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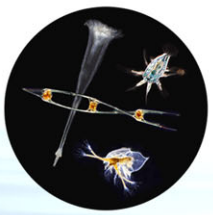

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Highly replicated sampling reveals no diurnal vertical migration but stable species-specific vertical habitats in planktonic foraminifera

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Diurnal vertical migration (DVM) is a widespread phenomenon in the upper ocean, but it remains unclear to what degree it also involves passively transported micro- and meso-zooplankton. These organisms are difficult to monitor by *in situ* sensing and observations from discrete samples are often inconclusive. Prime examples of such ambiguity are planktonic foraminifera, where contradictory evidence for DVM continues to cast doubt on the stability of species vertical habitats, which introduces uncertainties in geochemical proxy interpretation. To provide a robust answer, we carried out highly replicated randomized sampling with 41 vertically resolved plankton net hauls taken within 26 hours in a confined area of 400 km^2 in the tropical North Atlantic, where DVM in larger plankton occurs. Manual enumeration of planktonic foraminifera cell density consistently reveals the highest total cell concentrations in the surface mixed layer (top 50 m) and analysis of cell density in seven individual species representing different shell sizes, life strategies and presumed depth habitats reveals consistent vertical habitats not changing over the 26

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hours sampling period. These observations robustly reject the existence of DVM in planktonic foraminifera in a setting where DVM occurs in other organisms.

KEYWORDS: Zooplankton; planktonic foraminifera; vertical habitat; patchiness; North Atlantic

INTRODUCTION

Every day, the upper ocean experiences one of the greatest migrations on the planet. Large portions of the pelagic ecosystem migrate vertically in the water column, ascending at dawn and descending with dusk. This movement, called diurnal or diel vertical migration (DVM), was first described by Groom and Loeb (1890). It has since been observed in all marine and freshwater environments involving a range of organisms from microscopic phytoplankton to large fish (Forward, 1976; Ringelberg, 2010). Several hypotheses have been proposed to explain DVM, the most common suggesting DVM evolved as an adaptation to evade predation (Zaret and Suffern, 1976; Stich and Lampert, 1981; Hays *et al.*, 2001). Through active transport of the mesopelagic community, the DVM generates the largest flux of biomass to the twilight zone on the planet (Steinberg *et al.*, 2002; Hays, 2003) and the metabolism of the migrating community can supply more than a third of remineralised total organic carbon in this oceanic layer (Steinberg *et al.*, 2000). This process is thus essential for the efficiency of the biological carbon pump (Bianchi *et al.*, 2013; Aumont *et al.*, 2018). Despite its pervasiveness, it took over a century of research to understand this phenomenon in its entirety, from cause to effect (Ringelberg, 2010).

DVM is known to occur among organisms ranging in size from small motile phytoplankton such as dinoflagellates (Eppley *et al.*, 1968; Blasco, 1978; Cullen and Horrigan, 1981; Schofield *et al.*, 2006; Jephson and Carlsson, 2009) to small motile zooplankton like ciliates (Pérez *et al.* 2000) and larger meso- and macrozooplankton and nekton. Depending on the physical setting and organism group, the vertical distances traveled during DVM can vary from meters to hundreds of meters (Ringelberg, 1964). Shallow migrations are typical for regions with strong physical gradients, such as in stratified lakes or areas affected by sea ice. In the open ocean, the migration depth is typically several hundred meters: pelagic shrimps, as an example, may ascend and descend up to 800 m in each daily cycle (Omori, 1974).

To participate in the deep pelagic DVM, the organisms must achieve considerable swimming speeds. This is plausible for actively swimming organisms, including small unicellular zooplankton. For example, tintinnids swim with speeds averaging 0.4 mm s^{-1} (Broglio *et al.*, 2001) and could theoretically reach deeper water in 6 hours, without taking sinking velocity into account. The necessity to achieve a certain speed to participate in the DVM raises the question of whether or not non-motile plankton can also participate. In the size range of most non-motile plankton, DVM cannot be observed in situ by optical or acoustic techniques and the study of DVM in these groups requires analysis of discrete plankton samples. Most observational studies have focused on larger organisms such as cladocerans, copepods and chaetognathes (Pearre, 1973), and despite their key role in carbon transport (Calbet and Landry, 2004), the behavior of smaller micro-zooplankton remains unclear. Non-motile micro- and meso-zooplankton such as planktonic foraminifera could potentially participate in DVM by regulating their buoyancy, but their participation in DVM is shrouded by observational uncertainty. As appropriately stated by Hardy (1956): "There are many unsolved puzzles of pelagic natural history, but one seems perhaps more baffling than any other: that of vertical migration."

