Paleoecological insights on latest Oligocene-early Miocene planktonic foraminifera from the J-Anomaly Ridge (IODP Hole U1406A)

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Abstract: This paper focuses on a paleoecological study conducted on planktonic foraminifera from upper Oligocene-lower Miocene deposits of the J-Anomaly Ridge (North Atlantic Ocean). Paleoclimatic studies are crucial to better comprehend how climatic changes occurred in the past and how they might influence global climate in the next few decades. Oceanic currents are the predominant vehicle for heat transport across the globe and therefore organisms living within the water mass can supply much information on paleoceanographic settings. In total, 53 samples from IODP Hole U1406A were selected in the core interval 96-24 CCSF-M to perform statistical analyses (R-mode cluster analysis, principal component analysis) to describe ecogroup distribution and a paleoclimatic curve based on shallow dwelling taxa. The species have been subdivided into three ecogroups referring to recent studies on planktonic foraminiferal paleoecology. The statistical analyses allowed a preliminary screening of the distribution of the foraminiferal assemblages in the biozonal interval of O7–M3. The ecogroup distribution curves revealed the behavior of each group along the section, highlighting the interconnection among the various habitats. Finally, the abundance of the surface taxa was used to trace a paleoclimatic curve (SDPC) describing the superficial water variations. Those results were compared with the Alkenone Sea Surface Temperature (SST) record from IODP Site U1404 and the $\delta^{18}O$ North Atlantic stack from the literature. This comparison showed a good match among the foraminiferal and geochemical data, allowing the correlation of SDPC and SST minima with well-known glacial events of the North Atlantic Ocean. This study supports the potential of census data of planktonic foraminifera in paleoclimatic studies when geochemical data are not available.

Key words: Planktonic foraminifera, early Miocene, North Atlantic, Newfoundland Ridge, paleoclimate, U1406

1. Introduction

The Newfoundland Ridge is a key study area in understanding the Oligocene-Miocene climatic history of the North Atlantic Ocean. In this area (Figure 1), the intersection of the North Wall Gulf Stream, the Deep Western Boundary Current (Labrador Current), and the Western Greenland Current plays a crucial role in the local and global climate, influencing sedimentation and water circulation in the western portion of the Atlantic Ocean and regulating thermohaline circulation (Laskar et al., 1987; Broecker, 1997; Townsend et al. 2004; Boyle et al., 2017). Many authors have studied this area (e.g., Boyle and Keigwin, 1987; Keller et al., 1987; Miller et al., 1991; Wright et al., 1991; Townsend et al., 2004; Boyle et al., 2017) to describe the glacial events of the northern hemisphere during the Neogene (cf. Brunner and Maniscalco, 1998). The aim of this paper is to contribute to the understanding of the paleoecological evolution of this area during the early Miocene using planktonic foraminifera collected at IODP Hole U1406A.

1.1. The J-Anomaly Ridge

Newfoundland Ridge (Canada) is a well-known study area due to its isolated position from downslope sedimentation, typical of the Grand Banks and canyon areas, which probably guarantees a more continuous stratigraphic record. The J-Anomaly Ridge extends southwestward from the southeastern portion of the Newfoundland Ridge and today is 4000 m deep. At this depth the oscillating Carbonate Compensation Depth (CCD) has influenced sedimentation since the Paleogene, especially during the Miocene (Maniscalco and Brunner, 1998), producing regional unconformities as described by Miller et al. (1985) and Keller et al. (1987). The contouritic currents also created significant regional hiatuses and unconformities during the Cenozoic (Boyle et al., 2017), hindering biostratigraphic and paleoecological reconstructions. In this region the sedimentary framework is determined by many factors. The sea floor is swept by the North Atlantic Deep Water (NADW), a collective term indicating the cold and high salinity water masses that originated by sinking
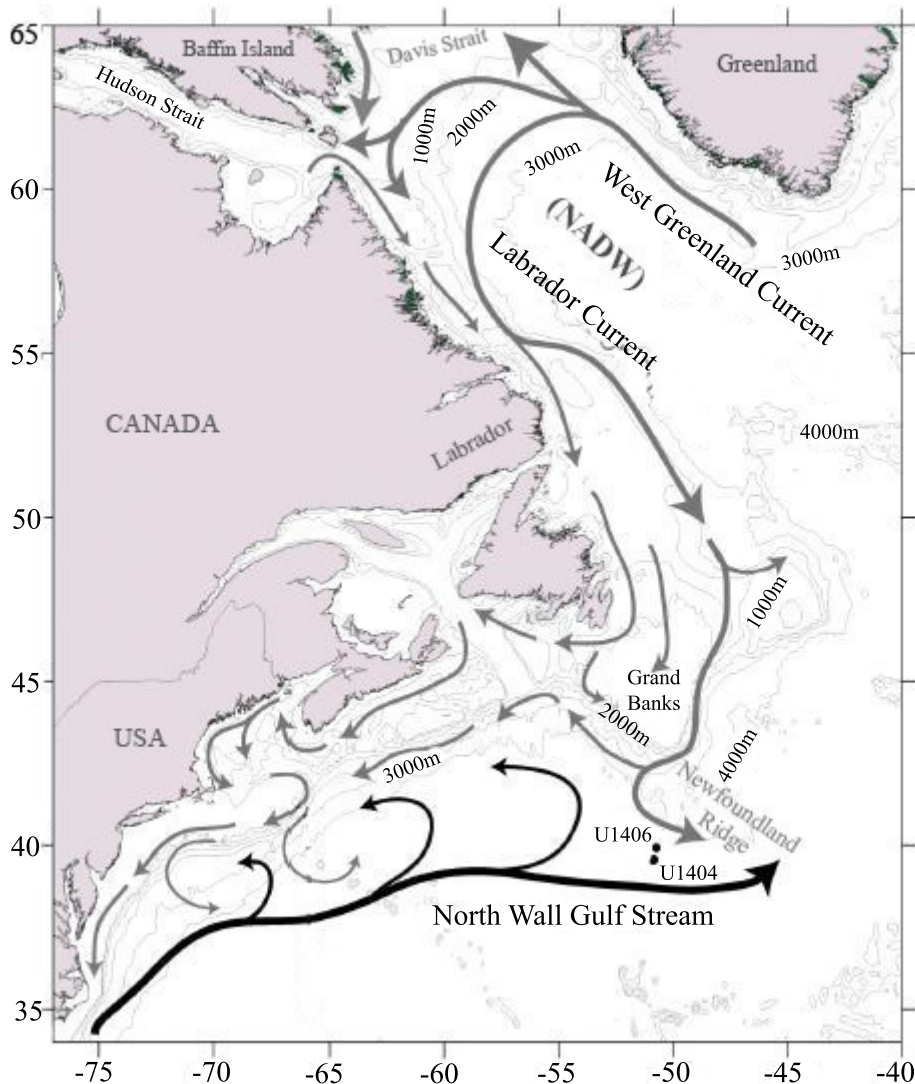
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Figure 1. Map of the present oceanic currents in the North Atlantic. The locations of IODP Site U1406 and IODP Site U1404 are indicated by black spots. The main isobaths are indicated, pinpointing the bathymetry of the studied sequence. All the major current systems are indicated with black and gray arrows (figure modified from Townsend et al., 2004).

in the Labrador Sea and Greenland-Norwegian Sea (Deep Western Boundary Current) as shown in Figure 1. These currents cause contouritic sedimentation, displacing the sediments for kilometers (currents flow >10 cm/s, Boyle et al., 2017). The interference of pelagic sedimentation with the oceanic currents allowed the formation of thick sediment drifts (more than 2 km) from the Paleogene to the present (Heezen and Hollister, 1964; Heezen et al., 1966; Tucholke and Mountain, 1979; Mountain and Tucholke, 1985; Rebesco et al., 1991, 2014; Faugères et al., 1999; Stow et al., 2002; Boyle et al., 2017). Despite their nature, the contouritic deposits recorded all the major climatic events, such as the Eocene Thermal Maximum (ETM), the Eocene-Oligocene climate transition, the Oligo-Miocene

Transition (OMT), and glacial-interglacial cycles during the Neogene. Understanding the climatic evolution of this area may therefore provide a major contribution to the paleoceanographic reconstruction of the North Atlantic Ocean.

