et al., 1996). However, *G. bulloides*'s maximum concentrations were observed in Iberia Margin and Canary region, both upwelling areas. Also, negatively correlated with chlorophyll *a* concentration and ML depth were also *G. crassaformis, T. sacculifer* and *G. ruber* pink. For *G. crassaformis* no mention on its preference for oligotrophic waters was found. In addition, this is typically considered a deep-dwelling species (e.g. Tedesco et al., 2007), which not explains its tendency for a shallow ML depth. However, most of the individuals found in our samples were juveniles and were present in low number, most probably not representing the entire population. On the other hand, *T. sacculifer* and *G. ruber* pink are thought to occur in warm oligotrophic and mesotrophic waters with *T. sacculifer* being associated with a shallow mixed layer (Fraile et al., 2008; Peeters and Brummer, 2002; Žarić et al., 2005), which is confirmed by our results.

Regarding the temperature, *G. ruber* pink is the species that exhibits the strongest correlation with this parameter. This species usually shows preference for warm waters (Fraile et al., 2008; Peeters and Brummer, 2002; Ufkes et al., 1998), increasing their abundance in summer and reflecting the warmest surface water conditions (Bé and Tolderlund, 1971; Deuser and Ross, 1989; Ganssen and Kroon, 2000), which is in agreement with our results. Being influenced also by the temperature in the ML depth, but showing a weak relation with the ML depth and chlorophyll *a* concentration appear to be *G. ruber* white*, G. rubescens, G. calida, P. obliquiloculata, N. dutertrei* and *T. quinqueloba*. The first three species have been associated with warm and oligotrophic conditions (Schulz et al., 2002; Storz et al., 2009; Žarić et al., 2005) and our observations suggest that the abundance of *G. ruber* white and *G. calida* increases with rising temperatures. Furthermore, *P. obliquiloculata* is considered a tropical to subtropical species (Bé and Tolderlund, 1971; Deuser et al., 1981) and *N. dutertrei* occurs in tropical to temperate upwelling systems (Fairbanks et al., 1982; Ufkes et al., 1998), which agrees with our results. However, T*. quinqueloba* inhabits preferentially colder waters (Bergami et al., 2009; Carstens et al., 1997; Kucera, 2007), which is the opposite of the results obtained for the CCA.

*G. scitula, G. hirsuta, N. pachyderma,* and *G. glutinata* exhibit a preference for colder temperatures in the ML. The first species has been suggested as an indicator of deep winter mixing (Schulz et al., 2002). In addition, *G. scitula* and *G. hirsuta* are usually considered deep-dwelling species (Hemleben et al., 1989; Ortiz et al., 1996; Schiebel and Hemleben, 2000; Rebotim et al., 2016), where it is usually colder than the surface part of the water column. *N. pachyderma* is known to prefer colder temperatures (Be, 1977; Hemleben et al., 1989) and *G. glutinata* has also been related to colder waters (Schiebel and Hemleben, 2000; Watkins et al., 1996). This agrees with the relative/absolute abundance trend to decrease along a higher temperature observed for *G. hirsuta* and *G. glutinata* (Fig. 3).

*N. incompta* and *G. siphonifera* correlate negatively with the three studied environmental parameters, indicating preference for low chlorophyll *a* in the ML, a shallow ML and a colder temperature. The fact that these species were ubiquitous through the three regions might be an explanation towards their lack of correlation to a specific environmental parameter. However, *N. incompta* has been previously associated to upwelling/filament waters (Meggers et al., 2002; Ufkes et al., 1998) or high food supply (Ortiz et al., 1995), which is not in total agreement with our results. It could be the case that the species is limited by nutrients as suggested by Pak and Kennett (2002). This would justify its presence at lower chlorophyll *a* concentrations in the ML and its abundance increase whenever the chlorophyll *a* concentrations peak, as would be the case in the winter upwelling in the Canary stations where its abundance was extremely high. *G. siphonifera,* typically occurs in warm oligotrophic waters and a shallow mixed layer (Peeters and Brummer, 2002; Schmuker and Schiebel, 2002), which in fact agrees with the position of this species in the canonical diagram opposing both chlorophyll *a* in the ML and a ML depth. However, *G. siphonifera* comprises at least 12 different genotypes to date, that are related with different chlorophyll concentrations (De Vargas et al., 2002; Weiner et al., 2014).

### 5.3 Comparison with plankton tows data from the Eastern North Atlantic

The CA of the plankton tows surface data from Ottens (1991) and Pujol (1980) and ours (Fig.7) shows that the existent datasets are comparable with ours. However, the Ottens (1991) study is situated to the west and both Ottens (1991) and Pujol (1980) cover a wider geographic area to the north and south in relation to ours. The broader coverage confirms the general trends seen in our data that the species composition changes along with a complex environmental gradient, with colder temperatures being associated with planktonic foraminifera species such as *T. quinqueloba*, *G. scitula*, *N. pachyderma,* and *N. incompta* and warmer temperatures with *G. ruber* white, *N. dutertrei, G. siphonifera, G. bulloides, O. universa,* and *T. sacculifer.*

The CA that contains a broader vertical range from the water column, including data from Bé and Hamlin (1967) and Cifelli and Bérnier (1976), also covers a larger geographic area, with the Bé and Hamlin (1967) stations being located north and south of our study area and Cifelli and Bérnier (1976) stations located to the south of the Canary Islands (Fig. 1, 8). Despite the geographic and temporal differences, both data sets agree well with our data and the observed relationship between faunal change and temperature, such as warmer species like *G. ruber* white and *N. dutertrei* being associated with the Cifelli and Bénier (1976) stations. The Bé and Hamlin (1967) stations are divided into two different groups, one that encompasses a colder species fauna such as *G. inflata* and *G. bulloides* and another that is related to warmer species such as *G. ruber* white or *T. sacculifer*. In the CA, our stations are positioned in between the Cifelli and Bénier (1976) and Bé and Hamlin (1967) stations, reflecting the typical Azores Front fauna, such as *G. truncatulinoides, G. falconensis, G. scitula, G. hirsuta,* and *N. incompta,* whereas *G. ruber* pink, *T. sacculifer, O. universa, N. dutertrei, G. ruber* white, and *G. siphonifera* are reflecting warmer conditions, probably off the southern Iberian Margin and near to Canary Islands.

### 5.4 Relationship between diversity and temperature

To understand to which extent temperature is the determinant factor in the planktonic foraminifera species distribution we plotted different diversity indices against the temperature in the ML (Fig. 8, Fig. 9). Species richness generally decreases with increasing temperature in the ML. The same tendency is observed for the Equitability index. This observation is in contrast to the general pattern of the latitudinal diversity gradient with species diversity increasing from the poles to the equator (Rosenzweig, 1995; Stehli et al., 1969). It is also at odds with observations from sedimentary assemblages (Rutherford et al., 1999). The studied region covers mid-latitude to subtropical settings straddling the temperature range where Rutherford et al. (1999) observed highest planktonic foraminifera diversity. Several studies suggested that diversity peaks at intermediate productivity levels (e.g. Waide et al., 1999), we also plotted the Shannon-Wiener and Equitability indexes against the chlorophyll *a* concentration in the ML. None of the diversity indexes seem to have a strong correlation with the increase of the chlorophyll a concentration.

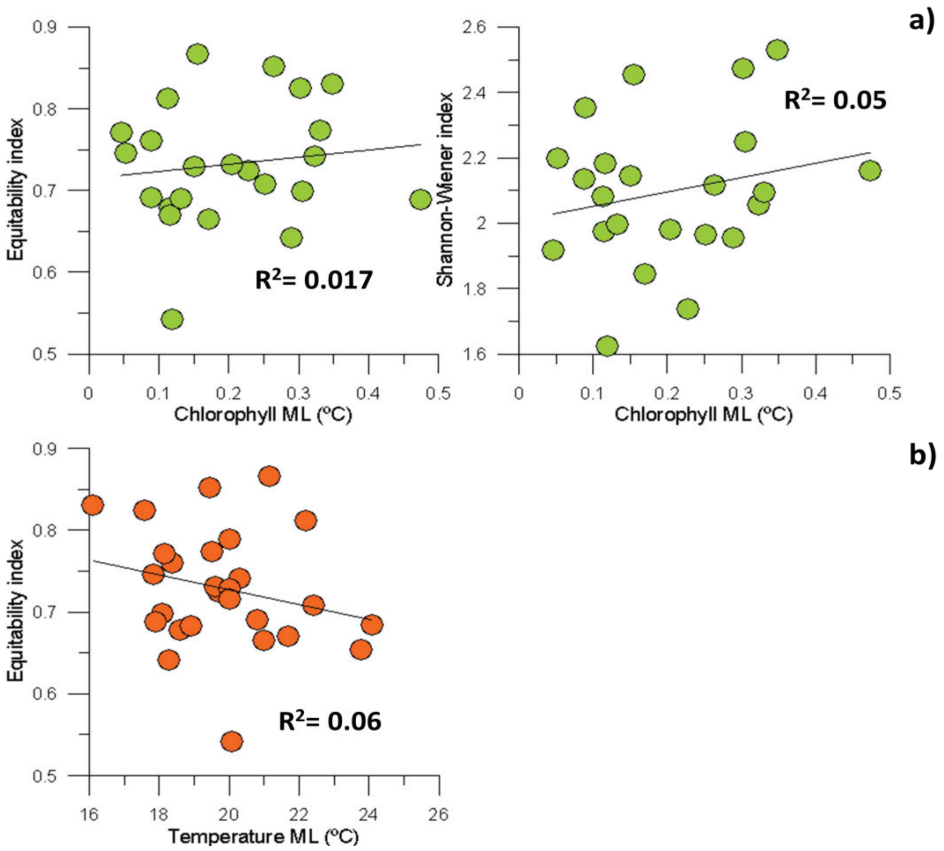

**Figure 9.** Each dot represents a single station with its respective **a)** chlorophyll *a* concentration and **b)** temperature in the ML depth plotted against the Equitability index and Shannon-Wiener index, respectively. Only the cases where the correlation was significant ($p>0.05$) are shown.

Because our samples were collected in different years, seasons and regions, we decided to verify the trends of our data also with the stations from Pujol (1980) and Ottens (1991) (Fig. 10). Here, the decrease of the Shannon-Wiener diversity index with the increase in the ML depth temperature is not visible, but there is no sign of a latitudinal diversity gradient either. Thus, although the latitudinal diversity gradient is strong in sedimentary assemblages, it does not seem to occur in the studied region in plankton samples. This could indicate that temperature is not the main factor determining the planktonic foraminifera diversity in the plankton. This would imply that the environmental preferences observed in sedimentary samples are the result seasonal and interannual superposition of distinct faunas, and the strong relationship to temperature is indirect.

## 6. Conclusions

To investigate which environmental factors determine the spatial distribution of planktonic foraminifera in the subtropical eastern North Atlantic, the abundance of 34 species was determined in vertically resolved plankton tows collected at 31 stations between 1995 and 2012, covering three distinct geographic areas. The resulting observations together form a coherent framework allowing to assess the factors affecting the spatial distribution and the species composition variability. In terms of the planktonic foraminifera relative abundances across the different regions, the fauna composition from the Canary Islands and Iberian Margin regions are more similar, with a greater percentage of warmer species compared to the Azores Front/Current region, in which the presence of deep-dwelling species is higher.

The assemblages in the studied area appear to be aligned along one principle gradient, which is not related solely to temperature. A secondary gradient appears when the fauna of the entire water column is analysed, separating stations with a higher contribution of the subsurface fauna. Most species are closely linked to either end of the gradient, indicating the distinct characteristics of each region and water masses, with *G. ruber* pink and *G. bulloides* occurring in the Canary Islands stations (except in winter), *G. hirsuta*, *G. scitula* and *G. truncatulinoides* appearing typically in the Azores Front/Current region and *T. sacculifer* making a distinction in the Iberian Margin stations.

A CCA reveals that the species are distributed evenly in the ecological space, with little redundancy, and seem to be influenced by a combination of mixed layer depth, temperature or chlorophyll *a* concentration. Some species, such as *G. ruber* pink showed a correlation towards a warmer temperature whereas *N. pachyderma* exhibits, as expected, the opposite behaviour. *G. truncatulinoides* seems to be more related to a deeper mixed layer depth, whereas *O. universa* correlated to a shallower mixed layer depth. *G. falconensis* shows preference for a higher chlorophyll *a* concentration, whereas *T. sacculifer* is linked to low chlorophyll *a* concentration conditions. Like the composition of the fauna, planktonic foraminifera diversity also does not seem to have a direct correlation with temperature, indicating that this factor is not individually responsible for diversity in the plankton.

In terms of paleoceanographic implications, the relationship between environmental parameters and faunal composition as seen in the sediment is thus the results of seasonal flux integration and does not strictly reflect primary affinities of the species.

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## Taxonomic Appendix

List of planktonic foraminifera species identified in the studied plankton tows.

*Berggrenia pumilio* (Parker, 1962)
Plate 3: 13 – 16
This species was only identified in the Azores and Iberian Margin samples, where it occurred commonly with similar abundances. The species is consistently small (<0.2 mm) and can be recognised by relatively heavily calcified shell with compact outline and smooth shiny surface appearance.

*Globigerina bulloides* (d'Orbigny, 1826)
Plate 1: 3 – 4
Present throughout the studied area, yet more abundant in the Canary and Iberian Margin stations.

*Globigerina falconensis* (Blow, 1959)
Plate 1: 13 – 14
Frequent through the studied area, with the highest abundances in the Azores region and at Canary stations during winter. This species could be distinguished from *G. bulloides* consistently by its slightly elongated chambers and narrow, asymmetrical aperture, commonly with lip.

*Globigerinella calida* (Parker, 1962)
Plate 1: 9
Appeared abundantly in similar numbers through the studied area. This species could be distinguished from *G. siphonifera* by its elongated chambers compared to the more spherical and compact chambers of *G. siphonifera*. In the adult stage, the coiling in *G. siphonifera* is nearly planispiral with the aperture becoming equatorial, whereas in *G. calida* the coiling remains trochospiral.

*Globigerinella siphonifera* (d'Orbigny, 1839)
Plate 1: 9 – 10
Common throughout the studied area in low numbers.

*Globigerinita glutinata* (Egger, 1893)
Plate 2: 1 – 4
This species occurred commonly throughout the studied area but more abundantly in the Azores and Canary winter stations.

*Globigerinoides ruber* (d'Orbigny, 1839)
White variety Plate 1: 17 – 18; Pink variety Plate 1: 15 – 16
The white variety was found abundantly in the Canary and Azores regions and in smaller numbers along the Iberian Margin. The distinction between *G. ruber* and *G. elongatus* was not done, since their characteristic features are not well developed among pre-adult individuals

that are abundant in the plankton (Aurahs et al., 2009). Therefore, this level of taxonomic resolution was not possible in our study. The abundance of the pink variety increased towards the south, with the highest numbers in the Canary region.