DVM has been suspected to occur in planktonic foraminifera since the beginning of the 20th century. Rhumbler (1911) was the first to observe larger numbers of planktonic foraminifera in surface nets taken during the day than during the night, and the same pattern has been reported in subsequent studies (Bé and Hamlin, 1967; Berger, 1969; Holmes, 1982). On the other hand, the participation of planktonic foraminifera in DVM contrasts with the existence of vertical habitat stratification among species (Fairbanks *et al.*, 1982; Pujol and Vergnaud Grazzini, 1995; Hull *et al.*, 2011; Rebotim *et al.*, 2017). Furthermore, no evidence was found for DVM in other replicated sampling studies such as that by Boltovskoy (1973). Remarkably, this controversy has never been resolved, and contradictory evidence continues to be presented both for (Field, 2004) and against (Manno and Pavlov, 2014) the presence of DVM in planktonic foraminifera. This is unfortunate considering how significant this phenomenon is for interpreting foraminifera-based paleo-proxies related to the understanding of their buoyancy control and for the evaluation of abundance data in vertical plankton tows. Because of the use of planktonic foraminifera as recorders of the state of the upper ocean in paleoceanographic studies,

there is a long history of reports identifying depth habitats and calcification depths of individual species (Fairbanks and Wiebe, 1980; Fairbanks *et al.*, 1982; Mulitza *et al.*, 1997; Lončarić *et al.*, 2006; Rebotim *et al.*, 2017). There is evidence for vertical segregation even among cryptic species (Weiner *et al.*, 2012). The existence of DVM would have profound consequences for the utility of such studies. Currently, planktonic foraminiferal abundance in depth-stratified plankton tows is interpreted assuming that DVM does not occur, and that their observed vertical distribution represents a stable depth habitat rather than a transient point on a daily migration trajectory (Rebotim *et al.*, 2017; Jentzen *et al.*, 2018). The existence of DVM would have profound consequences for the interpretation of the abundances and composition of assemblages "caught" at one point in time.

The lack of an authoritative answer to the existence of DVM in planktonic foraminifera is likely the consequence of unsuitable sampling approaches and reflects the fact that foraminifera are mainly used and studied as paleoceanographic tracers rather than as living organisms. Consequently previous sampling approaches were not designed to answer this question. In order to resolve the persisting uncertainty, we designed and executed a dedicated experiment using randomized continuous sampling over a full day-night cycle across the upper 300 m of the water column in a small area of 400 km^2 in the eastern tropical North Atlantic (Fig. 1).

MATERIAL AND METHODS

Sampling strategy and sample processing

The principle prerequisite for an unambiguous determination of the presence or absence of DVM is sampling in an oceanic (offshore) area with sufficient replication carried out in a region and at a time when DVM in other plankton groups occurred. To meet this prerequisite, we designed and implemented a novel sampling scheme during the RV Meteor cruise M140 (Kucera and Siccha, 2017) that took place between August 11th and September 5th, 2017 in the eastern tropical North Atlantic (Fig. 1) where DVM in larger plankton has been previously documented (Longhurst and Harrison, 1989). During the cruise, the existence of DVM in larger plankton (>5 mm) was monitored by an acoustic Doppler current profiler (ADCP) and having established its regular presence and extent (Fig. 2), a location in the vicinity of the sediment trap mooring M3 (Korte *et al.*, 2017; Fig. 1) was selected for sampling. To assess the existence of DVM in planktonic foraminifera, we followed a hyper-replicated sampling scheme (Fig. 1) using a multi-plankton-sampler (MPS, Hydrobios, Kiel) equipped with five nets (100 µm mesh size, 0.25 m^2 opening) and plastic net buckets, closing sequentially at successive discrete depths during the upcast. This system allowed us to collect individuals larger than 100 µm (no clogging was observed). The MPS was equipped with a pressure sensor, allowing net opening at precisely determined depths, and a flow meter to directly determine the volume of water filtered by each net.

The sampling scheme was designed to repeatedly sample a 20 × 20 km region for 26 hours with a total number of 41 stations. The sampling positions in the 20 × 20 km area are shown in Fig. 1, and the time (using UTC throughout the manuscript) and coordinates of station's sampling positions are given in Table I. The vertical depth intervals for sampling were randomly generated alternating between a shallow sampling scheme with depth intervals ranging from 15 m to 35 m and a deep sampling scheme with depth intervals ranging from 30 m to 70 m, covering the upper 300 m of the water column (Table I). The alternation of the two resolutions allowed us to cover the upper ocean (including the surface mixed layer and seasonal thermocline) at a higher resolution and at the same time sample to depths covering the observed DVM depth of the larger zooplankton determined from ADCP echo intensities (Fig. 2). The randomization of depth intervals allows a more precise estimate of the vertical abundance profile than sampling with fixed intervals, provided, as was the case here, the sampling is sufficiently replicated. In total, we obtained 205 vertically stratified plankton net samples (Fig. 1).

All plankton samples were processed directly on board by manually separating and enumerating all planktonic foraminifera from the entire sample, distinguishing between empty and cytoplasm-bearing shells on the basis of cytoplasm color and shell transparency. To assess the existence of DVM on species level, the separated foraminifera at ten randomly selected stations were identified and counted on the species level following the SCOR WG138 taxonomy as implemented in Siccha and Kucera (2017) (Table I, Fig. 1). For the species *Orbulina universa*, adult specimens with a spherical last chamber were differentiated from pre-adult trochospiral stages. Based on the estimates of the filtered volume, the counts were converted to concentrations and expressed as the number of individuals per cubic meter (Tables S1 and S2).