In the Neogene, the late Oligocene-early Miocene represents a transitional interval. Starting from the ETM, global climate went through multiple phases until the latest Oligocene, which was generally considered warm and ice-free, but glaciations occurred at the Oligocene-Miocene boundary, leading to the middle Miocene Climatic Optimum, and afterwards to the Middle Miocene cooling (Keller et al., 1987; Miller et al., 1991; Spezzaferri, 1995; Zachos et al., 1997, 2001, 2008; Boulila et al., 2011).

However, a paleoecological study on planktonic organisms requires an understanding of how these water masses interact today with living organisms in terms of nutrients, temperature, and seasonal productivity.

1.2. Modern North Atlantic
At present, the North Atlantic shows high biological productivity owing to nutrient-rich deep waters and winter mixing. This process renews the nutrient concentration in surface waters, favoring the winter-spring plankton bloom. This is followed by a strong vertical stratification during the summer, established by freshwater additions and the warming of superficial layers. Tides can enhance the vertical mixing, amplified by local effects, and further stimulating nutrient fluxes to promote higher levels of plankton production. All these processes affect planktonic foraminiferal assemblages, influencing their latitudinal distribution (Townsend et al., 2004). Also, the dynamics of the North Atlantic subpolar and subtropical gyres strongly determine the main features of this region, where the major current systems include the Labrador Current and the North Wall of the Gulf Stream. The Labrador Current is a cold, low-salinity coastal current originating on the west coast of Greenland from glacial melting (Chapman and Beardsley, 1989). At the Davis Strait (Greenland - Baffin Island) this current splits with one branch flowing north into Baffin Bay and the other crossing Davis Strait, where the West Greenland Current, the Baffin Land Current (Baffin Bay), and Hudson Bay waters (Hudson Strait) merge. This broad current extends from the continental shelf over the continental slope and rise and is commonly known as the Labrador Slope Water. It continues to flow south before subdividing again into two currents, mostly flowing along the outer edge of the Grand Banks (Chapman and Beardsley, 1989). A continuous equatorward coastal current system extends from Newfoundland south to the Middle Atlantic Bight, which interacts with slope waters north of the Grand Banks, and the Gulf Stream.

The northwest Atlantic continental shelf waters can therefore be subdivided into multiple regional systems, all interconnected to some extent to a coastal current flowing equatorward that has its origins in the Labrador Sea shelf. Within this context, shelf and slope waters mix in complex ways both at the surface and at depths and can be important in setting levels of primary production (Townsend et al., 2004). All these processes strongly affected the amount of biogenic sedimentation (calcareous and siliceous micro- and nannofossils) during the last million years. Miller and Fairbanks (1983) suggested that isotopic data from the North Atlantic and eastern Pacific Ocean evidenced the similarity of the late Oligocene-middle Miocene oceanic circulation of the western North Atlantic to the present configuration.

2. Materials and methods
This study is based on the analysis of 53 samples from the IODP Hole U1406A (J-Anomaly Ridge, 40°21′N, 51°39′W; Figure 1) belonging to lithological Unit II – an Oligo-Miocene nannofossil ooze 180 m thick (Norris et al., 2014). Following van Peer et al. (2017), the core composite depth below seafloor scale has been adopted. Thus, the samples span from 96 to 23.4 m. Above this interval a reworked Miocene-Pleistocene calcareous plankton assemblage has been recorded (Fabbrini et al., 2019), preventing a reliable biostratigraphic interpretation. Fabbrini et al. (2019) also reported two hiatuses in the upper portion of IODP Hole U1406A, the most relevant at 38.85 m (2.10 Ma long) and another one at 34.05 m (inferred to be 0.6 Ma long). The lowest hiatus involves the Biozone M2–M3 limit and thus the Aquitanian-Burdigalian boundary. The total investigated interval was constrained between Biozones O7 and M3 (Wade et al., 2011). For simplicity, samples are indicated in terms of their depth expressed in meters from the seafloor.

2.1. Sample preparation and analysis setup
Sediment samples (10 mL in volume) were oven dried at 40 °C and their dry weight was measured. Thereafter, the samples were soaked in distilled water and then washed through a 63-µm sieve. This is the same dataset used for a biostratigraphic study published by the same authors (Fabbrini et al., 2019). For this study, 53 samples were used and treated statistically. The original foraminifera census data were collected counting 300 specimens per sample on the fraction >125 µm. Each sample was observed under a stereomicroscope by picking out the planktonic foraminifera tests and gluing them onto microslides, where species level identification was conducted, mainly referring to the *Atlas of Oligocene Planktonic Foraminifera* (Wade et al., 2018). Before performing the statistical analyses, each species was assigned to an ecogroup, mainly following Aze et al. (2011), while the geographic distribution was based on Wade et al. (2018) and Schiebel and Hemleben (2017).

The ecogroups indicate specific environmental conditions based on calcification depth, different water temperatures, upwelling conditions, and nutrient supply (Table). The environmental factors are all closely linked together, creating dynamic ecosystems. For this reason, we decided to measure the abundance (relative percentage in respect to the total of counted individuals per sample) of each ecogroup to evaluate their reciprocal interactions. In parallel, we studied the behavior of each species using multivariate analyses as a first screening tool. A final paleoclimatic model was created combining all these results and data.

2.2. Statistical methods
We converted the census data of planktonic foraminifera in relative percentages. The statistical analyses were

Table. List of taxa and their ecogroups.

Taxon	Ecogroup	Reference	Climatic index	Reference
Globigerina bulloides	1	Aze et al. (2011)	Cool-temperate	Spezzaferri (1995, 2002, 2018)
Globigerinoides gr.	1	Spezzaferri et al. (2018)	Warm	Hemleben et al. (1989)
Globoturborotalita connecta	1	Spezzaferri et al. (2018)	Warm-temperate	Kennett and Srinivasan (1983)
Globoturborotalita occlusa	1	Stewart et al. (2004)	Warm-temperate	Wade et al. (2018) and references therein
Globoturborotalita ouachitaensis	1	Sexton et al. (2006)	Warm-temperate	Olsson et al. (2006)
Globoturborotalita pseudopraebulloides	1	Pearson and Wade (2009)	Warm-temperate	Wade et al. (2018)
Globoturborotalita woodi	1	Pearson et al. (1997)	Warm-temperate	Spezzaferri (1994, 1995)
Paragloborotalia kugleri	1	Leckie et al. (2018)	Warm-temperate, Upwelling	Leckie et al. (2018)
Paragloborotalia pseudokugleri	1	Leckie et al. (2018) and references therein	Warm-temperate, Upwelling	Spezzaferri (1994)
Trilobatus gr.	1	Spezzaferri et al. (2018)	Warm	Hemleben et al. (1989)
Dentoglobigerina baroemoenensis	3	Wade et al. (2018)	Warm	Kennett and Srinivasan (1983)
Dentoglobigerina globularis	3	Wade et al. (2018)	Warm	Spezzaferri (1994)
Dentoglobigerina larmeui	3	Pearson and Wade (2009)	Cosmopolitan	Spezzaferri (1994)
Globigerinella gr.	3	Aze et al. (2011)	Low to middle latitudes	Spezzaferri et al. (2018)
Globoquadrina dehiscens	3	Keller et al. (1985)	Cosmopolitan	Pearson and Shackleton (1995)
Paragloborotalia acrostoma	3	Aze et al. (2011)	Warm-temperate	Leckie et al. (2018)
Paragloborotalia nana	3	Poore and Matthews (1984); Matsui et al. (2016)	Cool-temperate	Spezzaferri (1995)
Paragloborotalia semivera	3	Aze et al. (2011)	Warm-temperate	Kennett and Srinivasan (1983)
Paragloborotalia siakensis	3	Pearson and Wade (2009)	Warm-temperate	Kennett and Srinivasan (1983)
Sphaeroidinellopsis disjuncta	3	Aze et al. (2011)	Low latitudes	Kennett and Srinivasan (1983)
Tenuitella angustiumbilicata	3	Wade et al. (2018)	Warm-temperate	Spezzaferri (1995)
Catapsydrax gr.	4	Aze et al. (2011); Coxall and Spezzaferri (2018)	Global, upwelling	Coxall and Spezzaferri (2018)
Dentoglobigerina binaiensis	4	Pearson and Shackleton (1995)	Warm	Pearson and Chaisson (1997)
Dentoglobigerina tripartita	4	Van Eijden and Ganssen (1995)	Cosmopolitan	Wade et al. (2018)
Dentoglobigerina venezuelana	4	Wade et al., (2018)	Warm-temperate	Kennett and Srinivasan (1983)
Globorotalia gr.	4	Aze et al. (2011)	Warm-temperate	Kennett and Srinivasan (1983)
Globorotaloides gr.	4	Poore and Matthews (1984)	Cool, upwelling	Spezzaferri (1995)
Globigerinita glutinata	-	Pearson (2001, 2009)	Cool-temperate/global	Spezzaferri (1995)