*Globorotalia crassaformis* (Galloway and Wissler, 1927)
Plate 2: 13 – 14
Rare, found only in the Azores and Iberian Margin areas. *G. crassaformis* was distinguished from *G. inflata* by its flat spiral side and more triangular chambers shape.

*Globorotalia inflata* (d'Orbigny, 1839)
Plate 2: 15 – 16
Common in small numbers throughout the studied area, found more abundantly in the Azores region.

*Globorotalia hirsuta* (d'Orbigny, 1839)
Plate 2: 17 – 18
This species was present in small numbers, except in the Azores region where its maximum abundance occurred.

*Globototalia truncatulinoides* (d'Orbigny, 1839)
Plate 2: 19 – 20
Very abundant in the Canary (winter samples) and Azores (winter and spring) regions. Almost absent in the remaining seasons in the Canary region and along the Iberian Margin.

*Globoturborotalita rubescens* (Hofker, 1956)
Plate 1: 19 – 20
Present throughout the studied area but with higher occurrences in the Azores and Canary regions (in winter).

*Hastigerina pelagica* (d'Orbigny, 1839)
Plate 1: 11 – 12
Rare, found only in the Canary and Azores regions and in low abundances.

*Neogloboquadrina dutertrei* (d'Orbigny, 1839)
Plate 2: 12
Rare throughout the studied area except for the winter station from the Canary region. This species was distinguished from *N. incompta* by the higher number of chambers in the last whorl, with specimens being considered as *N. dutertrei* when they had more than four chambers. In samples counted by different taxonomists, some specimens were initially identified as *Neogloboquadrina* P/D intergrade. Since those authors also distinguished *N. incompta*, and because there is no evidence for the presence of a different *Neogloboquadrina* species, these specimens were here considered as belonging to the species *N. dutertrei*.

*Neogloboquadrina incompta* (Cifelli, 1961)
Plate 2: 7 – 8
Frequent throughout the studied area, with high concentrations at the Canary winter stations.

*Neogloboquadrina pachyderma* (Ehrenberg, 1862)
Plate 2: 5 – 6
Present throughout the studied area but in low numbers. Where it was rare and its occurrence was concomitant with *N. incompta,* we have considered it as the rare sinistral form of *N. incompta* (Darling et al., 2006). Where it was present more abundantly, it was considered as *N. pachyderma.* The reason why the encountered species could not be dismissed a sinistral variant of *N. incompta* is illustrated if Figure A1, which shows that ratio between the sinistral and dextral form varied from 0.1 to above 1.

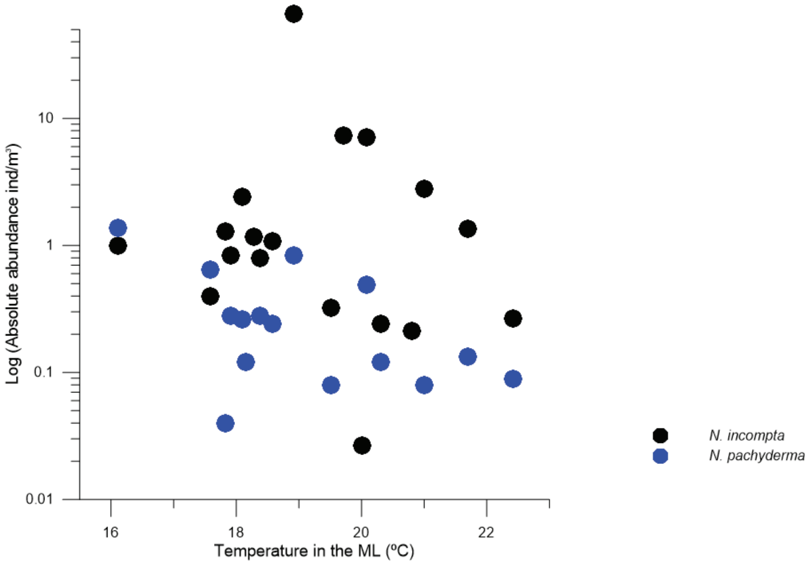


**Figure 10.** *N. pachyderma* and *N. incompta* absolute abundances for all the stations, with the respective temperature in the ML.

*Orbulina universa* (d'Orbigny, 1839)
Plate 1: 1 – 2
Common in small numbers, except in Iberian Margin. The "Biorbulina" form was rare and only found in two stations along the Iberian Margin.

*Pulleniatina obliquiloculata* (Parker and Jones, 1865)
Plate 2: 9 – 11
Rare along the Iberian Margin and around the Azores Islands where most of the individuals found were juveniles. These were identified as juvenile by the lack of the final chamber that is added in a streptospiral manner and covers the juvenile umbilical aperture (Plate 2: 9 and 10) in comparison the adult stage (Plate 2: 11). Abundant in the stations from the Canary region, especially in the winter stations.

*Tenuitella fleisherei* (Li, 1987)
Plate 3: 17 – 18

Found with minor concentrations in Iberian Margin and around the Azores. The species is consistently small (<0.2 mm) and can be recognised by its five or more curved chambers, which are laterally compressed.

*Tenuitella iota* (Parker, 1962)
Plate 3: 9 – 10
This species was only identified and counted in the Iberian Margin and Azores Islands samples, occurring frequently in Azores region but being very rare or absent in Iberia Margin. It has four slightly curved chambers with visible pores, an umbilical-extraumbilical aperture and a hispid surface.

*Tenuitella parkerae* (Brönnimann and Resig, 1971)
Plate 3: 11 – 12
This species was identified and counted only in the Iberian Margin and Azores samples, where it was present in small numbers. This small-sized (<0.2 mm) species is characterised by radially elongated chambers and smooth and shiny shell surface.

*Trilobatus sacculifer* [=*Globigerinoides sacculifer*] (Brady, 1877)
Plate 1: 6 – 8
Common throughout the studied area but very abundant at two of the stations located on the Iberian Margin. Specimens with and without a sac-like final chamber were found, but not counted separately following André et al. (2013).

*Turborotalita clarkei* (Rögl and Bolli, 1973)
Plate 3: 5 – 8
Rare along the Iberian Margin and the Azores. It was not identified and counted in the Canary Islands stations. *T. clarkei* can be distinguished from *T. quinqueloba* by its smaller size (<0.2 mm), and compact outline reflecting heavy calcification, lacking the ampullate final chamber that is frequently observed in *T. quinqueloba*.

*Turborotalita humilis* (Brady, 1884)
Plate 3: 1 – 2
This species was present in low numbers throughout the studied area, except for the Canary region during winter where it was present in exceptionally high numbers.

*Turborotalita quinqueloba* (Natland, 1938)
Plate 3: 3 – 4
Common with similar abundances throughout the studied area but not a dominant species.

*Globorotalia scitula* (Brady, 1882)
Plate 3: 19 – 20
Present through the studied area with maximum abundances in the surroundings of Azores Islands. This species is distinguished from *G. hirsuta* by its smaller size and smooth, shiny shell. Yet it can be very similar to *G. hirsuta* juvenile specimens.

### Plate 1

**1-2:** *Orbulina universa* from station Ib-F 12, 1- adult specimen of "Biorbulina" form, 2- adult specimen of *O. universa*; **3-4:** *Globigerina bulloides* collected at Ib-F 12, 3- juvenile specimen, 4- adult individual; **5:** *Globigerinella calida,* adult specimen from Ib-F 12 ; **6-8:** *Trilobatus sacculifer* collected at Ib-F 12*,* 6- juvenile specimen, 7- adult specimen without a sac-like final chamber, 8- adult specimen with a sac-like final chamber; **9-10:** *Globigerinella siphonifera* from Ib-F 12*,* 9- juvenile specimen, 10- adult specimen; **11-12:** *Hastigerina pelagica* from POS 383-163*,* 11- juvenile specimen, 12- adult specimen ; **13-14:** *Globigerina falconensis* from POS 383-173*,* 13- juvenile specimen , 14-adult specimen; **15-16:** *Globigerinoides ruber* white adult specimens from Ib-F 12; **17-18:** *Globigerinoides rube*r pink collected at Ib-F 12; **19-20:** *Globoturborotalita rubescens* from POS 383-173, 19- juvenile specimen , 20- adult specimen.

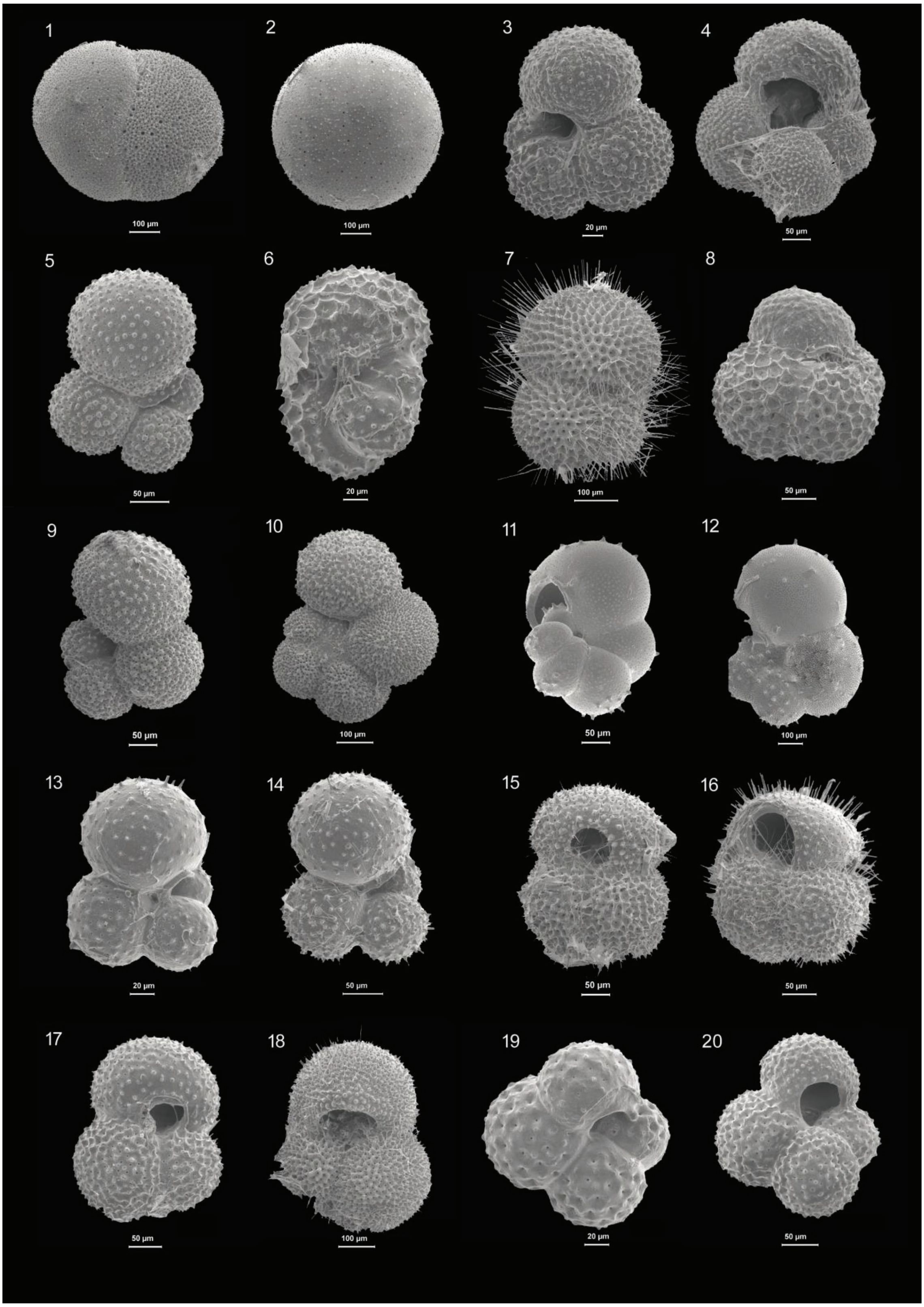
### Plate 2

**1-4:** *Globigerinita glutinata* from POS 383-161, adult specimens without bulla; **5-6:** *Neogloboquadrina pachyderma* from Ib-F 6, 5- juvenile specimen, 6- adult specimen, **7-8:** *Neogloboquadrina incompta* from POS 383-161, 7-juvenile specimen, 8- adult specimen; **9-11:** *Pulleniatina obliquiloculata* from POS 383-161, 9-10 – juvenile specimens, 11- adult specimen; **12:** *Neogloboquadrina dutertrei* adult specimen from POS 383-161; **13-14:** *Globorotalia crassaformis* sampled in POS 377-696, 13- juvenile specimen, 14- adult specimen; **15-16:** *Globorotalia inflata* from Ib-F 12, 15- juvenile 16- adult specimen; **17-18:** *Globorotalia hirsuta* from POS 383-161, 17- juvenile specimen, 18- adult specimen; **19-20:** *Globorotalia truncatulinoides* from POS 377-704, 19- juvenile specimen, 20- adult specimen.

### Plate 3

**1-2:** *Turborotalita humilis* from POS 334 -72, 1- juvenile specimen, 2- adult specimen with apertural flange covering the umbilicus; **3-4:** *Turborotalita quinqueloba* from POS 384-273; **5-8:** *Turborotalita clarkei* from POS 384 -273; **9-10:** *Tenuitella iota* from POS 383-161, 9- juvenile specimen, 10- adult specimen; **11-12:** *Tenuitella parkerae* from POS 384-273; **13-16:** *Berggrenia pumilio* from POS 384-273; **17-18:** *Tenuitella fleisheri,* from POS 383-161; **19-20*:*** *Globorotalia scitula* from POS 383-161, 19- juvenile specimen, 20- adult specimen.