Acquisition and treatment of environmental parameters

The vertical position of larger particles (mainly zooplankton) in the water column was tracked by measuring

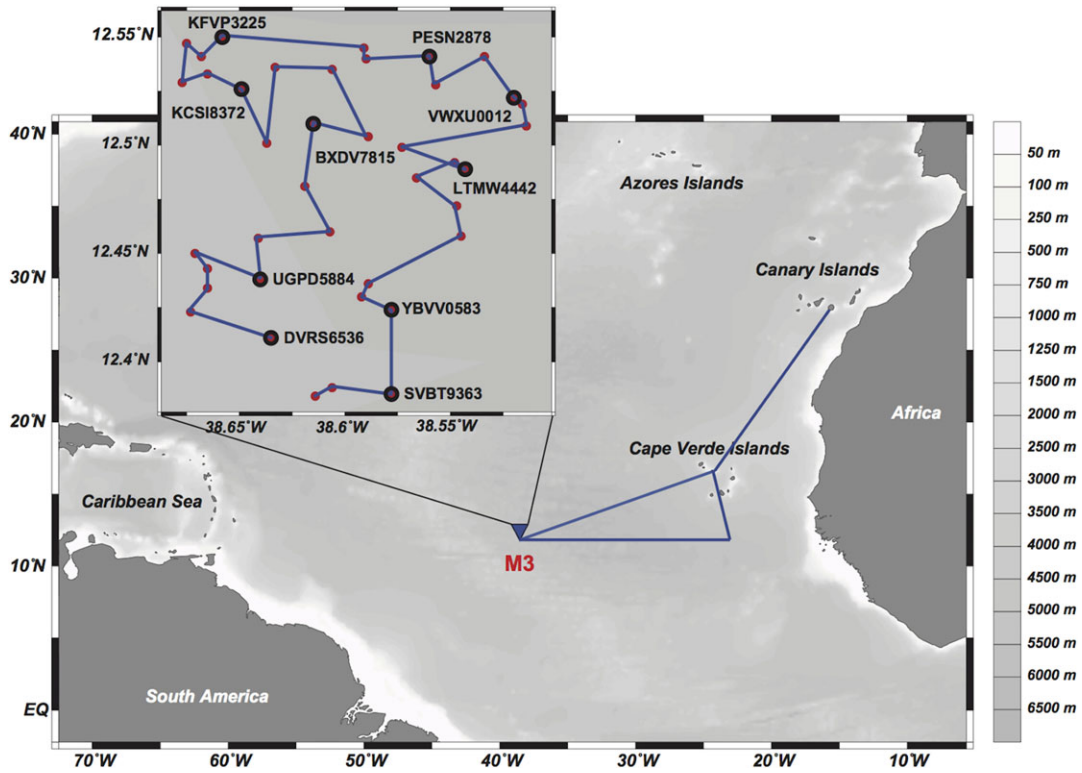

Fig. 1. Sampling area in the subtropical North Atlantic Ocean. Line = cruise track of M140, triangle = station M3 sampling zone, dots = sampled stations (41), black-circled dots = sampled stations processed to the species level and their labels (10). Gray scale shows bathymetry.

their velocity in the vertical plane with ADCP. We used a 75 kHz ADCP that record particles larger than about 5 mm from 12 August to 5 September 2017, with a break on 26 August for a port call in Mindelo, Cabo Verde (Fig. 2). The ADCP data were post-processed with the software package OSSI19 (Ocean Surveyor Sputum Interpreter, version 1.9), developed at the GEOMAR in Kiel, which also corrects for the misalignment angle. The MPS used for plankton sampling was equipped with a conductivity-temperature-depth probe (CTD) with fluorescence and oxygen sensors and five Niskin bottles, providing simultaneous, directly co-registered *in situ* records of physical parameters and water chemistry. Salinity, temperature (°C), chlorophyll *a* (Chl-*a*, in mg m^{-3}) and oxygen concentration (µmol kg^{-1}) were measured continuously during the downcast and upcast. The CTD profiles were obtained for each of the 41 net hauls and served as a confirmation that the plankton hauls sampled the same water masses.

Data analyses

All statistical analyses were performed in RStudio v. 1.1.456 running R v. 3.4.2 (RStudio Team, 2015). If planktonic foraminifera take part in the DVM, then their average depth habitat and concentration at a given depth should vary predictably between day and night. To test this hypothesis, we first compared the day and night populations (as a group and per species) with respect to the observed depths of maximum concentration (mode) and total concentration throughout the entire sampled interval using a simple Mann and Whitney *U* test (Mann and Whitney, 1947) (*P*-values have Bonferroni correction). Day (06:30 to 18:45) and night hours (18:45 to 06:30) were defined by the civil twilight hours and the migrating trajectory of the zooplankton (Fig. 2).

The highly replicated sampling design allowed us to probe vertical abundance patterns further and assess the predictability of the vertical distribution not related to a strict day-night pattern. To this end, we used a series of generalized linear mixed effects models (GLMM; Williams, 1982) designed to predict the observed foraminifera density (*FD*) as a function of time and sampling depth as implemented in the R-package "lme4" v.1.1-18-1 (Bates *et al.*, 2015). The models were built around three fixed and two random effects selected with regard to the specifically employed sampling strategy. The fixed effects are (i) the mean net depth *d* (is foraminifera density influenced by the sampling depth?—i.e. do the foraminifera have a preferred