performed using the paleontological software PAST (Paleontological Statistics, Ver. 3.18; Hammer, 2017). The statistical methods employed were multivariate ordination analyses in order to characterize the variations hidden in the fossil assemblage and in the dataset. For this purpose, R-mode cluster analysis investigated the components of the dataset and its spatial distribution. Principal component analysis (PCA) was used to describe the reciprocal behavior of each species in the assemblage. We followed the same methodology applied by Antonarakou et al. (2007) to set up the data for the analyses. Species with <1% abundance and belonging to the same ecogroup were summed together to avoid background noise. With respect to the original dataset of Fabbrini et al. (2019), all samples with fewer than 250 counted specimens were excluded, indicating intervals affected by dissolution at the sea floor. Fossil preservation was indicated by benthos/plankton and fragments/plankton ratios (Fabbrini et al., 2019). High values of both of these indicators highlight intervals affected by strong chemical dissolution, indicating ocean floor acidification or oscillating CCD.

Preliminary statistical screening allowed the identification of the maximum similarity between samples in terms of their counted fossil assemblage. R-mode cluster analysis allowed the characterization of the assemblages.

2.3. Paleoclimatic model (Shallow Dwellers Paleoclimatic Curve: SDPC)

The paleoclimatic model was created in two phases: after the recognition of three of the ecogroups identified by Aze et al. (2011), we investigated the local behavior of these taxa using multivariate and ordination analyses, identifying the most sensitive taxa in this assemblage. Such taxa were then plotted on a Shallow Dwellers Paleoclimatic Curve (SDPC). This curve was created modifying the method described by Cita et al. (1977), who proposed for the first time a single curve based on Pleistocene planktonic foraminifera to pinpoint paleoclimatic variations. Cita et al. (1977) discriminated planktonic foraminifera in latitudinal terms of warm, warm-temperate, cool-temperate, cool, and upwelling indices. Today, isotopic studies allow planktonic foraminifera to be separated into ecogroups according to habitat and geographic distribution (e.g., Mortyn et al., 2003).

In order to describe the ocean/atmosphere interaction and to represent a more reliable surface water temperature model, we used only species living in the mixed layer (Ecogroup 1). Thus, only species belonging to Ecogroup 1 were employed to trace the SDPC. Following the literature and our statistical analysis, species were weighted positively if having warm-water and oligotrophic affinity and negatively if possessing cold-water and eutrophic affinity. Thus, the SDPC was constructed as the sum of positive taxa (warm taxa living in the open-ocean mixed

layer) and negative taxa (cold taxa of the open-ocean mixed layer).

3. Results and discussion

3.1. Ecogroup division

Following Aze et al. (2011), there are three ecogroups recognized in this assemblage: Ecogroup 1- open-ocean mixed layer, Ecogroup 3 - thermocline, and Ecogroup 4 - subthermocline taxa (Table). No taxa belonged to Ecogroup 2 (Aze et al., 2011); barren shallow-dwelling taxa symbionts are represented in this assemblage. In the following paragraphs species sharing the same habitat and lifestyle are described together as a group, while species needing special mention are described individually (although grouped together for analytical purposes).

3.1.1. Ecogroup 1

These taxa live and calcify their tests in the open-ocean mixed layer, where water temperature is higher, CO_2 is less abundant, and trophic conditions are more dynamic. This ecogroup favors warm-temperate water conditions with a deep thermocline and thus a thicker mixed layer due to stronger stratification of the water column. The isotopic ratios of these taxa show the lowest $\delta^{18}O$ and the highest $\delta^{13}C$ values among all foraminifera, with the high $\delta^{13}C$ due to the presence of algal symbionts in their tests (Spezzaferri, 1995; Aze et al., 2011; Schiebel and Hemleben, 2017). The components of this group (Table) are *Globigerina bulloides*, *Trilobatus* gr. (*T. immaturus*, *T. primordius*, *T. trilobus*, and *Globigerinoides subquadratus*), *Paragloborotalia kugleri* gr. (*P. kugleri* and *P. pseudokugleri*), *Globoturborotalita* gr. (*G. connecta*, *G. occlusa*, *G. pseudopraebulloides*).

Globigerina bulloides calcifies its test between 30 and 50 m depth (Spero and Lea, 1996; Niebler et al., 1999) at equilibrium conditions, as indicated by its stable isotope ratios (Curry and Matthews, 1981; Kahn and Williams, 1981; Deuser and Ross, 1989; Sautter and Thunell, 1991; Spero and Lea, 1996). Aze et al. (2011) reported *G. bulloides* in Ecogroup 2 as a symbiont-barren species, which was later confirmed by Schiebel and Hemleben (2017) and Spezzaferri et al. (2018). In addition, Aze et al. (2011) listed another species (*G. praebulloides*) as a symbiont-bearing species (Ecogroup 1) in specimens from the Oligocene-Miocene transition in the Ceara Rise (Pearson et al., 1997). *Globigerina praebulloides* was then synonymized with *Globigerenella obesa* by Spezzaferri et al. (2018); thus, specimens previously identified as *G. praebulloides* were reassigned as *G. bulloides* and as *Globoturborotalita pseudopraebulloides* when presenting a cancellate wall texture. However, no pictures were provided of *G. praebulloides* specimens by Pearson et al. (1997), preventing their identification as *G. bulloides* or as *G. pseudopraebulloides*. Moreover, very little information is available about the paleoecology of *G. bulloides* in the

earliest Miocene, leading us to assign our *G. bulloides* to Ecogroup 1 instead of Ecogroup 2.

Trilobatus immaturus, *T. primordius*, *T. trilobus*, and *Globigerinoides subquadratus* are grouped together because they show similar isotopic ratios typical of the open-ocean mixed layer habitat in warm and warm-temperate waters. This group is rare or absent in areas of strong upwelling conditions (Kennett and Srinivasan, 1983; Spezzaferri, 1995).

Paragloborotalia kugleri and its ancestor *P. pseudokugleri* both show very low δ18O ratios, indicating a superficial habitat. These taxa favored high-productivity water (eutrophic conditions), especially at low and middle latitudes (e.g., Leckie et al., 2018).

In the *Globoturborotalita* group, *G. ouachitaensis* was reported in the mixed layer by Sexton et al. (2006) and was indicated by Pearson and Wade (2009) as a shallow and warm taxon during the Eocene due to negative δ18O values. *Globoturborotalita connecta* and *G. woodi* were reported by Spezzaferri et al. (2018) as shallow dwellers, falling with the others into the *Globoturborotalita* group.