## Plate 1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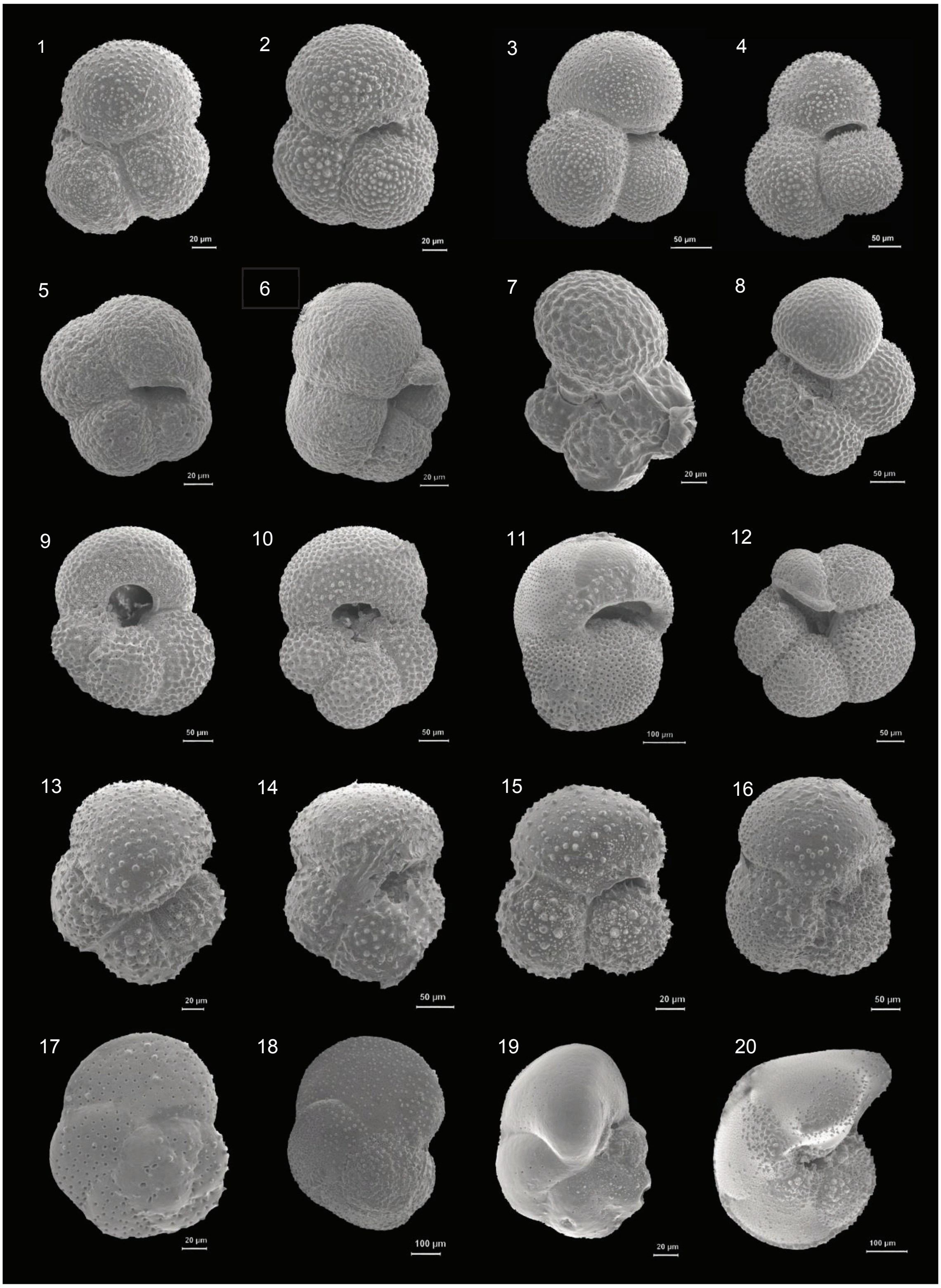
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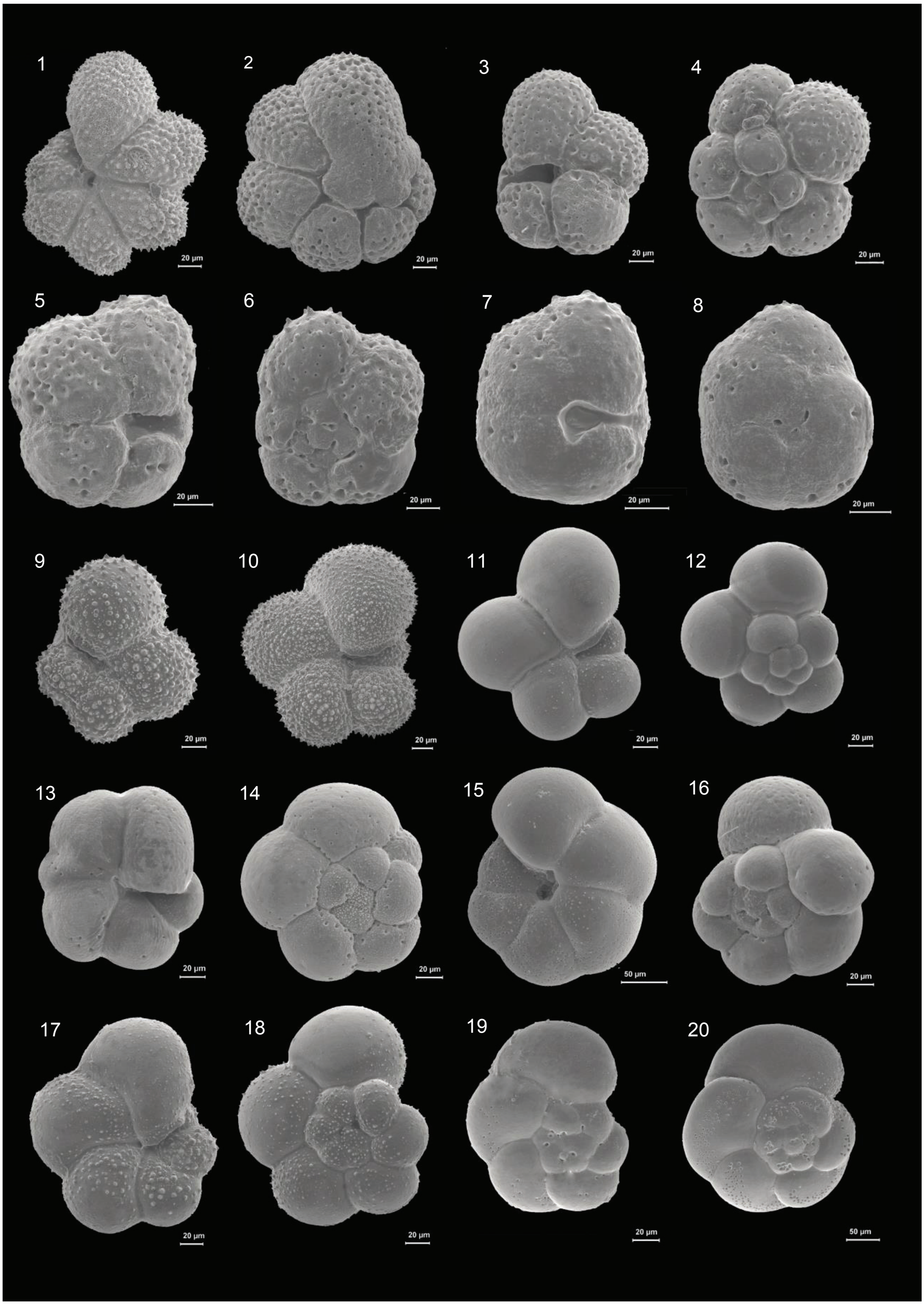
## Plate 3



# Chapter 4

## 4.1 Third case study

### Calcification depth of deep-dwelling planktonic foraminifera from the eastern North Atlantic constrained by stable oxygen isotope ratios of shells from stratified plankton tows

Andreia Rebotim, Antje H. L. Voelker, Lukas Jonkers, Joanna J. Waniek, Michael Schulz, Michal Kucera

**Status:** Submitted to Journal of Micropaleontology

# Calcification depth of deep-dwelling planktonic foraminifera from the eastern North Atlantic constrained by stable oxygen isotope ratios of shells from stratified plankton tows

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## Abstract

Stable oxygen isotopes ($\delta^{18}O$) of planktonic foraminifera are one of the most used tools to reconstruct environmental conditions of the water column. Since different species live and calcify at different depths in the water column, the $\delta^{18}O$ of sedimentary foraminifera reflects to a large degree the vertical habitat and interspecies $\delta^{18}O$ differences can thus potentially provide information on the vertical structure of the water column. However, to fully unlock the potential of foraminifera as recorders of past surface water properties, it is necessary to understand how and under what conditions the environmental signal is incorporated into the calcite shells of individual species. Deep-dwelling species play a particularly important role in this context, since their calcification depth reaches below the surface mixed layer. Here we report $\delta^{18}O$ measurements made on four deep-dwelling *Globorotalia* species collected with stratified plankton tows in the Eastern North Atlantic. Size and crust effects on the $\delta^{18}O$ signal were evaluated showing that a larger size increases the $\delta^{18}O$ of *G. inflata* and *G. hirsuta,* and a crust effect is reflected in a higher $\delta^{18}O$ in *G. truncatulinoides.* The great majority of the $\delta^{18}O$ values can be explained without invoking disequilibrium calcification. When interpreted in this way the data imply depth-integrated calcification with progressive addition of calcite with depth to about 300 m for *G. inflata* and to about 500 m for *G. hirsuta*. In *G. scitula*, despite a strong subsurface maximum in abundance, the vertical $\delta^{18}O$ profile is flat and appears dominated by a surface layer signal. In *G. truncatulinoides*, the $\delta^{18}O$ profile follows equilibrium for each depth, implying a constant habitat during growth at each depth layer. The $\delta^{18}O$ values are more consistent with the predictions of the Shackleton (1974) paleotemperature equation, except in *G. scitula*, which shows values more consistent with the Kim and O'Neil (1997) prediction. In all cases, we observe a difference between the level where most of the specimens were present and the depth where most of their shell appears to calcify.

**Key words:** planktonic foraminifera, stables oxygen isotopes, plankton tows, deep-dwelling species

## 1. Introduction

Stable isotope ratios in the shells of fossil planktonic foraminifera have been the backbone of paleoceanography for more than half a century. This is because during calcification, planktonic foraminifera record the physical and chemical conditions of the surrounding water and the fossil/sedimentary signal can be used to estimate water column properties, such as temperature, salinity or ocean stratification (Emiliani, 1954; Mulitza et al., 1997; Pak and Kennett, 2002; Shackleton, 1974; Simstich et al., 2003; Steph et al., 2009; Williams et al., 1979). However, already the first study using isotope ratios ($\delta^{18}O$) in foraminifera (Emiliani, 1954) revealed species-specific offsets that were attributed to differences in calcification depth among species. This hypothesis was later confirmed by observations from plankton tows (Bé and Hamlin, 1967; Berger, 1969; Duplessy et al., 1981; Fairbanks et al., 1980). Thus, according to their preferred habitat depth, certain species appear to consistently reflect conditions in the surface, others have a more variable calcification habitat and some appear to occur mainly below the mixed layer (Berger, 1969; Fairbanks et al., 1980, 1982; Kemle-von Mücke and Oberhänsli, 1999; Ortiz et al., 1995). Estimates of calcification depth based on $\delta^{18}O$ values in sedimentary shells are complicated by factors like non-linear growth during ontogenetic vertical migration and encrustation (Bemis et al., 1998; Fairbanks et al., 1982; Hemleben et al., 1989; Lohmann, 1995; Mulitza et al., 1997; Simstich et al., 2003). This implies that the proxy signal of the adult shell which is dominantly preserved in the sediment integrates the vertical range where each species lived and calcified (e.g. Birch et al., 2013; Kemle-von Mücke and Oberhänsli, 1999; Steinhardt et al., 2015; Wilke et al., 2009).

In addition, several studies have reported that the isotopic composition of shells of some planktonic foraminifera deviate from the predicted theoretical value for the ambient seawater in which they calcified (e.g. Birch et al., 2013; Fairbanks et al., 1980; Spero and Lea, 1996). These deviations have been attributed to ontogenic or size effects (Bemis et al., 1998; Deuser et al., 1981; Spero and Lea, 1996), symbiont photosynthesis and respiration (Spero and Lea, 1993; Wolf-Gladrow et al., 1999), calcification rate (Ortiz et al., 1996; Peeters et al., 2002), gametogenic or secondary calcite (Bé, 1980; Bouvier-Soumagnac and Duplessy, 1985; Duplessy et al., 1981; Lončarić et al., 2006), and carbonate-ion concentration (Itou et al., 2001; Spero et al., 1997). Size effect due to shell development has been reported in numerous studies with higher $\delta^{18}O$ values for larger size fractions (Berger, 1969; Kroon and Darling, 1995; Peeters et al., 2002; Spero and Lea, 1996) and also observed in culture experiments of the species *Globigerina bulloides,* which when kept under constant temperature and seawater oxygen isotope conditions, showed a $\delta^{18}O$ increase up to 0.8 ‰ with increasing size (Spero and Lea, 1996). The crust effect, i.e. the addition of a secondary crust in waters deeper (and thus often colder) than the waters of initial shell growth, is common in some planktonic foraminifera species during a later stage of their life cycle (Hemleben et al., 1985; Orr, 1967). The secondary crust can contribute up to a third to the total shell mass and therefore skew the result towards a heavier $\delta^{18}O$ value (Bé, 1980; Bouvier-Soumagnac and Duplessy, 1985; Duplessy et al., 1981; Schweitzer and Lohmann, 1991).

The majority of recent advances in understanding the incorporation of the oxygen isotopic signal are based on the evaluation of signals in foraminiferal shells collected from core-top sediments (e.g. Birch et al., 2013; Cléroux et al., 2007; Durazzi, 1981; Ganssen and Kroon, 2000; Mulitza et al., 1997; Steph et al., 2009). Using core-top shells makes a direct assessment of the isotopic signal incorporation in relation to the environmental conditions of the surrounding seawater at the time of calcification difficult, because the sedimentary signal represents a flux-weighted (seasonal) average of the vertical habitat, integrated over time. A more direct approach is using vertically resolved plankton tows, which allow a direct comparison between the isotopic composition of the shells and the seawater, the vertical abundance distribution of a species and the *in situ* environmental data (e.g., temperature, salinity) at time of collection. The majority of the studies using plankton tows focused on surface and intermediate dwelling species whereas deep-dwelling species remain poorly constrained (but see Lin et al., 2011; Mulitza et al., 2003; Peeters and Brummer, 2002). This is unfortunate, because combining signals from deep dwellers with those from surface and intermediate dwelling species is a potentially powerful method to obtain information on the water column structure (Cléroux et al., 2013; Mohtadi et al., 2007; Mulitza et al., 1997; Steph et al., 2009).

Thus, to fully unlock the potential of the geochemical composition of deep-dwelling planktonic foraminifera as a proxy for subsurface conditions, new observations from the water column are needed. Here we present data from stratified plankton tows in the subtropical Northeast Atlantic and assess how (or if) the proxy signal preserved in the shells integrates environmental information across the vertical habitat of the foraminifera. We focus on the $\delta^{18}O$ signal of the four deep dwelling species *G. truncatulinoides*, *Globorotalia hirsuta, G. inflata,* and *Globorotalia scitula*. These species were chosen because they are abundantly present in our samples and occur alive until at least 300 m water depth (Rebotim et al., 2017).

We assessed the potential impacts of shell size and secondary calcification, determined which paleotemperature equation best predicts the isotopic signal of each species, and tested where calcification occurred and if continued during a presumed ontogenetic vertical migration of the species.