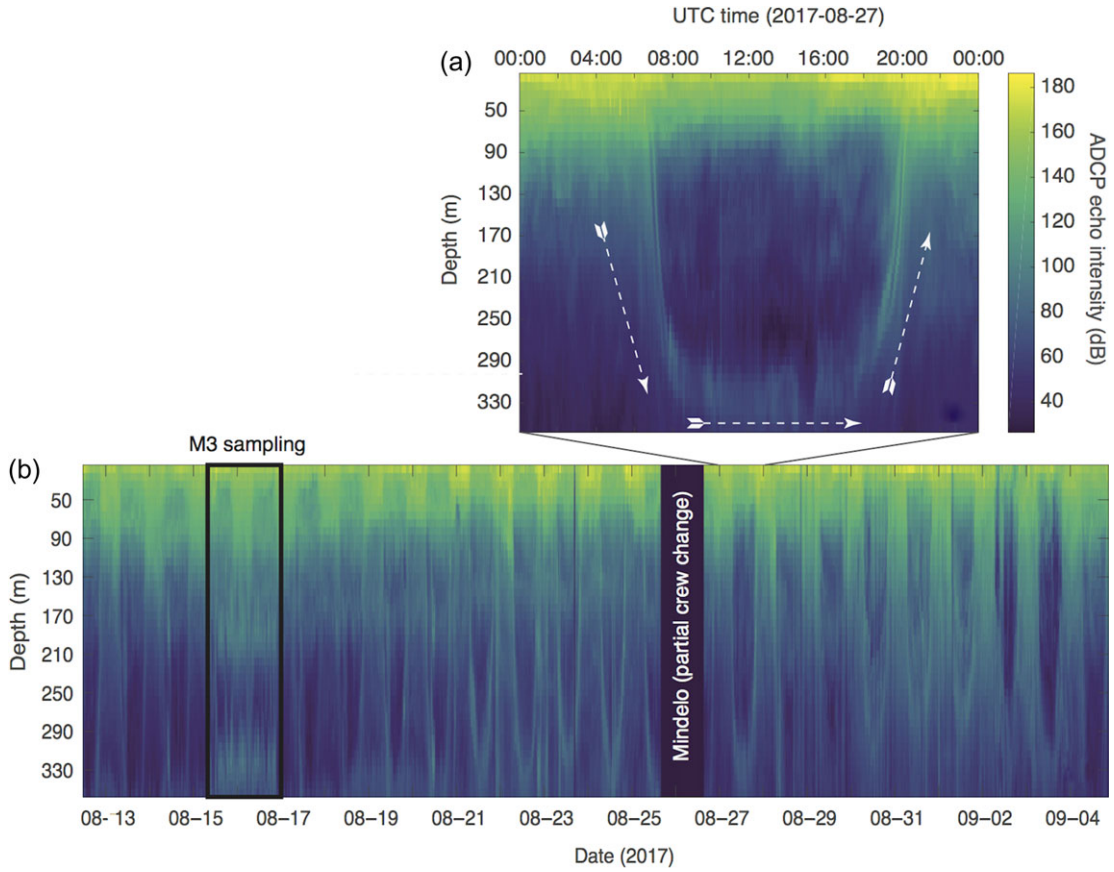

Fig. 2. ADCP-derived echogram (75 kHz), from the surface to 350 m depth and spanning. (**a**) 24 hours from August 27th 2017, 00:00 to August 28th 2017, 00:00 UTC (dashed white arrows = inferred diurnal vertical migration (DVM) trajectory of the large zooplankton and small nekton), (**b**) the entire cruise (black rectangle = M3 sampling period), showing the reproducibility and extent of the DVM pattern. Color scale = echo intensity (dB).

vertical habitat?), (ii) the time of day t (is overall foraminifera density changing with time?) and (iii) the relationship between net depth and time (do foraminifera occur at different depths with time—i.e. do they show vertical migration?). The chosen random effects are (i) the station ST as station positions were randomized and (ii) the mean net depth nested within station as net depths intervals were randomized per station. The specific models investigated (including an unknown error term ε) can be summarized as follows:

$$FD_1 = d + t + d * t + \varepsilon|ST + d{:}\ ST$$

$$FD_2 = d + t + \varepsilon|ST + d{:}\ ST$$

$$FD_3 = d + d * t + \varepsilon|ST + d{:}\ ST$$

$$FD_4 = t + d * t + \varepsilon|ST + d{:}\ ST$$

$$FD_5 = d + \varepsilon|ST + d{:}\ ST$$

$$FD_6 = t + \varepsilon|ST + d{:}\ ST$$

The models used the Gamma distribution, which fit the distribution data best according to a maximum likelihood fitting using the R-package "fitdistrplus" v. 1.0–9 (Delignette-Muller and Dutang, 2015), and the log as a link function as is customary with abundance data (McDonald, 2009). These models were tested for the group as a whole and for each of the seven most abundant species. In each case, the best fitting model was chosen for further interpretation using the corrected Akaike information criterion (AIC_c, Akaike, 1974, Table S3). The AIC_c was determined in all cases using the R-package "sme" v. 1.0.2. The coefficients of determination (R^2) for the GLMMs where calculated with the R-package "MuMIn" v. 1.42.1, using the trigamma function.

Table I: M3 26-hours sampling area station names, locations, time (dd/mm/yy hh:mm:ss) and depth intervals (m).