3.1.2. Ecogroup 3

This group lives between the dynamic superficial water layers and the colder and denser water below the thermocline, thus showing higher values of δ18O and lower values of δ13C than Ecogroup 1. This group comprises (Table) *Dentoglobigerina larmeui* gr. (*D. larmeui*, *D. baroemoenensis*, *D. globularis*, *Globoquadrina dehiscens*), *Globigerinella* (*Globigerinella obesa*), *Tenuitella* gr. (*Tenuitella angustiumbilicata*, *T. munda*), *Paragloborotalia* gr. (*P. acrostoma*, *P. nana*, *P. siakensis*, *P. semivera*), and *Sphaeroidinellopsis disjuncta*.

Globigerinella obesa is a thermocline species abundant in tropical and warm-temperate conditions (Spezzaferri, 2002), and the tenuitellids (according to Pearson et al., 2018, *Tenuitella* and *Tenuitellinata* belong to the same genus, *Tenuitella*) also prefer warm habitats (Pearson, 1997; Pearson and Wade, 2009). *Paragloborotalia acrostoma* was considered a warm/warm-temperate species by Spezzaferri (2002), while *Paragloborotalia siakensis* and *P. semivera* are typical of warm conditions, but with isotopic ratios indicating they are upper thermocline dwellers (Pearson and Wade, 2009; Leckie et al., 2018). *Paragloborotalia nana* had an upper thermocline habitat as well, even though also documented at high latitudes (Matsui et al., 2016; Leckie et al., 2018). *Globoquadrina dehiscens* is considered a cosmopolitan species with an erratic and variable lifestyle (Pearson and Shackleton, 1995), but it is reported as an intermediate dweller by Keller et al. (1985). In this paper, this taxon is considered as a thermocline inhabitant (Table) following Aze et al. (2011) and is grouped together with its ancestor *Dentoglobigerina larmeui*, another thermocline inhabitant (Pearson and Wade, 2009; Wade et al., 2018).

Sphaeroidinellopsis disjuncta is most likely a descendant of *G. woodi* (Kennett and Srinivasan, 1983) and stable isotope data classify it as a thermocline calcifier (Aze et al., 2011). It is especially abundant at low latitudes and during warm and temperate conditions (Kennett and Srinivasan, 1983).

3.1.3. Ecogroup 4

In previous literature, these taxa are sometimes referred to as "deep dwellers" because their life cycle occurs mostly below the thermocline. These taxa are characterized by the highest values of δ18O and the lowest of δ13C (Poore and Matthews, 1984; Spezzaferri, 1995; Aze et al., 2011; Schiebel et al., 2017 and references therein). Higher abundance of these taxa indicates a thinner mixed layer and thus a more superficial thermocline (Kennett et al., 1985; Ravelo and Fairbank, 1990). In fact, where the thermocline is more superficial the habitat for these taxa is wider, allowing them to proliferate. As summarized in the Table, the components of this group are *Catapsydrax* gr. (*C. dissimilis*, *C. unicavus*), *Dentoglobigerina venezuelana* gr. (*D. binaiensis*, *D. tripartita*, *D. venezuelana*), *Globorotalia* gr. (*G. praescitula*, *G. miozea*), and *Globorotaloides* gr. (*G. stainforthi*, *G. suteri*). *Catapsydrax* gr. and *Globorotaloides* gr. have the highest δ18O values (Poore and Matthews, 1984; Coxall and Spezzaferri, 2018), indicating a superficial thermocline or strong upwelling conditions. *Dentoglobigerina tripartita* is a cosmopolitan species, but a change in its habitat was documented in the early Oligocene (van Eijden et al., 1995). Stewart et al. (2012) reported *D. venezuelana* as a deep dweller during the adult stage, while it is reported as a thermocline dweller by Si et al. (2018). No consensus exists on the habitat of different morphotypes (adult or preadult calcification stage), leading to uncertain isotopic analyses (Gasperi and Kennett, 1993; Pearson and Shackleton, 1995; Pearson et al., 1997; Nathan and Leckie, 2009; Pearson and Wade, 2009; Aze et al., 2011; Stewart et al., 2012; Si et al., 2018). For these reasons, we distinguished no morphotypes in this study, considering *D. venezuelana* as a morphologically variable taxon (Table). *Globorotalia praescitula* is the ancestor of *Gl. miozea*; indeed, the specimens here identified as *Gl. miozea* show intermediate features between the two taxa. Thus, *Gl. miozea* is grouped together here with *Gl. praescitula* in Ecogroup 4 as a subthermocline dweller. *Gl. praescitula* was reported as a temperate to tropical species by Kennett and Srinivasan (1983) and low to middle latitudes by Aze et al. (2011).

3.2. Cluster analysis

Hierarchical cluster analysis allowed us to pinpoint different distributions and preferential patterns in the fossil assemblage. The cophenetic correlation index result was 0.82 for R-mode with the Euclidean distance, indicating good reliability (coph. corr. > 0.75). Cutting

at a 0.3 similarity value (Figure 2), the R-mode analysis identified two main clusters (A and B in Figure 2) and an outgroup formed by *Globigerinella* gr. (the taxon is rare but regularly distributed along the entire section). Cluster A is composed of *Globorotalia* gr., *S. disjuncta*, and *Trilobatus* gr., which is clearly determined by the different spatial distribution of these taxa. In fact, taxa grouped in Cluster A reach their peak abundance in the upper portion of the section. The presence of *Globorotalia* gr. and *S. disjuncta* can be linked to their first appearance in the fossil record that occurred during the time interval of hiatus H1 (Fabbrini et al., 2019). Cluster B comprises
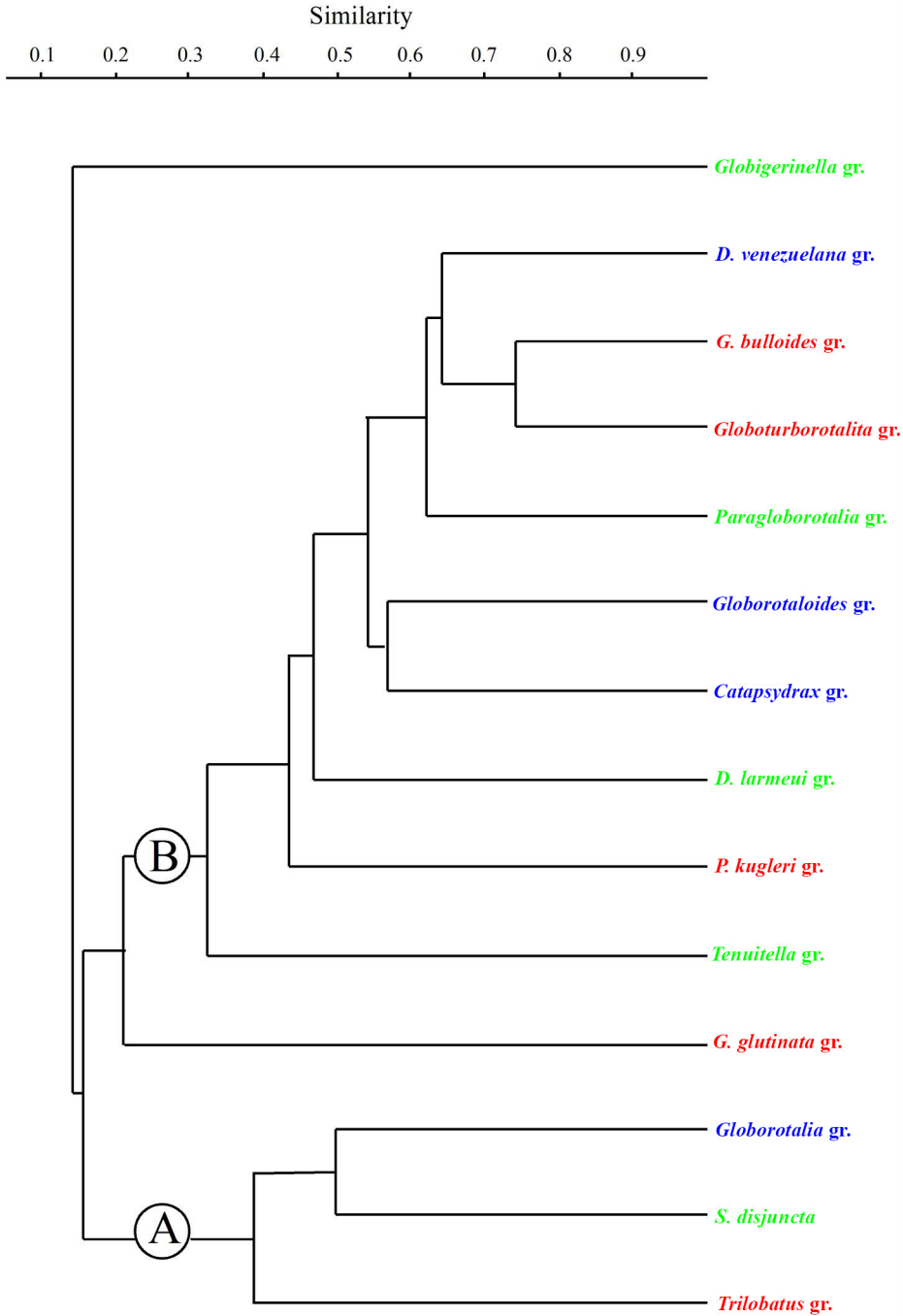