## 2. Regional setting

The study area lies between the Azores Islands and the western Iberian Margin, a region influenced by the Azores Current, the Mediterranean Outflow Water and seasonal upwelling (Fig. 1). The Azores Current extends from the southern branch of the Gulf Stream (Sy, 1988) to the Gulf of Cadiz between 32° and 36° N (Gould, 1985; Klein and Siedler, 1989), defining the northern limit of the subtropical gyre. Its width varies from 60 to 150 km and its vertical extension can reach 2000 m (Alves et al., 2002; Gould, 1985). The Azores Current is associated with a thermohaline front – the Azores Front, which acts as a border between two different 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 north-eastern North Atlantic (Gould, 1985; Storz et al., 2009). This creates an abrupt change in temperature (~4° C) and in the water column structure across the Azores Front, influencing the distribution of planktonic organisms, including foraminifera (Alves et al., 2002; Schiebel et al

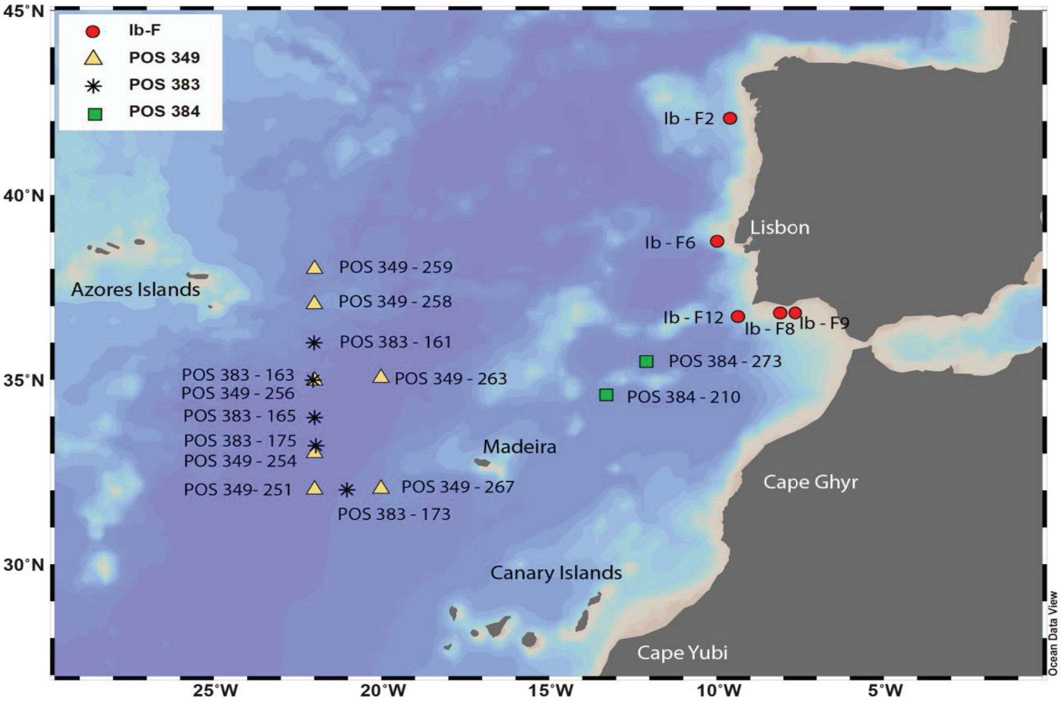


**Figure 1.** Stations in the eastern North Atlantic where planktonic foraminifera for this study were collected from stratified plankton hauls (Table 1). These include 14 stations discussed in Rebotim et al. (2017) and 5 additional stations from the POS 349 campaign. Station symbols are coded by cruises.

2002a, 2002b). According to a 42 years-long time series study, the position of the Azores Front varied between 30° N and 37.5° N (Fründt and Waniek, 2012). Southeast of the Azores Islands, the Azores Current splits into a northern branch that approaches the Portugal Current, a southern branch that connects to the Canary Current and a eastern branch that flow to the Gulf of Cádiz and also along the western Iberian margin – Iberian Poleward Current (Barton, 2001; Peliz et al., 2005; Sy, 1988). The latter, transports at the subsurface, eastern North Atlantic Central water from subtropical origin (Ríos et al., 1992). The Portugal Current flows southward along the western Iberian margin, carrying at the subsurface eastern North Atlantic Central Water but of subpolar origin. The North Atlantic Central Water masses form a permanent thermocline that can extend as deep as 800 m (van Aken, 2001). Because of the combination of large seasonality and the presence of strong gradients in water column structure, the region is particularly suitable to study the calcification behavior of the deep-dwelling species under variable conditions (Fig. 1, Table 1).

## 3. Material and methods

Planktonic foraminifera were sampled during four oceanographic campaigns between 2007 and 2012 in the eastern North Atlantic (Fig.1, Table 1). The collection, preservation and treatment of all samples is described in detail by Rebotim et al. (2017). Cytoplasm-bearing shells were picked from two size fractions (150 – 300 µm and >300 µm; referred to as small- and large-sized, respectively); except in samples of cruise POS 349 where shells were merged across all sizes in the fraction >150 µm. For the species *G. truncatulinoides* only the sinistral variant was selected. With the exception of the POS 349 samples, specimens with encrusted and non-encrusted shells were separated. Depending on the species and the size fraction, between 3 and 20 specimens were used for the stable isotope analyses.

Stable oxygen isotope measurements were performed at MARUM, University of Bremen, using a Finnigan MAT 251 isotope ratio mass spectrometer coupled to a Kiel I or Kiel III automated carbonate device. Isotope ratios are expressed in the $\delta$-notation and calibrated to the Vienna Pee Dee Belemnite (VPDB) scale using the NBS-19 standard. Analytical precision of an in-house carbonate standard (Solnhofen limestone) over the measurement period was ≤0.04 ‰ (1 s.d.). The oxygen isotopic data will be available online through the www.pangaea.de.

To determine which paleotemperature equation best describes the foraminifera $\delta^{18}O$, we calculated oxygen isotope equilibrium values ($\delta^{18}O_{eq}$) using temperature and salinity data

**Table 1 –** Cruise and stations, location, time (day/month /year), depth intervals of the collected samples.

| **Cruise** | Station | Latitude | Longitude | Date | Depth intervals (m) |
|---|---|---|---|---|---|
| **Poseidon 349** | 251 | 32.000 | -22.000 | 09/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 254 | 33.000 | -22.000 | 10/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 256 | 35.000 | -22.000 | 11/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 258 | 37.000 | -22.000 | 12/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 259 | 38.000 | -22.000 | 13/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 263 | 35.000 | -20.000 | 16/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 267 | 35.000 | -20.000 | 18/4/07 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| **Poseidon 383** | 161 | 36.000 | -22.000 | 22/4/09 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 163 | 35.000 | -22.000 | 23/4/09 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 165 | 34.000 | -22.000 | 23/4/09 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 173 | 32.000 | -21.000 | 25/4/09 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| | 175 | 33.150 | -22.000 | 26/4/09 | 0-100, 100-200, 200-300, 300-500, 500-700 |
| **Poseidon 384** | 210 | 34.600 | -13.290 | 12/5/09 | 0-100, 100-200, 200-300, 300-400, 400-700 |
| | 273 | 35.500 | -12.090 | 21/5/09 | 0-100, 100-200, 200-300, 300-400, 400-500 |
| **Iberia-Forams** | 2 | 42.090 | -9.500 | 11/9/12 | 0-25, 25-80, 80-200, 200-300 |
| | 6 | 38.760 | -9.980 | 12/9/12 | 0-70, 70-140, 140-240, 240-340, 240-540 |
| | 8 | 36.800 | -8.040 | 13/9/12 | 0-60, 60-120, 120-240, 240-400 |
| | 9 | 36.810 | -7.710 | 13/9/12 | 0-90, 90-180, 180-270, 270-360 |
| | 12 | 36.720 | -9.370 | 15/9/12 | 0-100, 100-200, 200-350, 350-550 |

obtained from CTD casts at the time of sample collection and the equations of Shackleton (1974) (1) and Kim and O'Neil (1997) (2):

$$\delta^{18}O_{eq} = \frac{4.38 - \sqrt{19.18 - 0.4 \times (16.9 - T)}}{0.2} + \delta^{18}O_w \qquad (1)$$

$$\delta^{18}O_{eq} = \frac{4.64 - \sqrt{21.53 - 0.36 \times (16.1 - T)}}{0.18} + \delta^{18}O_w \qquad (2)$$

where T denotes temperature in °C and $\delta^{18}O_w$ the $\delta^{18}O$ of seawater. For the Shackleton (1974) equation, the $\delta^{18}O$ values from the ambient seawater were converted from VSMOW to VPDB scale by subtracting 0.2 ‰, which was the current conversion at that time (e.g. Pearson, 2012), whereas for the Kim and O'Neil (1997) equation, the $\delta^{18}O$ values were converted from VSMOW to the VPDB scale by subtracting 0.27 ‰ (Hut, 1987). Seawater $\delta^{18}O$ was estimated using a regional $\delta^{18}O_w$ – salinity relationship (Fig. 2) based on previous measurements in the study area (25°N to 45°N and 5°W to 35°W) (Voelker et al., 2015), covering the top 700 m of the water column, since this is the maximum depth used for the collection of planktonic foraminifera (Eq. 3).

$$\delta^{18}O_w = 0.5956 * S - 20.829 \; (3)$$

where $S$ denotes *in situ* salinity at the time of collection. The prediction error calculated for the seawater $\delta^{18}$O estimation was 0.12 ‰. We then compare the oxygen isotope ratios with the vertical distribution of the analysed foraminifera species, as described in Rebotim et al. (2017) and Rebotim (2009) for the POS 349 cruise samples.

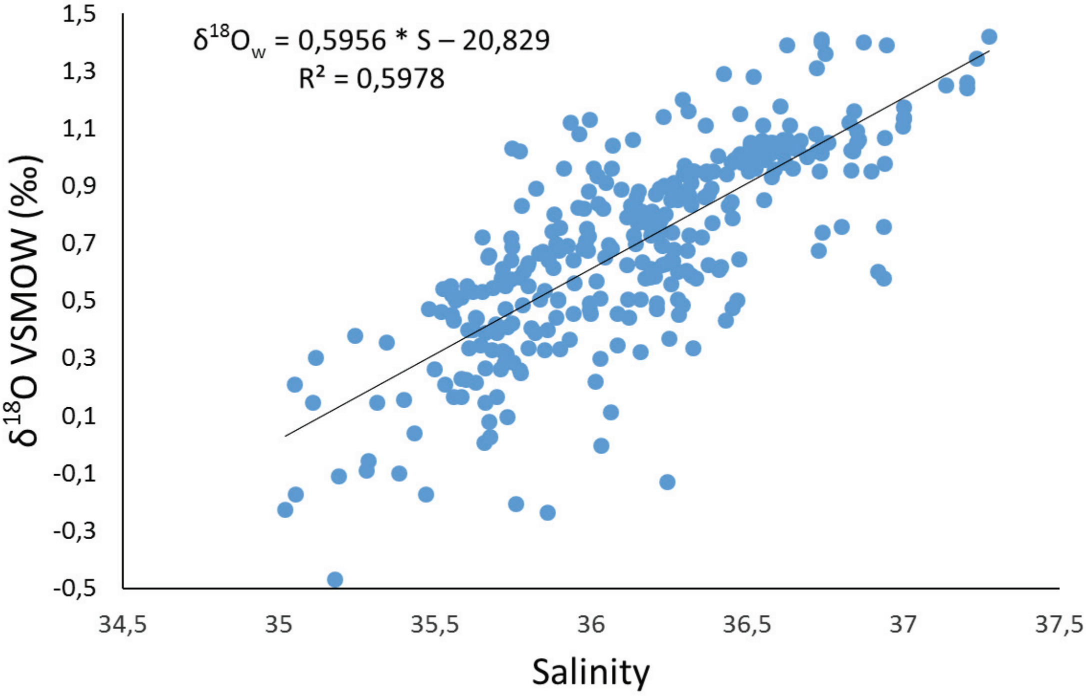


**Figure 2.** Regional linear regression of salinity versus $\delta^{18}O_w$ for the eastern North Atlantic Ocean based on data extracted from Voelker et al. (2015). The relationship is based on $\delta^{18}O_w$ values (per mil VSMOW) from depths between 0 and 700 m and within the region between 25° – 45°N and 5° – 35°W.

## 4. Results

### 4.1 Size and crust effects on the $\delta^{18}$O of the shell

To understand the $\delta^{18}$O variability in our data, we evaluate the effects of shell size and secondary encrustation (Fig. 3, 4, 5, 6). A potential size effect is observed in non-encrusted *G. hirsuta*, where $\delta^{18}$O values of larger shells are on average 0.32 ‰ more positive (Table 2). The same may hold for encrusted *G. inflata*, but the effect appears larger (0.59 ‰ for Azores and 0.56 ‰ for Iberia). The crust effect in this species is almost insignificant for the Iberian Margin sample (0.04 ‰) but it is negative for the sample from Azores region (-0.12 ‰). Our data do not show a clear indication for a size effect in *G. truncatulinoides*. However, in this species encrusted small shells have consistently more positive $\delta^{18}O$ values than non-encrusted shells (Table 2). The effect of encrustation is unclear for *G. inflata* and could not be evaluated for *G. hirsuta* (Table 2). Note that all measurements in *G. scitula* were made on uniform samples, preventing assessment of a size effect.

**Table 2 –** Size effect between non-encrusted and encrusted specimens and crust effect between specimens with and without crust for the individuals grown under similar conditions, sorted by region.

| **Species** | Size Effect | | | | Crust Effect | |
|---|---|---|---|---|---|---|
| | Non-encrusted | | Encrusted | | Small size | |
| | N | Mean $\Delta\delta^{18}O_{(large - small)}$ ± Standard deviation (‰) | N | Mean $\Delta\delta^{18}O_{(large – small)}$ ± Standard deviation (‰) | N | Mean $\Delta\delta^{18}O_{(crust – no crust)}$ ± Standard deviation (‰) |
| ***G. truncatulinoides***<br>**Azores Front/Current** | 3 | -0.09 ± 0.22 | 3 | -0.03 ± 0.12 | 5 | 0.27 ± 0.11 |
| ***G. hirsuta***<br>**Azores Front/Current** | 12 | 0.32 ± 0.18 | | N/A | | N/A |
| ***G. inflata***<br>**Azores Front/Current** | 1 | -0.14 | 1 | 0.59 | 1 | -0.12 |
| **Iberian Margin** | | N/A | 1 | 0.56 | 1 | 0.04 |

## 4.2 Offsets from equilibrium $\delta^{18}O$ in the surface layer

Since planktonic foraminifera have been hypothesized to migrate downwards in the water column during growth, a specimen may contain an integrated isotope signature from all depths above the level where it was collected. This integration effect is smallest in the near surface layer, where migration is likely to be minimal and thermal and isotope gradients are small. Measurements in the surface layer are therefore most suitable to evaluate departures from equilibrium calcification. To this end, we determined the offsets from the two tested equations for the upper 100 m. In this interval, *G. inflata* and *G. truncatulinoides* show the smallest offsets from the Shackleton equation, with median offsets of -0.03 ‰ and -0.07 ‰ (Fig. 7, 8). *G. hirsuta* reveals a difference of -0.11 ‰ from the median value of Shackleton (1974) and 0.11 ‰ from the Kim and O'Neil (1997) $\delta^{18}O_{eq}$ estimate (Fig. 7, 8); thus the $\delta^{18}O$

values seem to be equally predicted by both equations. For *G. scitula* we have only a single measurement in the top layer, showing an offset of -0.06 ‰, from the estimation from Shackleton (1974) and a deviation of 0.18 ‰ from the Kim and O'Neil (1997) prediction (Fig. 7, 8).