Station	Longitude	Latitude	Date	Time	Net depth intervals (m)
DVRS6536	**−38.635**	**12.411**	**15/08/2017**	**15:45:40**	**0–31, 31–60, 60–75, 75–107, 107–140**
DEAY9146	−38.673	12.423	15/08/17	16.35:20	0–41, 41–93, 93–162, 162–221, 221–285
HTOL2787	−38.665	12.434	15/08/17	17:13:00	0–30, 30–46, 46–69, 69–96, 96–100
KXGN9928	−38.665	12.443	15/08/17	17:44:38	0–47, 47–96, 96–148, 148–189, 189–249
CHPF6756	−38.671	12.450	15/08/17	18:15:01	0–19, 19–39, 39–67, 67–92, 92–119
UGPD5884	**−38.640**	**12.438**	**15/08/2017**	**19:00:11**	**0–50, 50–106, 106–148, 148–184, 184–233**
HQXN9213	−38.641	12.457	15/08/17	19:33:57	0–20, 20–39, 39–71, 71–101, 101–135
KLIR1433	−38.607	12.460	15/08/17	20:11:00	0–44, 44–106, 106–167, 167–224, 224–259
DPHE0358	−38.619	12.481	15/08/17	20:51:00	0–17, 17–36, 36–53, 53–78, 78–97
BXDV7815	**−38.615**	**12.510**	**15/08/2017**	**21:27:00**	**0–31, 31–83, 83–125, 125–193, 193–262**
KEOP2594	−38.589	12.504	15/08/17	22:18:00	0–33, 33–50, 50–66, 66–92, 92–122
RKBH7315	−38.606	12.535	15/08/17	22:53:00	0–41, 41–103, 103–169, 169–223, 223–288
JSNU7217	−38.633	12.536	15/08/17	23:39:00	0–21, 21–40, 40–62, 62–81, 81–106
QAWN5578	−38.637	12.501	16/08/17	0:15:00	0–68, 68–120, 120–179, 179–232, 232–263
KCSI8372	**−38.649**	**12.526**	**16/08/2017**	**1:01:00**	**0–33, 33–61, 61–78, 78–101, 101–117**
DWBR7439	−38.665	12.533	16/08/17	1:28:00	0–48, 48–104, 104–155, 155–200, 200–267
KLEI3823	−38.677	12.529	16/08/17	2:06:00	0–25, 25–49, 49–84, 84–115, 115–140
KSEW1407	−38.675	12.547	16/08/17	2:40:00	0–63, 63–127, 127–172, 172–226, 226–291
SFRO8584	−38.668	12.541	16/08/17	3:18:00	0–33, 33–51, 51–74, 74–108, 108–141
JMGX4246	−38.657	12.551	16/08/17	3:50:00	0–67, 67–124, 124–162, 162–218, 218–251
KFVP3225	**−38.658**	**12.550**	**16/08/2017**	**4:38:00**	**0–29, 29–56, 56–78, 78–112, 112–129**
LTCV6182	−38.590	12.540	16/08/17	5:15:00	0–46, 46–103, 103–170, 170–232, 232–281
POEA7741	−38.591	12.545	16/08/17	5:47:00	0–30, 30–58, 58–90, 90–113, 113–143
PESN2878	**−38.560**	**12.541**	**16/08/2017**	**6:24:00**	**0–60, 60–107, 107–176, 176–246, 246–311**
CFSR7546	−38.557	12.528	8/16/2017	7:04:00	0–32, 32–53, 53–79, 79–114, 114–140
VRNH6358	−38.534	12.541	8/16/2017	7:40:00	0–46, 46–94, 94–134, 134–195, 195–260
VWXU0012	**−38.520**	**12.522**	**16/08/2017**	**8:18:00**	**0–22, 22–49, 49–71, 71–101, 101–124**
BLJO8338	−38.516	12.519	16/08/2017	8:45:00	0–67, 67–119, 119–173, 173–209, 209–275
JDNV3664	−38.514	12.509	16/08/2017	9:32:00	0–25, 25–54, 54–88, 88–110, 110–142
MYCH4584	−38.573	12.499	16/08/2017	9:59:00	0–48, 48–86, 86–152, 152–213, 213–278
LTMW4442	**−38.543**	**12.489**	**16/08/2017**	**10:47:00**	**0–30, 30–64, 64–80, 80–102, 102–130**
CCWG8688	−38.548	12.492	16/08/2017	11:13:00	0–41, 41–98, 98–155, 155–170, 170–236
DKZQ8406	−38.566	12.485	16/08/2017	11:46:00	0–21, 21–41, 41–70, 70–97, 07–124
GNSP5424	−38.547	12.472	16/08/2017	12:28:00	0–41, 41–100, 100–141, 141–207, 207–270
APYC0820	−38.545	12.458	16/08/2017	13:10:00	0–28, 28–44, 44–66, 66–90, 90–110
UEWC3556	−38.589	12.436	16/08/2017	13:56:00	0–46, 46–96, 96–154, 154–217, 217–271
QLDT2681	−38.592	12.430	16/08/2017	14:27:00	0–29, 29–61, 61–82, 82–112, 112–130
YBVV0583	**−38.578**	**12.424**	**16/08/2017**	**15:06:00**	**0–48, 48–96, 96–144, 144–203, 203–268**
SVBT9363	**−38.578**	**12.385**	**16/08/2017**	**15:56:00**	**0–35, 35–98, 98–141, 141–181, 181–225**
FUSH5410	−38.606	12.388	16/08/2017	16:37:00	0–34, 34–50, 50–84, 84–103, 103–131
MHIH2462	−38.614	12.384	16/08/2017	17:07:00	0–45, 45–97, 97–142, 142–195, 195–241

Boldface values and text highlight taxonomically processed stations.