Figure 2. R-mode cluster dendrogram. The two clusters are indicated by letters A and B. In red are indicated the species belonging to Ecogroup 1, in green species from Ecogroup 3, and in blue species from Ecogroup 4.

two elements. The first one is *Globigerinita glutinata* and the second is a subcluster made of *Catapsydrax* gr., *D. larmeui* gr., *D. venezuelana* gr., *G. bulloides* gr., *Globorotaloides* gr., *Globoturborotalita* gr., *Paragloborotalia* gr., *P. kugleri* gr., and *Tenuitella* gr. As shown in Figure 2, *Globigerinita glutinata* contrasts with all the other members of cluster B, suggesting a different distribution with respect to all the other taxa. In fact, *G. glutinata* is the dominant species of the fossil assemblage. Similar behaviors occur inside cluster B for taxa belonging to the same ecogroup, such as *Catapsydrax* gr. and *Globorotaloides* gr., *Globigerina bulloides*, and *Globoturborotalita* gr.

3.3. Principal component analysis (PCA)

Ordination analysis allowed the behavior of apparently similar taxa to be clarified (Figure 3). The PCA plot indicates clearly the predominance of *Globigerinita glutinata*, which is weighted positively in terms of the PC1 and therefore significantly different from all the other taxa. This analysis also pinpoints the different distribution of *Paragloborotalia* gr. with respect to the other taxa.

In fact, *Paragloborotalia* gr. is weighted positively for PC1 and PC2, but PC2 influences the distribution of this group. *Paragloborotalia* gr. species belong to Ecogroup 3 (Aze et al., 2011; Leckie et al., 2018) and were common in tropical to subtropical waters, especially in tropical upwelling areas, as are some modern *Neogloboquadrina* (Leckie et al., 2018).

Globigerinita glutinata, still living today, is reported as an opportunistic species belonging to Ecogroup 1 (Schiebel and Hemleben, 2017) and inhabiting the uppermost mixed layer (water depth < 75 m). It is a cosmopolitan species spreading within a wide range of temperature and salinity, which can survive both in oligotrophic and eutrophic conditions (Hemleben et al., 1989; Mazumder et al., 2009). Sometimes its presence is associated with the spring bloom, triggered by newly available nutrients at the end of the winter mixing and increased solar irradiation (Casford et al., 2002). According to Schiebel et al. (2017), *G. glutinata* decreases in abundance from low to high latitudes. It can be transported to subpolar or polar areas, becoming dominant in the assemblage during the summer. At lower latitudes *G. glutinata* blooms are linked to nutrients and food production at the depth of the seasonal thermocline (Schiebel et al., 2001). Stangeew (2001) documented *G. glutinata* as the major constituent of the foraminiferal summer assemblage in the Labrador Sea (south of Greenland).

Globigerina bulloides is weighted positively for both principal components. Thus, it is closely related to *G. glutinata* and belongs to Ecogroup 1. *Globigerina bulloides* inhabits the mixed layer, withstanding large fluctuations in temperature, salinity, and density of the water column. This species is more abundant in high productivity
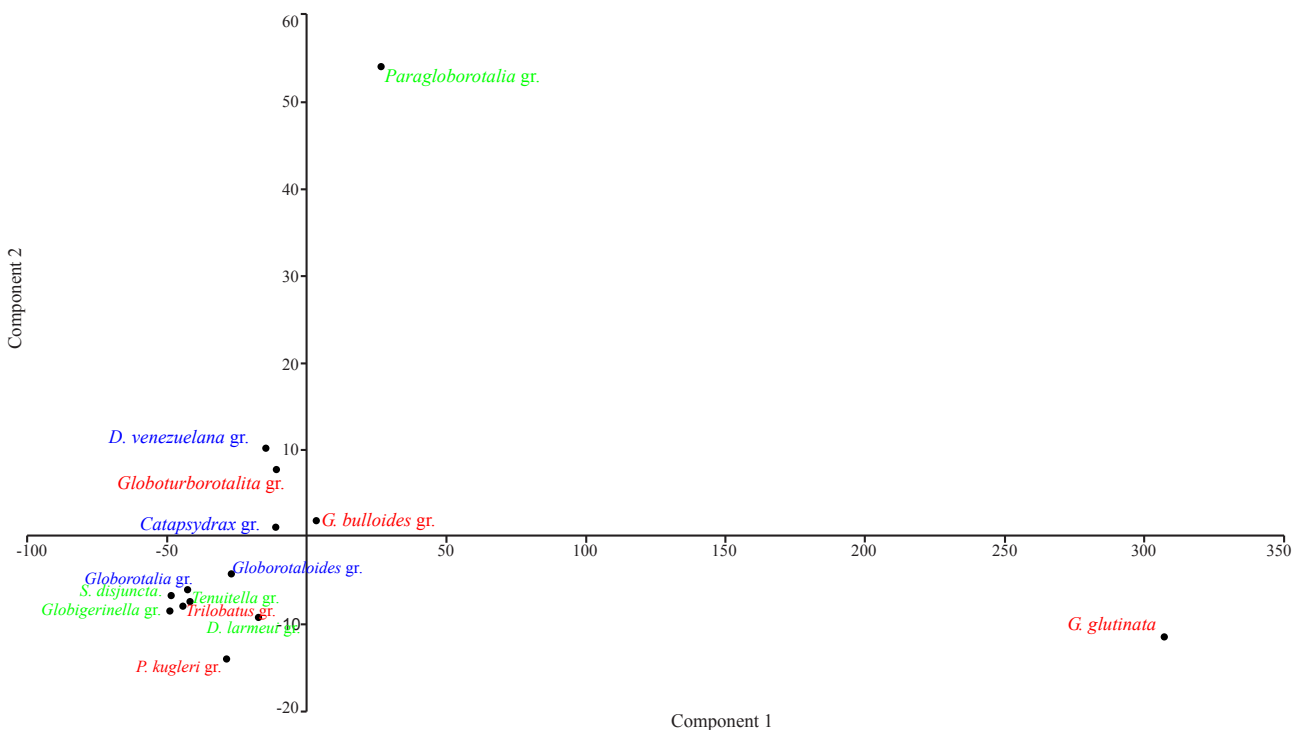

Figure 3. Principal component analysis plot. In red are indicated the species belonging to Ecogroup 1, in green species from Ecogroup 3, and in blue species from Ecogroup 4.

environments and is influenced by upwelling conditions, strong seasonal mixing, and fresh water inputs (Rohling et al., 1993).

Globoturborotalita gr. is weighted negatively for PC1 as opposed to *G. bulloides*. Both belong to Ecogroup 1 but have different climatic affinities. *Globoturborotalita* gr. inhabited preferentially warm waters at low and mid latitudes. In this group, *G. pseudopraebulloides* and *G. occlusa* were widespread and abundant, while *G. connecta* was cosmopolitan but generally rare.