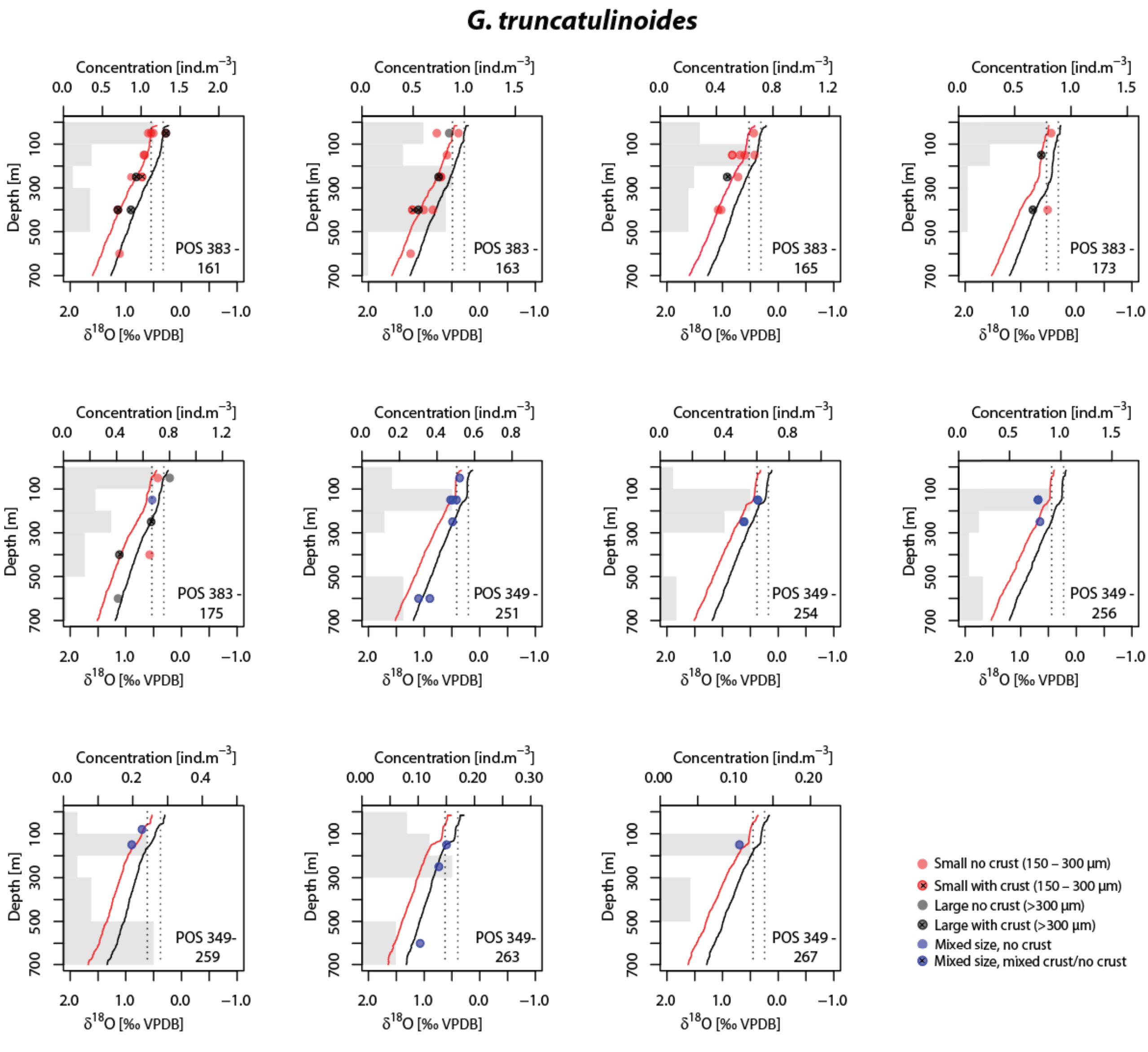


**Figure 3**. Vertical profiles of $\delta^{18}$O and concentration (grey bars, ind/m$^3$) of *G. truncatulinoides* in the upper 700 m of the water column at all stations (Fig 1) with sufficient number of individuals for oxygen isotope analysis. Red line shows $\delta^{18}O_{eq}$ for calcite based on the Shackleton (1974) equation, black line shows the same using the Kim and O'Neil (1997) equation. Dashed lines indicate the mean $\delta^{18}O_{eq}$ values of the upper 100 m. The area between the dashed and solid line for each equation delimit the space of $\delta^{18}$O values that can be explained without requiring disequilibrium calcification.

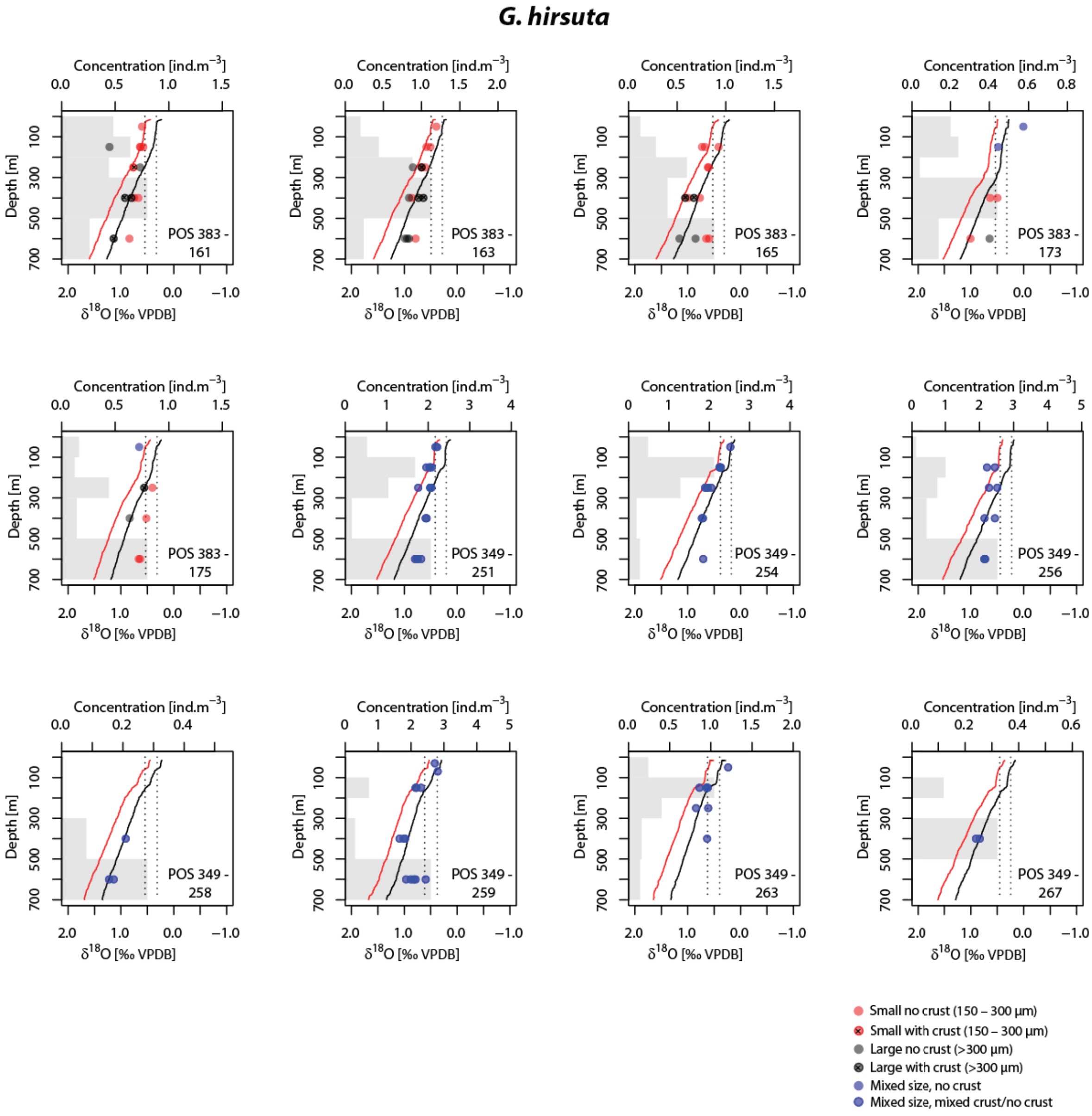
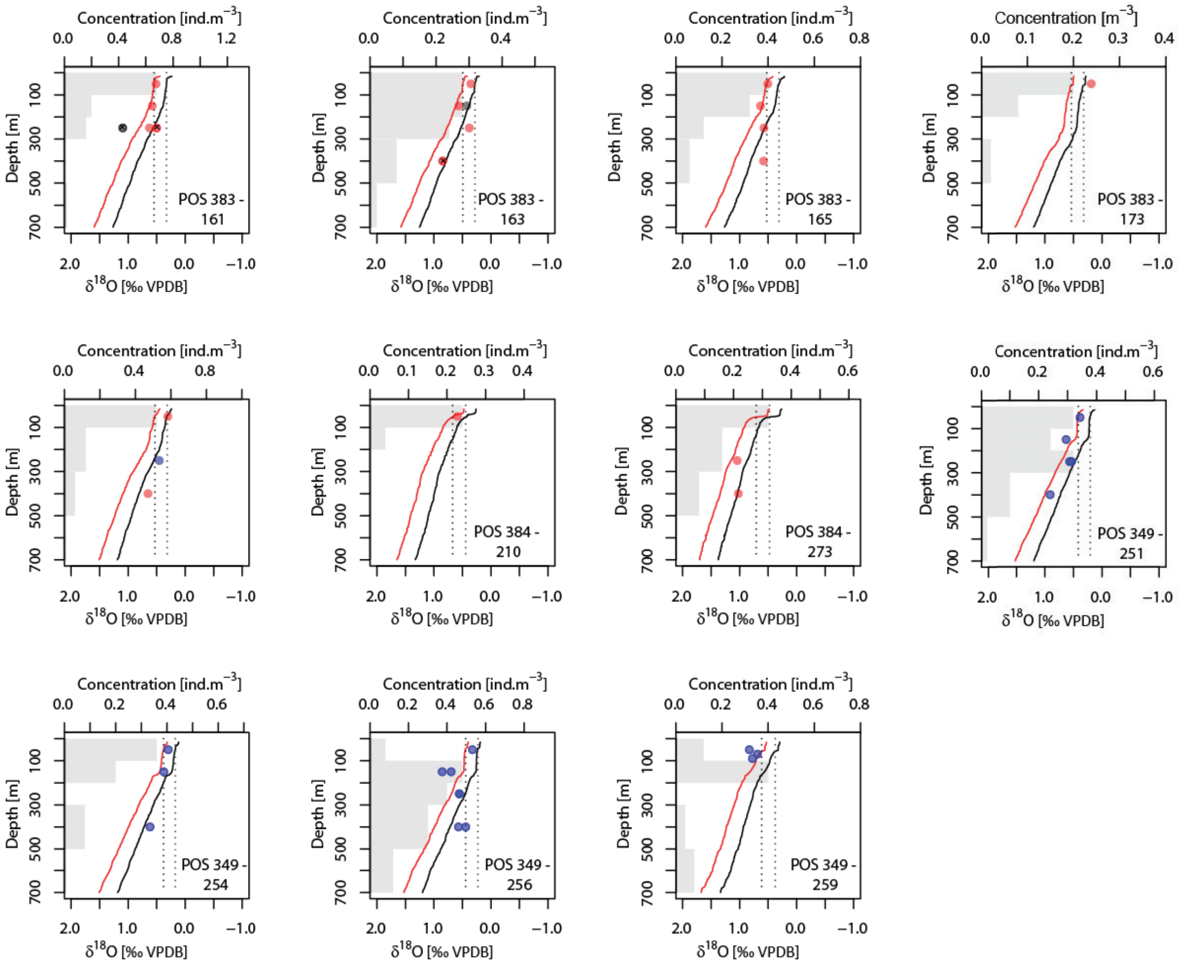


**Figure 4**. As Fig. 3 but for *G. hirsuta*.

## *G. inflata*

**a) Azores Front/ Current**



**b) Iberian Margin**

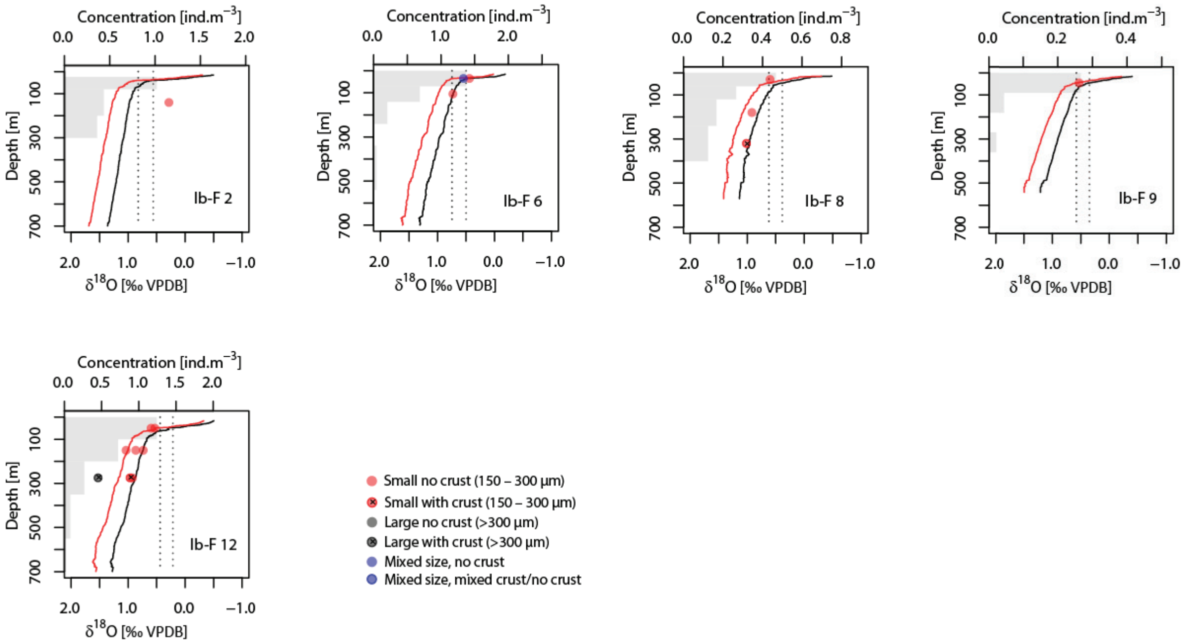


**Figure 5**. As Fig. 3 but for *G. inflata,* shown separately for **a)** stations in the Azores Front/ Current region and **b)** stations along the Iberian Margin.