RESULTS

Water column properties

The ADCP data revealed the presence of a persistent pattern of DVM in larger zooplankton, manifested by a distinct reduction in particle load in the surface layer during night accompanied by a clear pattern of descent beginning at approximately 06:00, reaching a maximum of 330 m depth around 13:00 and returning to surface at 20:00 (Fig. 2). This pattern was observed every day, including during the M3 sampling, providing evidence that large zooplankton migrated vertically during the experiment/plankton towing. During all 41 net hauls, the CTD profiles recorded simultaneously with the plankton collection showed a similar vertical profile, suggesting we did succeeded to continuously sample the same water column (Fig. 3). All CTD profiles show a clear surface mixed layer extending to 50 m depth. The stable, high values of oxygen concentrations from the surface to 100 m and potential density (θ) < 25.8 kg m^{-3} suggest that the salinity maximum water (TSW), also called subtropical underwater, extended to that depth. Below the TSW lay central waters, with a density 25.8 < θ < 27.1 kg m^{-3} and oxygen concentrations from 1.25 mg m^{-3} to 0.30 mg m^{-3} (Stramma *et al.*, 2008). Beneath this transitional water mass, the deeper casts encountered the oxygen minimum zone (OMZ, [O_2] < 0.30 mg m^{-3}) that can extend down to 500 m depth (Varela *et al.*, 2008). The fluorescence profiles indicate the presence of a well-developed and stable deep

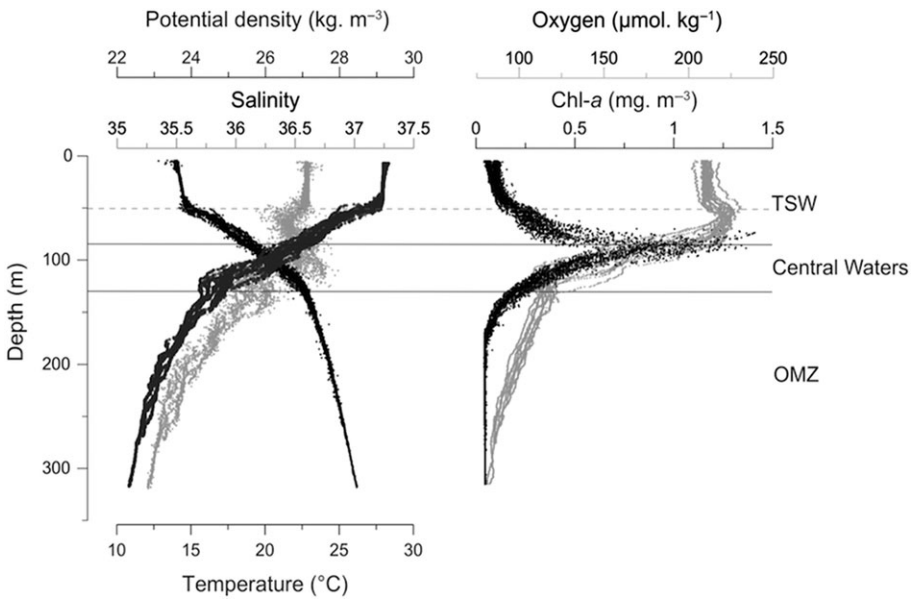

Fig. 3. Composite CTD profiles from the surface to 350 m depth (potential density, salinity, temperature, oxygen and chlorophyll-*a* concentrations) at the 10 stations in the M3 sampling area for which planktonic foraminifera were identified to species level. The encountered water masses are highlighted with black lines and labels (TSW = salinity maximum water, OMZ = oxygen minimum zone) and the dashed gray line illustrates the mixed layer limit.

chlorophyll maximum (DCM) across all stations, reaching Chl-*a* values of 1.3 mg m^{-3} at 100 m depth (right at the base of the TSW), similar to earlier observations in this region (Sauzède *et al.*, 2015).

Planktonic foraminifera vertical distribution

The maximum concentration of living planktonic foraminifera, i.e. cytoplasm-bearing shells occurred consistently in the surface mixed layer between 0 and 50 m (Fig. 4), well above the DCM (≈100 m depth) and ranged from 4 to 331 ind. m^{-3} (raw counts [27; 1185] individuals per individual sample, Table S1), with a median of 31.3 ind. m^{-3}, testifying to the high variability between stations and indicating relatively low standing stocks typical of oligotrophic gyre areas (Ufkes *et al.*, 1998). Below 50 m, the concentration decreased by an order of magnitude, with a median of 3.75 ind. m^{-3} and a maximum of 23 ind. m^{-3} (raw counts [0; 320] individuals per individual sample, Table S1). The species counts performed at 10 stations (Fig. 1, Table I) revealed the presence of 35 morphospecies of living planktonic foraminifera including typical tropical and subtropical species such as *Globigerinita glutinata* and *Globigerinoides ruber* (Bé, 1977, Table S2) and with a wide size spectra ranging from 100 to >300 µm. Among the 35 species, we analyzed the six most abundant ones (>5%) that occurred at every station. These species representing collectively more than two-thirds of the overall assemblage include *G. glutinata* (21.2%), *G. ruber* white (16.9%), *Globigerinella siphonifera* (8.5%), *Orbulina universa* adults (7.8%), *Globigerinella calida* (7.4%) and *Tenuitella fleisheri* (6%) (Fig. S1). Out of these, *G. ruber* white and *G. glutinata* often inhabit surface waters and together with *O. universa*, *G. calida* and *G. siphonifera* are symbiont-bearing species. In addition, we also analyzed the second most abundant deeper-dwelling species *Globorotalia crassaformis* (3.4%) that occurred at every station. As shown in Figs 5 and 6, the vertical distribution of the concentration of living specimens of these species reveals distinct depth habitats.