Trilobatus gr. and *Paragloborotalia kugleri* gr. (*P. kugleri* and *P. pseudokugleri*) are weighted negatively in terms of PC1 and PC2, which is completely opposite to *G. bulloides*. These two groups inhabited the warm water of the mixed layer as suggested by their isotopic signatures. They were global taxa preferring warmer conditions at low and middle latitudes.

Trilobatus gr. (and *Globigerinoides*) are oligotrophic taxa typical of well-stratified water masses, absent or very rare in upwelling regions (Spezzaferri et al., 2018 and references therein), where oceanic currents mix the water masses creating eutrophic conditions and high primary productivity and algal blooms. Thus, *Trilobatus* gr. indicates warm and strongly stratified water columns. The stratification of the water column is the main controlling factor of the distribution of this group (Rohling et al., 1997). Living taxa such as *Globigerinoides ruber* and *Trilobatus sacculifer* live close to the surface, preferring low nutrient conditions during summer months in areas where solar radiation is highest (Hemleben et al., 1989).

Paragloborotalia kugleri gr. favored eutrophic conditions mostly in tropical to subtropical environments (Leckie et al., 2018 and references therein). Pearson and Wade (2009) suggested a symbiotic association in *P. pseudokugleri* based on stable isotope data. This group preferred eutrophic conditions in temperate to high-latitude waters.

All taxa belonging to Ecogroup 4 are weighted negatively for PC1 as opposed to *G. glutinata*, *G. bulloides*, and *Paragloborotalia* gr. (Figure 3). At a closer look, interesting details emerge: *Catapsydrax* gr. and *Globorotaloides* gr. are weighted differently for PC2, even though they have similar isotopic signatures, typical of subthermocline habitats, and both showed affinities to high productivity conditions. In fact, *Catapsydrax* gr. was global, especially common at high latitudes and in upwelling regions. *Globorotaloides* gr. was global, but more common at low and middle latitudes. *Globorotalia* gr. is weighted similarly to *Globorotaloides* gr. The living *G. scitula* is a descendant of *G. praescitula* and associated with cool water conditions (Rohling et al., 1993). Other living taxa such as *Globorotalia crassaformis* inhabit a subthermocline habitat in equatorial areas and superficial waters at polar/subpolar latitudes (Schiebel et al., 2017).

Dentoglobigerina venezuelana gr. are weighted the same as *Catapsydrax* gr. In fact, their isotopic signatures indicate deep water habitats, even if some authors documented shallower habitats (Poore and Matthews, 1984; Wade et al., 2007; Beltran et al., 2014; Moore et al., 2014). These taxa might have changed habitats during their life cycle, migrating to deep water in the adult stage (Wade et al., 2018). They were global but particularly abundant at low and middle latitudes.

Taxa belonging to Ecogroup 3 are weighted negatively for both PCs, sharing similarities with taxa of Ecogroups 1 and 4 (Figure 3). Thermocline dwellers show intermediate isotopic signatures with respect to other ecogroups (e.g., Aze et al., 2011), and inhabiting the thermocline level they may be more tolerant to latitudinal and thermal variability.

Dentoglobigerina larmeui was cosmopolitan, recorded even at polar latitudes at DSDP Site 407 (Poore, 1979). Pearson and Wade (2009) and Aze et al. (2011) proposed an upper thermocline habitat based on the isotopic signature. *D. globularis* was widespread in low to middle latitudes. Biolzi (1983) suggested a mixed layer habitat but the species was not illustrated, preventing a reliable identification. Wade et al. (2007) showed variable isotopic ratios, but Aze et al. (2011) classified this taxon in Ecogroup 3. *Globoquadrina dehiscens* was also cosmopolitan and classified as an intermediate dweller by Keller (1985). Pearson and Shackleton (1995) suggested this species as erratic and variable; it was placed in Ecogroup 3 by Aze et al. (2011).

Tenuitella gr. was not reported by Aze et al. (2011) but was described by Pearson et al. (2018) as an inhabitant of the warm surface mixed layer, following suggestions by earlier authors (Poore and Matthews, 1984; van Eijden and Ganssen, 1995; Pearson et al., 1997; Pearson and Wade, 2009). *Tenuitella* was documented from the tropics to high latitudes. *Globigerinella* gr. was reported by Aze et al. (2011) in Ecogroup 3 at thermocline depth. These taxa are documented from low to middle latitudes and are particularly abundant in oligotrophic tropical areas (Spezzaferri et al., 2018). Even if *Globigerinella siphonifera* today inhabits the mixed layer and is a symbiont-bearing species, it is not known if it has changed habitat with respect to its ancestral taxon (*G. praesiphonifera*) or if the carbon isotope offset is a vital effect.

Sphaeroidinellopsis disjuncta was shown in Ecogroup 3 as a thermocline dweller by Aze et al. (2011) and inhabited mostly low latitudes (Kennett and Srinivasan, 1983). PCA therefore allowed species with contrasting behavior, such as *Globoturborotalita* gr. and *G. bulloides* and *Trilobatus* gr., to be separated (Figure 3).

3.4. Ecogroup distributions and paleoclimatic observations

We plotted the distribution of the ecogroups vs. depth/magnetostratigraphy to infer the changes occurring in the water column and the stratification of changing

foraminiferal habitats. Three curves (Figure 4) were produced, summing together the census values of all the species belonging to the same ecogroup (Table). These curves enable the reciprocal behaviors of these groups to be compared. The curves indicate clearly that ecological variations occurred. In fact, the mixed-layer dweller curve (Ecogroup 1) and the deep-dwelling taxa curve are in opposition (Ecogroup 4), suggesting a reciprocal influence between the habitats. All the shallow dwellers' minima correspond to deep dwellers' maxima (Figure 4). On the other hand, the intermediate dweller curve (Ecogroup 3) depicts more complex behavior. At some points they mirror the shallow dweller taxa and at others they resemble deep dwellers. This ambivalent behavior could be linked either to real intermediate habitat conditions or to misinterpretation of some taxa. Higher abundance of Ecogroup 1 can be related to a mixed-layer expansion allowing superficial taxa to proliferate. The vertical expansion of the mixed layer might be induced by multiple factors. Increased supply of warmer superficial water masses from the North Wall Gulf Current could cause the expansion of the superficial mixed layer and deepening of the thermocline.