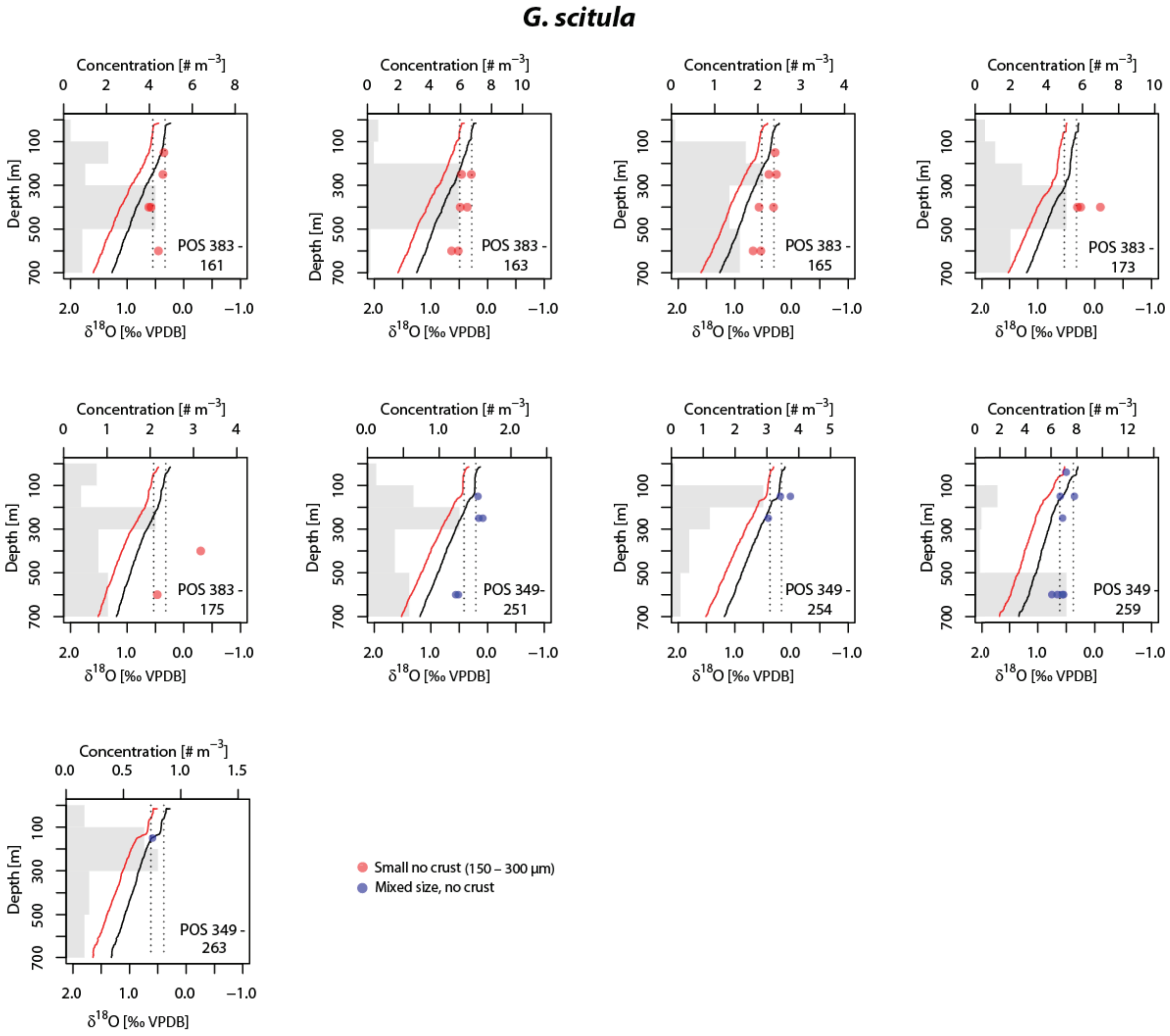


**Figure 6**. As Fig. 3 but for *G. scitula.* No different size fractions have been distinguished since no specimens > 250 µm were found.

*G. hirsuta* coincide in most of the cases with the presence of a secondary crust or a greater size fraction. *G. inflata* $\delta^{18}$O values turn slightly positive until approximately 300 – 500 m (Fig. 5). In comparison, the $\delta^{18}$O values of *G. inflata* are more positive (0.56 – 0.95 ‰) in the stations from the Iberian Margin (Fig. 5b) than the $\delta^{18}$O data from the plankton tows from Azores region (0.19 – 0.91 ‰) (Fig. 5a), reflecting seasonal temperature differences, namely end of summer for Iberian Margin and spring for Azores. The $\delta^{18}$O values of *G. scitula* (Fig. 6) remain similar across all depths, with $\delta^{18}$O values falling closer to the Kim and O'Neil (1997) estimation than the Shackleton (1974) line (Fig. 7, 8). This species exhibits the lowest $\delta^{18}$O values, between 0.12 and 0.67 ‰.

## 5. Discussion

### 5.1 Size and crust effects in $\delta^{18}$O

To assess to what degree the stable isotopic signatures of the individual species could be interpreted in terms of equilibrium offsets and calcification habitat, we first evaluate the effects of ontogeny on the isotope ratios of the shells. This is essential, because our analysis is based on specimens that were alive during collection and therefore represented different stages in the ontogeny. We focus our comparison on studies of plankton-derived material, to avoid the complication of having to consider factors like seasonal integration in the interpretation of size-related trends in sedimentary material (Ezard et al., 2015; Hernández-Almeida et al., 2011). Since few parallel measurements were possible on samples with different shell size or encrustation from the same tow intervals (Fig. 3, 4, 5, 6; Table 2) and the sample sizes are small, our analyses allow the evaluation of shell size and secondary encrustation effects only to a limited extent. The observed trends can, nevertheless, be compared to previous observations on the studied species and to estimate the potential magnitude of the size-related offset and compare it to the magnitude of isotopic variation with depth among the species.

Our observations on non-encrusted *G. hirsuta*, for which we have most data, show that larger specimens have heavier $\delta^{18}$O values, consistent with previous findings (Ganssen, 1983; Hemleben et al., 1985; Niebler et al., 1999). In this species, we also observe that small individuals are present at all depths, but the $\delta^{18}$O values from deeper specimens are consistent with a surface signal, suggesting that these specimens may represent descending individuals that have not yet added any calcite at depth. An enrichment in the $\delta^{18}$O values with size was also observed for encrusted specimens of *G. inflata* (+0.58 ‰), which agrees with what was reported by other authors (Ganssen, 1983; Lončarić et al., 2006; Niebler et al., 1999). In a study performed in the same region, larger specimens of *G. truncatulinoides* were found to be isotopically heavier by 0.4 ‰ (Wilke et al., 2009), which is also in agreement with previous studies in other regions (Hemleben et al., 1985; Lončarić et al., 2006). The small sample size could potentially explain the apparent absence of a size effect on the $\delta^{18}$O of *G. truncatulinoides* in our data.

Heavier $\delta^{18}$O in larger specimens could be explained by “vital effects” likely related to calcification rate (Spero and Lea, 1996; Bemis et al., 1998). Alternatively, the same pattern could be explained by ontogenetic vertical migration with a descending trajectory and continued calcification. In this model, the isotopically lighter small specimens at a given depth would represent individuals which calcified at a shallower depth and have not yet added new

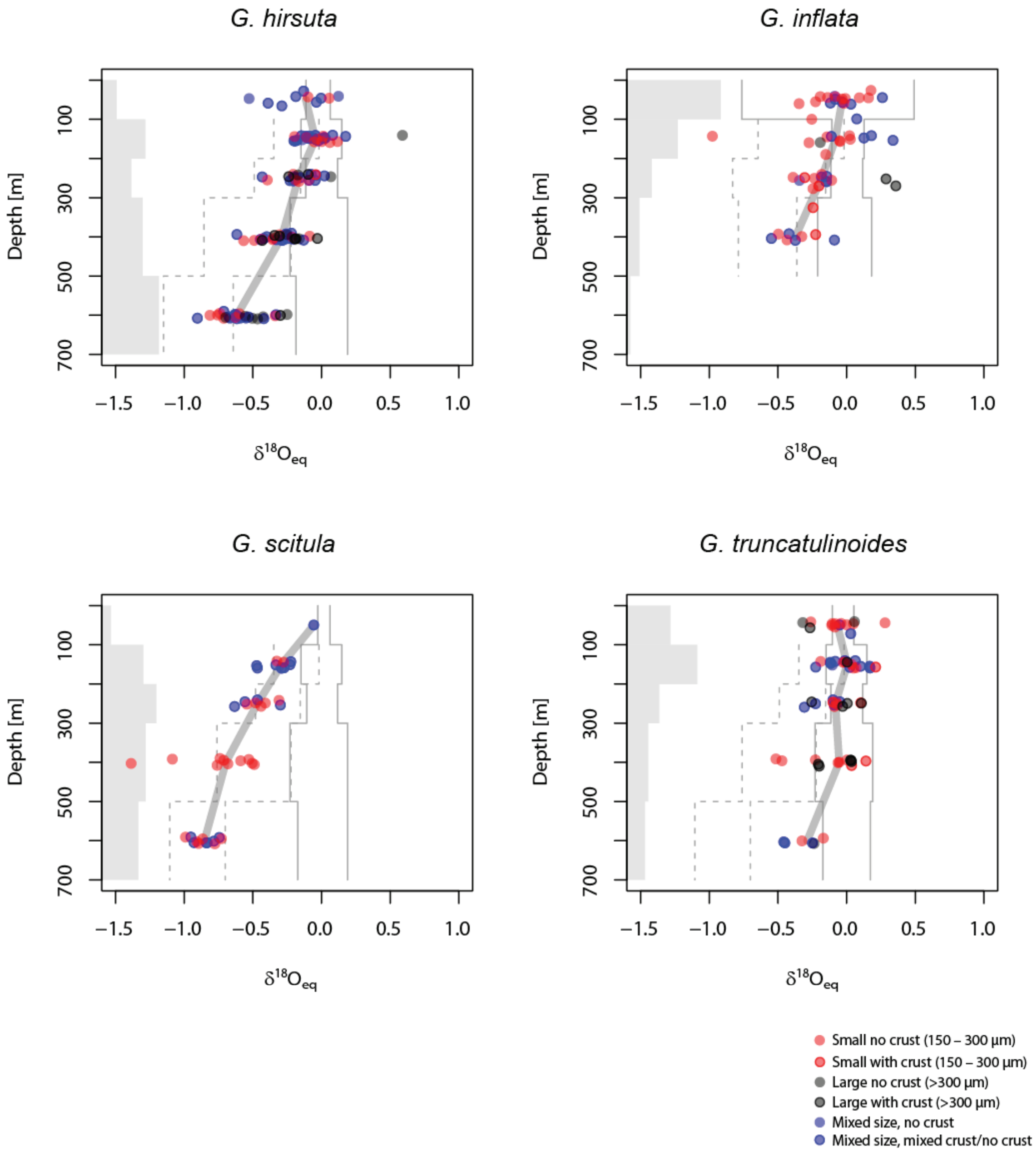


**Figure 7.** Summary across all stations for which respective foraminifera data are available of the offsets between the $\delta^{18}$O of the respective species at a given depth from the equilibrium $\delta^{18}$O at that depth calculated using the Shackleton (1974) paleotemperature equation. Solid lines represent the range of $\delta^{18}O_{eq}$ at each depth across all stations. Dashed lines show the range of offsets from the mean near surface (0-100 m) $\delta^{18}O_{eq}$ values at a given depth. Thick grey line shows the median profile of $\delta^{18}$O offsets for each species. Relative shell concentrations (averaged across all stations where the respective species is present and normalised) are indicated with the grey bar plots. Note that these serve only to qualitatively assess the vertical abundance pattern and no scale bar is given.

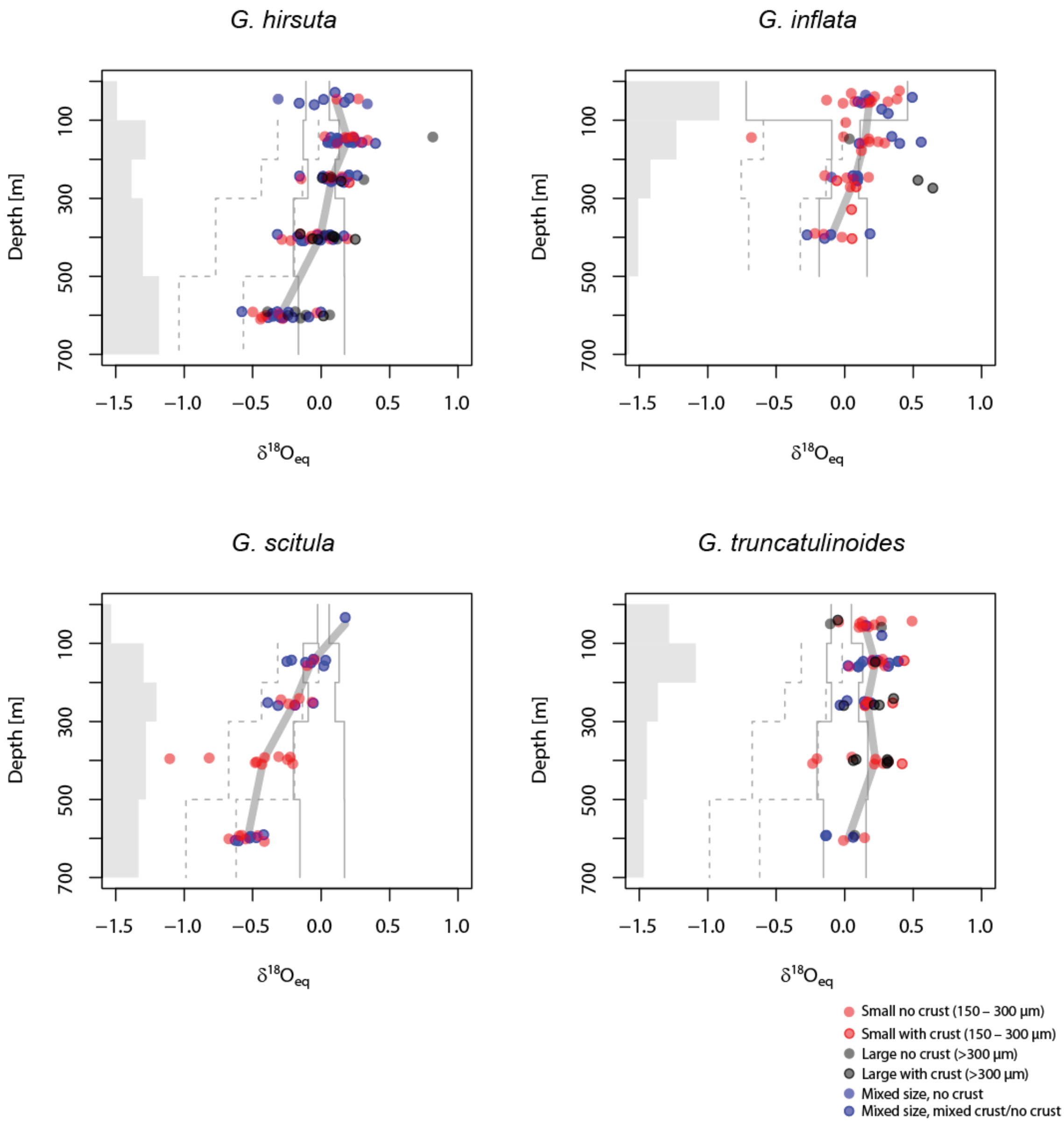


**Figure 8.** Same as Fig. 9 but using the Kim and O'Neil (1997) paleotemperature equation.

calcite at the depth where they were collected. Indeed, once these "ontogenetic migrants" add calcite at depth, they also increase in size and are then no longer considered "small". These two alternative explanations would leave a different depth-related signature. A "vital effect" would remain constant with depth, whereas ontogenetic vertical migration should cause an increase in the offset between small and large specimens with depth. In our limited data, the observations for *G. hirsuta* appear consistent with ontogenetic vertical migration, but the data for *G. truncatulinoides* do not.