The concentration of planktonic foraminifera as a group (all species) in the surface mixed layer appeared to vary with time. However, this variability does not follow a pattern of DVM. A direct comparison of total concentrations and of the depths of maximum abundance between stations sampled during the day and night revealed no significant differences in a *U* test ($P > 0.05$), suggesting the population does not migrate vertically in pace with daylight (Fig. 7, Table II). Results from the GLMM corroborate these observations as they indicate from the ΔAIC_c that the best fitting model is FD_3 which shows a significant relationship with depth *d* only (Table III). Consequently, the main factor controlling the distribution of living planktonic foraminiferal populations and their variability is depth-related and independent of time on a day/night time scale. We

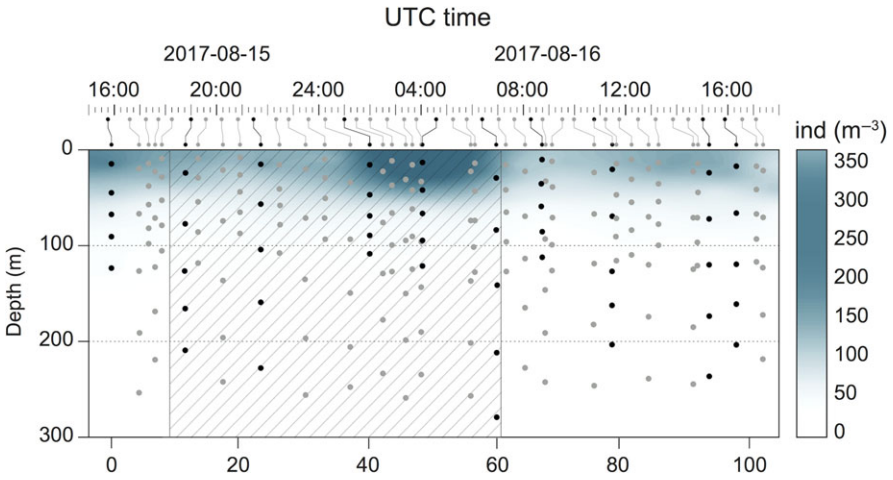

Fig. 4. Concentration of living planktonic foraminifera (color scale) in the water column from 15 August 2017 15:45 to 16 August 2017 17:45 UTC (black dots = average depth of net samples processed to the species level, gray dots = average depth of the other net samples) in the M3 area. The time scale highlights the exact sampling hour for each station and hatched area highlights the hours of night.

conclude that planktonic foraminifera as a group do not take part in any kind of DVM.

Next, we analyzed the distribution of the most important species to explore the possibility that only some species participate in the DVM. We observe that *Globigerinoides ruber* white and *Globigerinita glutinata* show a stable unimodal vertical distribution, inhabiting essentially the same surface mixed layer (upper 50 m), with maximum density of 23 and 30 ind. m^{-3}, respectively (Figs 5 and 6). The highest concentrations of *G. glutinata* occurred during the beginning of the 26 hours sampling period (15:45 on 15 August) until 16 August early morning (06:24), decreased to ≈10 ind. m^{-3} for stations sampled at 06:24, 08:18 and 10:47 before rising again for the two last stations. Abundances of *G. ruber* across the sampling area with time showed more variability with three areas of high densities encountered around 15:45 on 15 August from 01:01 to 04:38 and from about 10:47 to 15:06 on 16 August (Fig. 6). For both species, their abundances and depths of maximum concentration did not significantly vary between day and night (*P*-value > 0.05, Fig. 7, Table II). The series of GLMM indicates that the distribution of *G. ruber* is significantly correlated with depth only (Table III). The best model for *G. glutinata* also identifies depth as the strongest factor (Table III), and a small but significant interaction between depth and time reflecting a slight difference in the depths of the initial and the last abundance maxima (not related in time to DVM). Therefore, neither *G. ruber* white nor *G. glutinata* participate in any kind of DVM.

Despite their large size and favorable shape (spherical shell) for rapid sinking, adult specimens of *O. universa* remained highly concentrated in a narrow depth zone around 100 m near the DCM throughout the sampling period (Figs 5 and 6). The concentrations of this species did not differ between day and night ($P > 0.05$, Fig. 7, Table II) but the depths of maximum abundances differed significantly ($P = 0.006$, Table II) between the day (mean 69.5 m) and night (mean 90 m). However, this is not confirmed by the GLMM analysis. Like for *G. ruber*, the best fitting model for *O. universa* is FD_5, suggesting both species have a fixed depth habitat irrespective of the time of day. Therefore, we conclude that the large spherical *O. universa* maintained a distinct and consistent subsurface abundance maximum and did not participate in the DVM either.

The deeper-dwelling *Globorotalia crassaformis* also showed a unimodal depth distribution, but as expected, its habitat reached much deeper, with living specimens found down to 280 m depth, while absent in the upper 100 m above the DCM at day and night (Fig. 5). The concentrations of this species remained low throughout the sampling, not exceeding 0.8 ind. m^{-3} (Fig. 6). Results from *U* tests revealed that *G. crassaformis* concentrations and depth habitat remained similar during day and night (Fig. 7, Table II) and the GLMMs confirms that only depth contributed significantly to the model that best explained its concentrations (Table III). For all four species, the GLMM models explained more than 50% of the variance, illustrating the stability of their depth habitat (Table III).