The relationship between thermocline fluctuations and SST were investigated by tracing the SDPC (Figure 4). We traced this curve based on the climatic curve published by
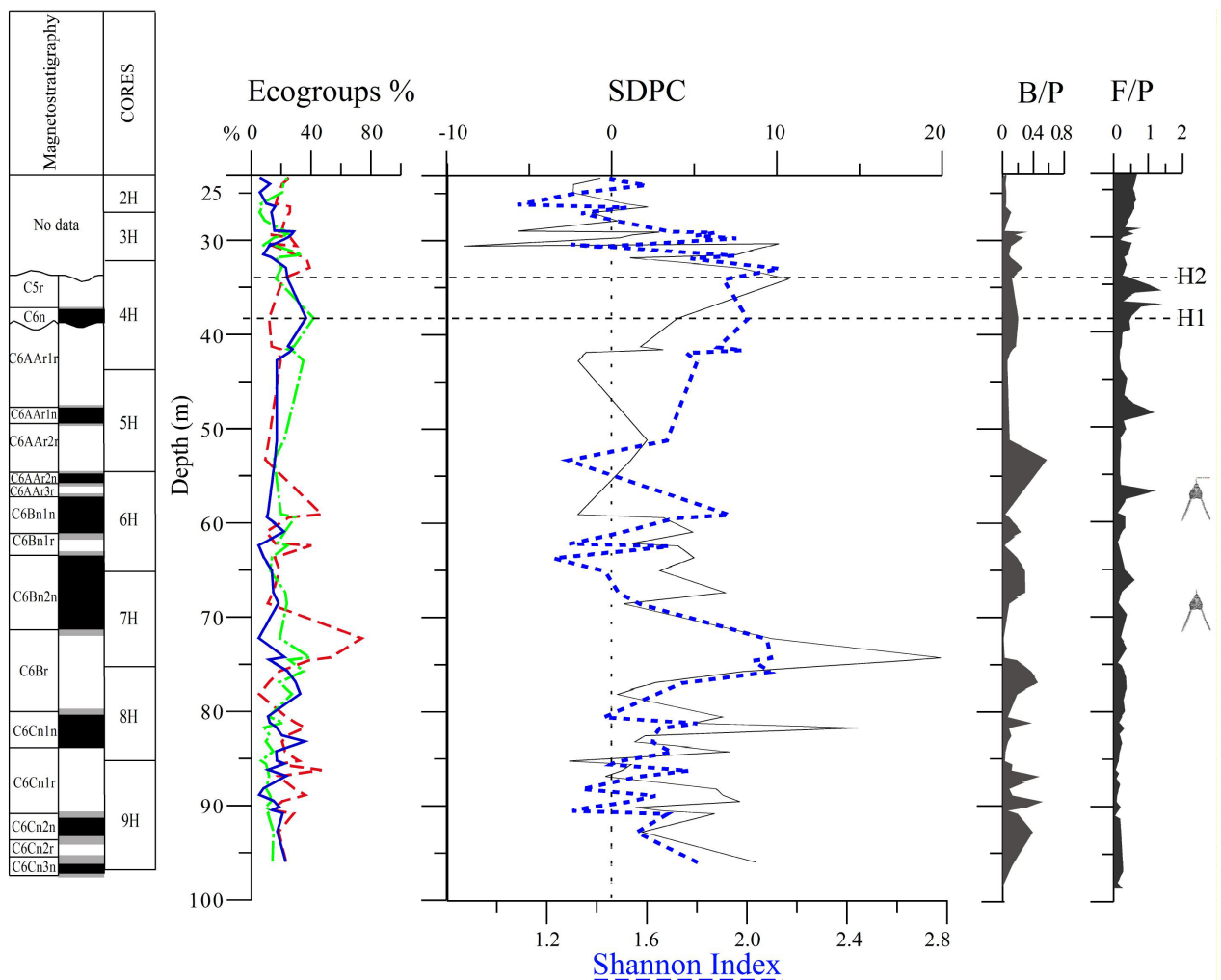

Figure 4. Ecogroup distribution and Shallow Dwellers Paleoclimatic Curve. From left to right are represented the magnetostratigraphic model (from Fabbrini et al., 2019), the three curves (dashed red line: Ecogroup 1; dotted green line: Ecogroup 3; blue line: Ecogroup 4) describing the ecogroups' abundances along the section, the Shallow Dwelling Paleoclimatic Curve (SDPC–black) and the Shannon index curve (dashed blue line), and benthos/plankton (B/P) and fragments/planktonic (F/P) foraminifera ratios. The symbols on the right-hand side show two intervals characterized by a higher presence of radiolarians. The horizontal dashed lines indicate the two hiatuses (H1, H2) recognized by Fabbrini et al. (2019).

Cita et al. (1977). Instead of using all taxa, we took into consideration only taxa from Ecogroup 1, as direct and more reliable indicators of the surface water conditions. The curve depicts higher superficial temperature when positive and lower temperatures when values are negative or decrease. Thus, the SDPC shows the relationship between 1) *Trilobatus* gr., *Globoturborotalita* gr., and *Paragloborotalia kugleri* gr. and 2) *Globigerina bulloides*. The SDPC shows great variability along the section, highlighting some intervals with negative values or strong decreases. The negative intervals at 87 m, 85 m, 58–56 m, 45–42 m, 32–30 m, 29–26 m, and 25–24 m represent dominance of *G. bulloides* over other mixed-layer taxa. This dominance could be associated with increased primary productivity in eutrophic conditions. A stronger influence of colder water masses of the Labrador Current and even increased upwelling conditions possibly induced *G. bulloides* to proliferate. Thus, all the negative peaks may be linked to stadial events or colder and more productive superficial water.

Higher species diversity is often linked to warmer conditions or interstadial conditions and is generally higher at low and middle latitudes rather than at polar/subpolar latitudes. The Shannon index describes species diversity and it can be used to evaluate the richness of the fossil assemblages.

In Figure 4 the two curves are plotted together, showing a similar trend. The general accordance between the two curves supports the connection between superficial water temperature and species diversity. A secondary observation can be made using radiolarians, which are abundant along the entire section (Norris et al., 2014), reaching their maximum abundance at two intervals (Figure 4). Both these intervals coincide with a fall of the SDPC. Radiolarians can be considered an indicator of cold waters, especially abundant at polar/subpolar latitudes, even though at 56 m their abundance can be attributed to a higher dissolution rate as shown by F/P and B/P curves (Figure 4).

The IODP Site U1406 was drilled at 3800 m water depth and its paleobathymetry is estimated at 3500 m in the early Miocene (Norris et al., 2014), making it vulnerable to CCD oscillations. The B/P ratio (benthic foraminifera/planktonic foraminifera) and F/P (planktonic fragments/planktonic foraminifera) are plotted here for comparison to evaluate the fossil preservation. High values of the two parameters suggest poor preservation due to chemical dissolution of foraminiferal tests, such as in four intervals: 77–75 m, 67–65 m, 61–59 m, and 38–34 m. The SDPC appears poorly related to B/P and F/P, suggesting limited influence of chemical dissolution on the SDPC, which presumably describes genuine climatic variations.

The studied section contains two hiatuses as described by Fabbrini et al. (2019), at 38.85 m and at 34.05 m (indicated with dashed lines in Figure 4). Even if the two hiatuses have been biostratigraphically well constrained, we preferred to cut the paleoclimatic model at H1 (38.85 m) in order to avoid misleading interpretations.