Another aspect that affects the $\delta^{18}$O is secondary calcification during the final stage of the ontogeny (e.g. Bé, 1980; Schweitzer and Lohmann, 1991). Among the studied species, this effect could be observed only in *G. truncatulinoides*, where encrusted specimens appear isotopically heavier by on average 0.27 ‰ (Table 2). For this species, the $\delta^{18}$O increase associated with the addition of a secondary crust has been explored by several authors, who found that the crust may account for 30% (Mulitza et al., 1997) to more than 50% (LeGrande, 2004; Lohmann, 1995) of shell mass (e.g. LeGrande, 2004; Lohmann, 1995; Mulitza et al., 1997). For *G. inflata,* the $\delta^{18}$O difference between non-encrusted and encrusted specimens is not significant or inconclusive (Table 2) and for *G. hirsuta* the lack of paired data does not allow us to assess this effect.

Typically, isotopically “colder” signatures in encrusted specimens have been explained by the addition of the crust at the end (associated with reproduction) or during the final stages of a descending ontogenetic trajectory (Hemleben et al., 1989). If this is true then we should observe encrusted specimens only at depth. Since we observe encrusted specimens at all depth (Fig. 3-6) then either the vertical ontogenetic migration has a limited magnitude or encrustation is not related to the end of the ontogeny. Either way, the heavier isotopic values in encrusted specimens could also reflect a different mode of biomineralization and be the result of a process akin to the size-related “vital effect”. Indeed, recent studies have shown that some planktonic foraminifera species form crusts with different geochemical composition from lamellar calcite grown under the same environmental conditions (Fehrenbacher et al., 2017; Jonkers et al., 2016).

These observations provide first-order constrains for the interpretation of the vertical isotopic profiles. Potential size and crust effects are not seen in all species and their magnitude is <0.5 ‰ (Table 2). Whereas the size effect could arise either from a vital effect or from ontogenetic vertical migration, the crust effect is more likely a result of a vital effect (different mode/rate of calcification).

### 5.2 Offsets from equilibrium $\delta^{18}$O in the surface layer

The first-order prerequisite to interpret isotopic signature in foraminifera is to constrain the presence and magnitude of isotopic disequilibrium (vital effect). Next to culture experiments, material from stratified plankton nets is the only way to directly determine to what degree the foraminiferal calcite was produced in isotopic equilibrium with the surrounding water. The classical ontogenetic vertical migration model with a descending trajectory (Hemleben et al., 1989; Lohmann, 1995) implies that most of the initial calcite shell is built in the surface water, even in deep dwelling species. To avoid the effect of ontogeny on the observed isotopic values, we here assess the degree of equilibrium calcification only in the surface layer. The equilibrium isotopic composition at each station and depth is constrained by *in situ* temperature and salinity measurements, but the estimate has to consider differences in paleotemperature equations commonly used for these (symbiont-free) species of planktonic foraminifera.

In this respect, the $\delta^{18}$O data of *G. truncatulinoides* show a small negative median offset from the Shackleton (1974) equation (Fig. 7) and a slightly larger, positive offset from the Kim and O'Neil (1997) $\delta^{18}O_{eq}$ prediction (Fig. 8). Lončarić et al. (2006) found in their Southeast Atlantic plankton-tow samples that above 100 m, the $\delta^{18}$O of large specimens (350 – 450 µm) showed a positive offset (approximately +0.2 ‰) from the Kim and O'Neil (1997) predicted values, whereas the offset was insignificant for small specimens. Ganssen (1983), based on a plankton-tow study that applied the Epstein and Mayeda (1953) paleotemperature equation, which gives values close to Shackleton's, stated that *G. truncatulinoides* (size fractions: 315 – 400 µm; 400 – 500 µm) calcified in equilibrium with the prediction in waters off Eastern North Africa. Near the Canary Islands and thus in vicinity of our study area, $\delta^{18}$O values for smaller (<280 µm) *G. truncatulinoides* specimens were significantly more negative (-0.22 – -0.40 ‰) than the predicted $\delta^{18}O_{eq}$ values (Kim and O'Neil equation) within the surface mixed layer (≈120 m) than their larger (280-440 µm) counterparts, whose values were only slightly negative or matched the predicted $\delta^{18}O_{eq}$ (see fig. 8 in Wilke et al., 2009).

Similarly, our *G. inflata's* $\delta^{18}$O values show a negligible negative median offset in relation to the Shackleton estimation (-0.03 ‰) (Fig. 7) and a larger, positive median offset for the Kim and O'Neil line (+0.18 ‰) (Fig. 8). The latter is in good agreement with the Lončarić et al. (2006) observations, in the upper 150 m of the Southeast Atlantic that showed an offset range between 0.01 and 0.25 ‰ for the 350 – 450 µm size fraction relative to the Kim and O'Neil estimation. For the smaller size fraction (200 – 300 µm) the offset was 0.02 ‰ (Lončarić et al., 2006), which is comparable to the Wilke et al. (2006) findings, who, also using plankton tows from the Southeast Atlantic, obtained an average offset in relation to Kim and O'Neil (1997) $\delta^{18}O_{eq}$ of +0.05 ‰ (except for one station) for the size fraction 250 – 355 µm in the mixed layer. For the samples where size fractions were taken into consideration, the large size fraction is associated with a larger offset, being more positive relative to Kim and O'Neil (1997) $\delta^{18}O_{eq}$. Using the Epstein and Mayeda (1953) paleotemperature equation, Ganssen (1983) reports an offset between -0.4 and +0.5‰ for the size fraction 200 – 400 µm, which is higher than our observed median deviation from the Shackleton's $\delta^{18}O_{eq}$, but smaller than the median offset from Kim and O'Neil's $\delta^{18}O_{eq}$.

Most of our $\delta^{18}O$ data points of *G. hirsuta* lie closer to Shackleton (1974) $\delta^{18}O_{eq}$ prediction (Fig. 4 and Fig. 7). For comparison, only plankton tow studies related to the Epstein and Mayeda (1953) $\delta^{18}O_{eq}$ are available. Hemleben et al., (1985) observed a positive offset (0.25 – 0.5 ‰) for the large size fraction of *G. hirsuta,* whereas an offset between -0.5 and +0.2 is reported (200 - 500 µm) by Ganssen (1983). The only $\delta^{18}O$ measurement available for *G. scitula* in the surface layer falls near the Shackleton prediction, presenting an insignificant offset (Fig. 7). Ortiz et al. (1996), using plankton tows from the northeastern Pacific, estimated a deviation from $\delta^{18}O_{eq}$ (based on Epstein and Mayeda (1953)) of less than -0.4 ‰ for a size fraction > 150 µm. Although the offset from Shackleton (1974) $\delta^{18}O_{eq}$ is apparently lower (-0.06 ‰) than the presented by the latter study, it is based on a single measurement and therefore inconclusive.

Thus, in our study, all four *Globorotalia* species show the same trends at the surface, i.e. a small or non-existing offset from the Shackleton (1974) equation, except for *G. scitula* where only a single data point is available. In that species, it is possible that our assumption of using values from the surface layer is incorrect, as this species clearly has a subsurface habitat (and abundance maximum) (e.g. Rebotim et al., 2017). At depth, the isotopic values of this species can only be explained by equilibrium calcification when the Kim and O'Neil equation is used (Fig. 7, 8), whereas for the remaining three species, the isotopic profiles at depth remain consistent with the Shackleton (1974) equation. The compilation of results from previous studies reveals considerable inconsistencies. These could be real, reflecting unconstrained processes (such as the hypothetical annual reproductive cycle in *G. truncatulinoides*; e.g., Schiebel and Hemleben, 2017) or they could reflect uncertainties in determining the *in situ* $\delta^{18}O$ of seawater from indirect measurements, which is considerable even in our region (Fig. 2).

### 5.3 Vertical patterns in foraminifera $\delta^{18}O$: evidence for calcification at depth?

In the presence of steep gradients in surface water properties, differences in vertical habitats among species or changes in the vertical habitat of a species during its ontogeny leave a signature in the sedimentary $\delta^{18}O$ signal that is at least as important to constrain as the magnitude of disequilibrium calcification. Once the degree of (dis)equilibrium calcification is constrained, the depth interval where calcification occurs can be determined. Whereas living depth is straightforward to constrain by observations (e.g. Rebotim et al., 2017), the concept of calcification depth requires explanation. Calcification depth could either be considered as a specific level in the water column where calcification appears to occur or it can, more realistically, as we will explain, refer to the portion of the water column where a species adds calcite to its shell.

Here, we determine the calcification depth assuming that vertical ontogenic migration occurs and that it can be described using a framework of a monotonously descending trajectory and continuous calcification. This framework is based on the hypothetical model by Hemleben et al. (1989) and it has been embodied in quantitative calcification models by e.g. Wilke et al (2009). In this model, and in the absence of a large or variable disequilibrium calcification, foraminifera $\delta^{18}$O at a given depth must fall between the surface $\delta^{18}$O equilibrium and the $\delta^{18}$O equilibrium at that depth. This framework produces for each vertical profile a theoretical $\delta^{18}$O space (Fig. 9). The vertical profile of the foraminifera $\delta^{18}$O within this space describes where the calcite of a specimen from a given depth has been added. If the profile is vertical, all calcite would have to originate from the same depth layer. Such a species would thus have a preferred calcification depth, which may be decoupled from its living depth. If the profile follows exactly the $\delta^{18}$O equilibrium prediction at each depth then all calcite must have been formed at the depth where a specimen was collected. Such a species may have a preferred living depth, but it has no preferred calcification depth.

This approach is fundamentally different from an attempt to determine (apparent) calcification depth from sediment or sediment-trap samples, which cannot be used to answer the question whether the calcification occurred during ontogenetic vertical migration. Inferred apparent calcification depth based on such material will always be shallower than the calcification zone identified from specimens from vertically resolved plankton net samples, even if the effect of seasonality can be removed from sediment samples or excluded in sediment trap samples. Isotopic offsets between species sampled in sediment material do not reflect the difference in their calcification depths. Rather, they reflect differences in the zone over which calcification occurred, modulated by the pattern of calcite addition during descent and seasonality.

Following the above framework, the vertical profile of *G. truncatulinoides* $\delta^{18}$O is consistent with equilibrium calcification following the Shackleton-based prediction from the surface down to 300 – 500 m (Fig. 3, 7). Below this depth, the isotopic signature remains constant, implying that calcification may cease below this depth. Other plankton tow studies reported that *G. truncatulinoides* calcified in the upper 200 m in the Sargasso Sea (Hemleben et al., 1985), whereas in the South Atlantic and eastern North Atlantic it was described as calcifying until 400 m (Lončarić et al., 2006; Wilke et al., 2009). Across all stations in this study, the vertical isotopic profile of this species appears to follow the end-member scenario of complete *in situ* calcification. Remarkably, the observed vertical profile of this species is most consistent with the absence of ontogenetic vertical migration. Despite the obvious variation in living depth captured by our sampling (Fig. 3), specimens outside of the dominant living depth always show an isotopic signature of the depth interval where they were found.

The calcification behaviour inferred from our data implies that a sedimentary isotopic signature of this species should reflect the dominant living depth at a given place. This would provide a new perspective on its variable calcification depth implied by previous studies. Using sediment traps in the Sargasso Sea, Deuser and Ross (1989) and Deuser et al. (1981) estimated that *G. truncatulinoides* records conditions at 200 m, which is shallower than our observations and could reflect signal integration over a broad depth zone that reaches to the surface. Studies based on surface sediments from the North Atlantic indicate calcification depths between 400 and 700 m (Durazzi, 1981), from 100 to 400 m (Ganssen and Kroon, 2000) and between 200 and 400 m (Cléroux et al., 2007). Other surface sediments studies from the Equatorial and South Atlantic estimated calcification depths below 250 m (Niebler et al., 1999), between 270 and 370 m (Steph et al., 2009) or from surface to 700 m (Mulitza et al., 1997). In a modelling approach, Lohmann (1995) estimated a calcification depth between the surface and 800 m and LeGrande (2004) proposed a single calcification depth at 350 m or 30% of the calcification at the surface and 70% at 800 m. The diversity of these estimates documents the difficulty to extract information on calcification depth in the absence of knowledge on the actual vertical and/or seasonal abundance of the studied species.

As with *G. truncatulinoides*, an increase in the $\delta^{18}$O values of *G. hirsuta* is observed until a depth of 300 – 500 m (Fig. 4). However, unlike *G. truncatulinoides,* the vertical isotopic profile of *G. hirsuta* shows a progressive deviation from the equilibrium at a given depth, consistent with the framework of continued calcification during descent. Below 300 m, the isotopic values in individual profiles appear to stabilise (Fig. 7, 8). This suggests that the calcification depth of *G. hirsuta* covers the top 300 m of the water column. In the Sargasso Sea, a plankton tow study indicated *G. hirsuta* also as calcifying in the first 200 m of the water column (Hemleben et al., 1985). In contrast, in a sediment trap study it reflected average conditions at 600 m (Deuser et al., 1981; Deuser and Ross, 1989) and based on surface sediments it was estimated to have a calcification depth below 250 m in South Atlantic (Niebler et al.,1999) and between 600 and 750 m in the Atlantic Ocean (Cléroux et al., 2013).

Such a large discrepancy could be explained by the addition of a significant amount of secondary calcite either below the sampling interval covered in this study (below 700 m).