In Figure 5 the final model is plotted against time. Using the age model provided by Fabbrini et al. (2019), the interval studied spans from 23.50 to 21.25 Ma. The SDPC and Shannon index curve have been smoothed for a direct comparison with the two other curves from literature: 1) the δ18O stack from the North Atlantic (Cramer et al., 2009) and 2) the Alkenone SST from IODP Site U1404 (Liu et al., 2018) using chemical data to reconstruct deep water temperature (from benthic foraminifera) and superficial water temperature (SST), respectively. The δ18O shows smoother oscillations with three minima, around 22.75 Ma, around 22 Ma, and at 21.25 Ma. Then it shows three maxima points, at 23.30 Ma, around 22.40 Ma, and around 21.60 Ma. The SST curve depicts more oscillations with five negative peaks and four main positive peaks. The temperature minimum is documented at 22.50 Ma, which corresponds to rising values of the δ18O stack. From 22 Ma upwards a good accordance between the two curves can be observed. The SDPC shows a generally good match with the δ18O, but a greater similarity to the Alkenone SST. In fact, until 23 Ma all the curves indicate a gradual lowering of the temperatures, suggesting a general cooling of the superficial water mass. At 23 Ma Boulila et al. (2011), among others, documented megahiatus Mi1 affecting the North Atlantic and potentially recognizable at global scale. Boulila et al. (2011) suggested a connection between such a megahiatus and the obliquity node at 22.98 Ma of long-period (~1.2 Ma) obliquity cycles as recognizable in the obliquity variation curve of Laskar et al. (2004). Following Miller et al. (1985), the megahiatus Mi1 occurs between the third-order sequence O7 and KW0 of the New Jersey sea shelf and encompasses the Oligocene/Miocene boundary. Megahiatus Mi1 is not documented in IODP Hole U1406A but a climatic signal corresponding to general oceanic cooling is clearly recorded by planktonic foraminifera and thus evident in the SDPC. At the end of the Mi1 event another SDPC drop occurs, coinciding with δ18O and SST low values. The SDPC also captures the same climatic improvement described by the SST warming, maybe linked to a short interstadial event around 22.80 Ma and not documented by the δ18O data. Around 22.60 Ma all three curves indicate rising temperature, first recorded by the Alkenone SST and by the SDPC and slightly later by the δ18O, further supporting the successful correlation of the SDPC with the Alkenone SST. At 22.50 Ma the SDPC and SST document a drastic fall of the superficial temperature and thus a strengthening of the Labrador
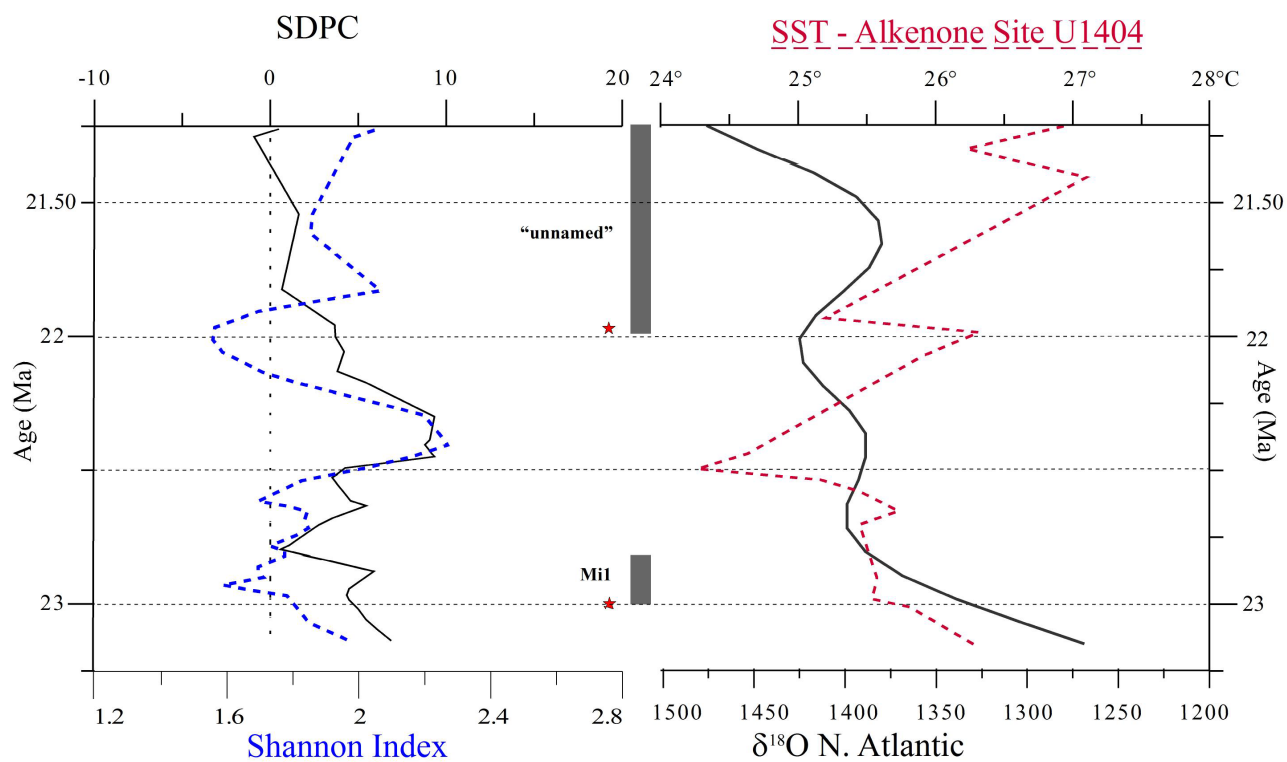
Figure 5. Comparison between present data (SDPC and Shannon index) and Alkenone SST (Liu et al., 2018) and δ¹⁸O North Atlantic data (Cramer et al., 2009). On the left a smoothed SDPC (black line) and the Shannon index curve (dashed blue) are plotted versus time (Ma) following the age model proposed by Fabbrini et al. (2019). The graphs terminate at (age?) owing to H1. On the right side, data from Alkenone SST from IODP Site U1404 (Liu et al., 2018) – red and dashed line – and the δ¹⁸O North Atlantic data (Cramer et al., 2009) – in black – are shown. The vertical gray boxes represent the regional megahiatuses (Boulila et al., 2011) associated with specific 1.2 Ma obliquity nodes (red stars).

current. This SST minimum is not recorded by the δ¹⁸O data, which in contrast suggest a higher temperature at the ocean floor.

The interval between 22.50 and 22 Ma seems to show no correspondence among the SDPC and SST. In fact, while the δ¹⁸O data show a temperature peak, perfectly mirrored by the SDPC (22.50–22.25 Ma), the SST shows a continuously rising trend. However, in this interval, the situation depicted by Alkenone data could partially represent the temperature oscillations at the J-Anomaly Ridge. In fact, in this interval, the SST curve is based on only two sample levels (22.40 Ma and 22.05 Ma; Liu et al., 2018). The SST peak at 21.99 Ma is evident in the smoothed SDPC, where the Shannon index mirrors the δ¹⁸O stack. Then all the curves fall coinciding with the temperature minimum recorded by the δ¹⁸O stack. At this age the Earth was in another nodal position (Laskar et al., 2004) and thus another megahiatus is documented in the North Atlantic by Boulila et al. (2011). The megahiatus linked to the "unnamed" event spans from 21.99 Ma to 21.20 Ma but is not documented in IODP Hole U1406A. Around 21.60 Ma the high values of δ¹⁸O are also documented by

a maximum in the SDPC. In this time frame the Alkenone SST of Liu et al. (2018) is affected by low sample resolution, thus not giving a complete record of the temperature variations. The SST peaks at 21.40 Ma, while δ¹⁸O and the SDPC are decreasing. At 21.30 Ma another minimum occurs in the SDPC and SST, during the steady lowering trend of the δ¹⁸O stack. In correspondence with H1 (38.85 m; Fabbrini et al., 2019) SDPC and SST increase rapidly, in contrast with the δ¹⁸O data. Thus, H1 is not directly linked to any regional megahiatus and occurred at the end of the "unnamed" glacial event.

3.5. Conclusions

The planktonic foraminifera quantitative distribution from IODP Hole U1406A reveals intriguing information about the paleoclimatic changes occurring in the North Atlantic Ocean during the uppermost Oligocene-lower Miocene interval. Following Aze et al. (2011), three foraminiferal ecogroups are recognized: Ecogroup 1 - open-ocean mixed layer with symbionts, Ecogroup 3 - thermocline, and Ecogroup 4 - subthermocline taxa. Results from statistical analyses suggest that Ecogroup 1 is the most suitable in reconstructing the sea surface variations, and

among the superficial water taxa, *Globigerina bulloides*, *Globoturborotalita* gr. and *Trilobatus* gr. are the most sensitive to environmental factors, such as superficial water temperature and trophic conditions. The SDPC presented in this paper accurately mirror the Alkenone SST data from Site U1404 (Liu et al., 2018) and the δ18O stack (Cramer et al., 2009). The Shannon–Weaver index also tends to primarily mirror the δ18O stack and secondarily the SST curve. The SDPC and the Shannon–Weaver index curve significantly drop in correspondence with the "Mi1" and "Unnamed" events reported by Boulila et al. (2011), indicating colder water conditions. Those events are visible at 22.90–22.80 Ma and at 21.95–21.90 Ma, respectively, perfectly fitting with the obliquity nodes of the Earth (Laskar et al., 2004). These relationships support the use of open-ocean mixed-layer (Ecogroup 1) planktonic foraminifera as sensitive indicators of SST, particularly where isotopic data are not available. The taxa

living in the mixed layer showed a close relation with the other taxa living in deeper levels of the water column, due to the connection of their habitats. In fact, the taxa living in the open-ocean mixed layer always present an opposite trend to the subthermocline-dwelling taxa, while the thermocline dwellers show intermediate features and seem more tolerant to ecological variations. This multiapproach study confirms the utility of the taxa inhabiting the open-ocean mixed layer to document SST and some ecological variations. Paleoecological data fit well with geochemical data and pinpoint the dynamic balance between the ecogroups and their habitat.

Acknowledgments

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