The vertical isotope profiles of *G. inflata* are similar to those of *G. hirsuta* (Fig. 5), consistent with equilibrium calcification and continuous addition of calcite until 200 – 300 m (Fig. 7, 8). Using plankton tows from the South Atlantic this species was reported as calcifying until 400 m (Lončarić et al., 2006), whereas in waters of the NW African upwelling system it is described as calcifying above 200 m (Ganssen, 1983; Wilke et al., 2006). Within the oligotrophic waters of the western Mediterranean Sea a calcification down to 500 m was indicated by van Raden et al. (2011). In contrast, studies based on surface sediments invoke calcification depths between 100 and 250 m in the South Atlantic (Niebler et al., 1999), 100 and 400 m in the eastern North Atlantic (Ganssen and Kroon, 2000), until 400 – 700 m in the North Atlantic (Durazzi, 1981), and an average calcification of 330 – 475 m in the Atlantic Ocean (Cléroux et al., 2013). In the case of this species, the overestimated calcification depth in the sediment-based studies likely reflects seasonality. *G. inflata* has been reported to reflect winter conditions (Deuser and Ross, 1989; Ganssen, 1983; Wilke et al., 2006; Jonkers and Kucera, 2015), which could be the reason why apparent calcification depth estimates that assume annual calcification are overestimated.

Contrary to the other species, *G. scitula* $\delta^{18}$O values appear to be more consistent with the Kim and O'Neil $\delta^{18}O_{eq}$ prediction and its vertical isotopic profiles appears more uniform (Fig. 8). This is consistent with a mode of growth where a large part of the shell calcifies at the top of the interval where the species lives (100 – 200 m) and very little calcite is added below. In contrast, Fallet et al. (2011) and Steinhardt et al. (2015), using sediment traps in the Mozambique Channel, postulated that *G. scitula* calcifies between 200 – 300 m. Greater calcification depth are also invoked in sediment-based studies. Steph et al. (2009b) estimated an apparent calcification depth for *G. scitula* of 300 m in the tropical eastern Atlantic, 200 m in the western Atlantic and below 200 m in the Caribbean. Niebler et al (1999) proposed a calcification depth below 250 m based on a transect of samples from the South Atlantic. Other factors than those considered in our study (e.g., Itou et al., 2001), may be required to explain the differences in calcification depth derived from our material and other studies.

### 5.4 Contrasting living and calcification depth

We note that for all species at most stations the isotopically inferred calcification depths differ from the observed dominant living depths (Fig. 7, 8). *G. truncatulinoides* shows maximum abundances in the upper 200 m of the water column but calcification occurs in equilibrium until 500 m. Highest abundances for *G. hirsuta* are observed below 300 m, yet it calcifies throughout the top 500 m. *G. inflata* has highest abundances near the surface, but continues to calcify down to 300 m. Finally, *G. scitula* is most abundant between 200 and 300 m, but its isotopic signal appears to derive from a shallower depth. The different calcification behaviours among the species imply that different aspects of their habitat have to be constrained to interpret their isotopic signatures in sediment samples. Since *G. truncatulinoides* appears to calcify at all depths, its isotopic signal in the sediment should be the result of integration of populations from different depths. Considering the variation in its depth habitat inferred from plankton tows (Rebotim et al., 2017) and its flux seasonality inferred from sediment traps (Jonkers and Kucera, 2015), the expected sedimentary signal should be weighted towards winter conditions around 100 m water depth. In *G. hirsuta* and *G. inflata*, a prediction of the sedimentary signal requires knowledge of the maximum depth to which calcification occurs and a model of how much calcite is added with depth, together with the knowledge of the seasonal flux pattern. In *G. scitula*, the isotopic signature seems to be dominated by conditions at the top of its living depth range, and we observe only a small addition of calcite below 500 m. This is in contrast to the great calcification depth postulated from observed habitat depth and sediment data, unless a significant modification of the isotopic signal occurs below the depth range covered by our study. Clearly, considering habitat depth alone is likely not sufficient to constrain the depth origin of isotopic signals in planktonic foraminifera.

## 6. Conclusions

Using stable oxygen isotope measurements on specimens from stratified plankton net samples, we provide new observations on calcification behaviour of the deep-dwelling planktonic foraminifera species *G. truncatulinoides, G. hirsuta, G. inflata* and *G. scitula*. To assess the potential of these species as a tool to reconstruct subsurface water column properties, we attempt to constrain where in the water column the environmental signal is incorporated in the chemical composition of the shell. We evaluate how the $\delta^{18}O$ signal is affected by shell size and the presence of crust, which paleotemperature equation best predicts the $\delta^{18}O$ values of each species and up to what depth the calcification continues.

We show that larger specimens of *G. inflata* and *G. hirsuta* appear isotopically heavier even when found at the same depth level, which we attribute to ontogenetic migration. A crust effect leading to heavier isotopic signal is observed for *G. truncatulinoides.* This effect likely reflects different mode or rate of biomineralization of the crust. These species appear to calcify in equilibrium with the prediction based on the Shackleton (1974) paleotemperature equation, whereas *G. scitula* appears better predicted by equilibrium calcification following the Kim and O'Neil (1997) equation.

We infer that *G. truncatulinoides* does not show a vertical ontogenetic migration and that its sedimentary signal is dominated by the depth and season where it is most abundant (around 100 m in winter). In contrast, *G. hirsuta* and *G. inflata* show isotopic profiles consistent with vertical ontogenetic migration and calcite addition until 300 – 500 m. Interpretation of their sedimentary signals will also require knowledge on the pattern of calcite addition with depth. *G. scitula* appears to add most of its calcite at the top of the observed living depth range, which seems at odds with its habitat depth and sediment-based calcification depth estimates. In all species we observe differences between living depth and calcification depth, implying that the knowledge of both is needed to interpret sedimentary proxy signals of these species.

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# Chapter 5

## 5. Conclusion and Outlook

### 5.1 Concluding remarks

The main purpose of this thesis was to contribute to a better understanding of the biology and ecology of planktonic foraminifera in the eastern North Atlantic. To this end, new abundance counts were generated for 71 samples from 17 vertically resolved plankton tow hauls. The counts were carried out exhaustively, enumerating in total 39 203 shells of 34 species in the size fraction >0.1 mm, discriminating between shells with and without cytoplasm. Together with additional data from the literature, the counts were analyzed alongside environmental parameters measured at the time of collection. The first two case studies (Chapter 2 and 3) assessed the vertical and biogeographic distribution of individual species and the potential environmental factors influencing their distribution. In the third case study (Chapter 4), the oxygen isotopic composition was measured in the shells of four deep-dwelling species to improve the understanding of their calcification behavior and thus to promote their use as a proxy of subsurface conditions. To this end, we defined their calcification depths and determined which paleotemperature equation is more suitable for each species.

The depth habitat of individual species was expressed as average living depth (ALD), allowing is to investigate the depth variability among the species as a function of environmental forcing (Chapter 2). Although the ALD of the different species varied, we could identify 1) species inhabiting consistently the surface waters (ALD above 100 m); 2) species occurring between the surface and intermediate waters (ALD between 50 and 100 m); and 3) species found mostly in subsurface waters (ALD mostly below 100 m). Some species like *G. ruber* and *T. iota*, exhibited a narrow range ALD, whereas the majority showed a wider range ALD. Species with a narrow habitat depth reflect a consistent preference for a well-constrained depth interval and would therefore be ideal for paleoceanographic reconstructions. For species showing variable ALD, the habitat depth was found to vary as a function of environmental variables (mixed layer depth, temperature or chlorophyll a concentration) and ontogeny (ontogenetic migration with a yearly or lunar cycle) and a considerable portion of the ALD variation thus seems to be predictable. In general, the different species apparently regulate their habitat depth according to the environmental and ontogenetic conditions (like temperature, chlorophyll concentration, water column structure, seasonality and lunar cycle) with each species showing a specific habitat depth and specific variations within it.

Regarding the biogeographic distribution (Chapter 3), across the three studied regions the overall faunal composition seems to be systematically related to the environmental conditions and in general, our data appear to be coherent with previous plankton tow studies done in the eastern North Atlantic (Bé and Hamlin, 1967; Cifelli, 1962; Ottens, 1991; Pujol, 1980). The Canary Islands and Iberian Margin show a higher occurrence of species with a preference for warmer temperatures such as *G. ruber* pink and *T. sacculifer,* whereas in the Azores Front/Current region the fauna is mostly composed of species associated with colder temperatures and deeper mixed layer depths, such as *G. hirsuta*, *G. scitula* and *G. truncatulinoides*. This suggests that each of the geographic areas exhibits a characteristic faunal composition with only few species occurring ubiquitously, these regional differences reveal most probably the prevailing hydrographic conditions. Importantly, we confirm that the ordination of species along environmental gradients when using plankton samples is not the same as when analysing sedimentary assemblages and that factors other than sea surface temperature are important for assemblages composition. Together with the lack of evidence for a latitudinal diversity gradient in the studied samples, these results imply that the community structure and the apparent strong effect of sea surface temperature on composition of sedimentary assemblages is the result of seasonal accumulation and multi-year averaging in the sediment.

To constrain the geochemical signal of deep-dwelling planktonic foraminifera (Chapter 4), we assessed how (or if) the oxygen isotopic signal present in the shells is an integration of the environmental conditions through their habitat depth. The effects of shell size and secondary/gametogenic calcification in the oxygen isotopic signal was investigated, with our results showing that larger specimens of *G. inflata* and *G. hirsuta* record a heavier isotopic signal even at the same depth, whereas a heavier isotopic signal was attributed to the presence of a crust in *G. truncatulinoides.* In addition, we also determined which of the paleotemperature equations best described the $\delta^{18}O$ values of each species. *G. inflata, G. hirsuta* and *G. truncatulinoides* seem to calcify in equilibrium with the Shackleton paleotemperature equation based prediction, whereas *G. scitula* is better predicted by the Kim and O'Neil paleotemperature equation. Finally, we attempted to define where calcification occurred in the water column, with for example *G. hirsuta* and *G. inflata* showing isotopic profiles consistent with calcite addition until 300 – 500 m.

Based on its habitat depth variability (Chapter 2) and the absence of a vertical ontogenetic migration in its oxygen isotopic signal (Chapter 4), *G. truncatulinoides* is most probably reflecting the isotopic signal in the depth and season where it is most abundant, i.e. around 100 m in winter, based on sediment trap seasonal fluxes (Jonkers and Kucera, 2015). *G. scitula* seems to calcify most of its shell at the top of the observed living depth range (100 – 200 m) (Chapter 4), which contrasts with the observed deeper habitat depth until 350 m (Chapter 2) and the greater calcification depths described in the literature based on sediment samples, unless a modification of the isotopic signal occurs below the depth range covered by our study. In all the studied species we observe differences between living depth (Chapter 2) and calcification depth (Chapter 4), implying that the information on both is required to use these species as a proxy of the water column conditions and interpret the sedimentary records with more reliability.

Regarding the vertical and biogeographic distribution, the study is limited by the nature of the method. Besides being a snapshot in time and space as already discussed in the introduction, planktonic foraminifera can have a patchy distribution on a temporal or spatial scale, usually caused by small to mesoscale hydrographic features such as fronts and eddies (e.g. Siccha et al., 2012). One of the major limitations is that the sampling was not continuous and in some of the locations, we do not even cover all the seasons, preventing us to assess the seasonality effect at these locations and masking probably some data artifacts caused by patchy distribution or climate variations, such as the unusually warm September during the Iberia-Forams cruise. In addition, by sampling with a 100 µm mesh size, most of the specimens in the juvenile stages are left out as well as the smaller species, which are typically smaller than 150 µm and usually do not figure in paleoceanographic studies (CLIMAP Project Members, 1976). Therefore, only a few observations on the distribution of these species in the plankton have been reported (Peeters and Brummer, 2002; Schiebel et al., 2002). Although the study of these specimens is challenging, here we provide new information on this undisclosed group of small species and introduce new possibilities to use them in paleoceanographic studies.

Other limitation concerning this work is the eventual presence of cryptic species impossible to differentiate merely by their morphology. Even though this is a strong possibility, we were aware of this problem and tried to bring this into discussion whenever it was the case. Furthermore, since most of the cryptic species are restricted geographically (Darling et al., 2000; Darling and Wade, 2008; de Vargas et al., 2001; De Vargas et al., 2002; Morard et al., 2015), the new knowledge on the ecology and biology of the individual species acquired here is a step further to future investigations on cryptic species' ecological preferences and vertical distribution. Despite of these limitations, I believe that the three case studies presented here contributed significantly to the improvement of the actual knowledge of the biology, ecology and biochemistry of individual planktonic foraminifera species, and ultimately to the interpretation of paleoceanographic records.

In conclusion, this work shows that planktonic foraminifera habitat depth and biogeographic distribution are predictable and reflect in-situ environmental conditions. Due to the fact that most of the environmental parameters are strongly interconnected between each other and to seasonality and hydrography, in most of the cases it is not possible to attribute a unique environmental parameter as a controlling factor of an individual species' vertical or regional distribution. Instead, each planktonic foraminifera species can be usually associated to more than one environmental factor.

## 5.2 Future perspectives

In order to interpret their fossil record in a more accurate way, the only way is to understand modern planktonic foraminifera such as their habitat depth, ecological needs and preferences and their calcification behaviour. We believe that the present thesis is a step forward into that direction by answering some of the existing questions. However, as in all works of this type other questions and/or suggestions arise. For example, in a future work of this type, *G. truncatulinoides* sinistral and dextral should be studied separately, as well as *G. ruber* white and the morphotype *G. elongatus.* A genetic analysis on *N. pachyderma* and *N. incompta* could be done to confirm or not the occurrence of these two species in our study area. In addition, since it was the first and until to date the only study on modern planktonic foraminifera species on the western Iberian Margin, it would be interesting to collect more samples in this area during other seasons of the year to observe how species fauna evolve seasonally. Also, much remains unknown concerning the ecological preferences of the smaller species such as *T. parkerae, T. fleisheri, T. iota, D. anfracta* and *T. clarkei* and their representativeness in the marine sediments. Only this knowledge will allow new the use of this species in paleoceanographic studies.

Furthermore, our last case study (Chapter 4) has demonstrated that the integration of the oxygen isotopic signal is complex and considering the habitat depth alone is not sufficient to clarify where in the water column the signal is incorporated and which conditions are the data reflecting. To fully unlock the geochemical signal in shells of planktonic foraminifera species, it is necessary to define the maximum depths where calcification occurs and to model how much calcite is added with depth for each species and associate this information with the seasonal flux pattern of each species. Such study would require access to a large amount of material from a vertically highly resolved profile. Thus, rather than a further synthesis of observations from different regions, a dedicated sampling scheme at one locality resolving more depths whilst providing enough material will be more beneficial.

Ideally, a work of this nature would be a compilation of a continuous, monthly and vertically resolved sampling strategy, covering all the seasons during at least one year. Such a study would benefit from sediment traps located nearby to the plankton tow sampling stations and collecting samples during the same period as the plankton tows. Moreover, it would be relevant to have core-top sediment samples from the same locations as the sediment traps. Combining the results from the three sampling types would allow clearly distinguishing which species are present in the water column and under which conditions (environmental factors, lunar cycle, season, depth interval), if specimens of all species arrive in the sediment trap cups, how flux rates vary throughout the year and finally, specimens of which species are present in the surface sediments and how representative for the environment they are.

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