In contrast, the species *Globigerinella calida*, *Globigerinella siphonifera* and *Tenuitella fleisheri* showed a more variable depth habitat, extending from the surface to below 200 m (Figs 5 and 6). The variability is not only

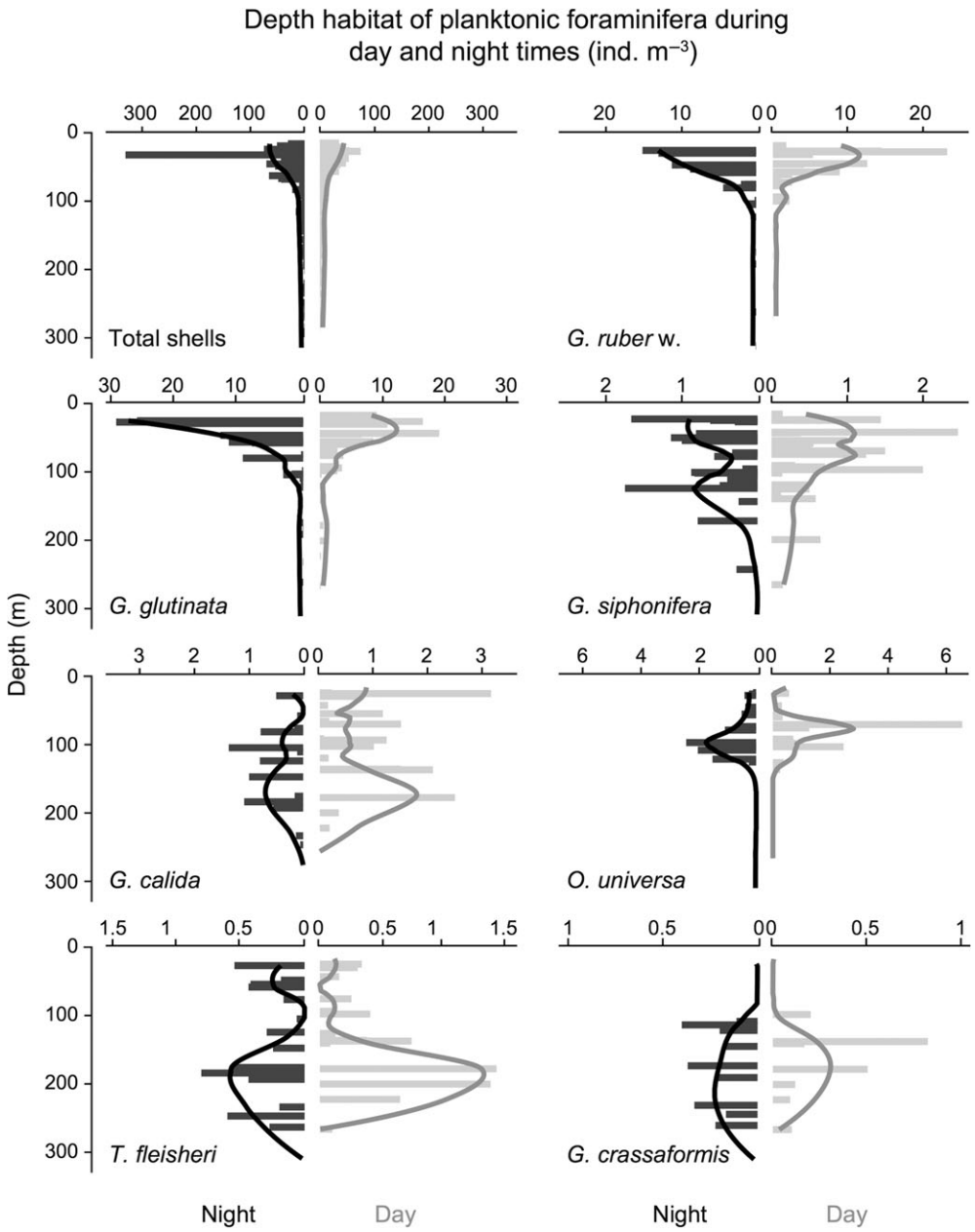

Fig. 5. Composite vertical distribution and concentration of total living planktonic foraminifera (total shells, $n = 41$ stations) and per species (*Globigerinoides ruber* white, *Globigerinita glutinata*, *Globigerinella siphonifera*, *Globigerinella calida*, *Orbulina universa*, *Tenuitella fleisheri*, *Globorotalia crassaformis*, $n = 10$ stations) during hours of day and night. Thick lines represent the smoothed distribution (locally estimated scatterplot smoothing, LOESS, Span = 0.5, formula = $y \sim x$). Bars are drawn at the middle of the collection interval of each net.

manifested in depth, but also in space/time: *G. siphonifera* and *T. fleisheri* fluctuated largely in depth distribution and abundance along the sampling track whilst *G. calida* almost disappeared at stations sampled from 01:01 to 10:47 hrs on 16 August (Fig. 6). The maximum abundances of the latter species occurred at two time periods. First, the species reached a maximum of 3.2 ind. m^{-3} at 15:45 on 15 August and again of almost 2 ind. m^{-3} at 15:56 on 16 August. Results from the GLMM series highlight this discrepancy, indicating that its abundance is only explained by time (t) (Table III, FD_6), as confirmed by the *U* test. However we find no significant differences between day and night concentrations and depth of maximum abundances for *G. calida* (Fig. 7, Table II), suggesting that its temporal abundance variability is not able to be explained by DVM.

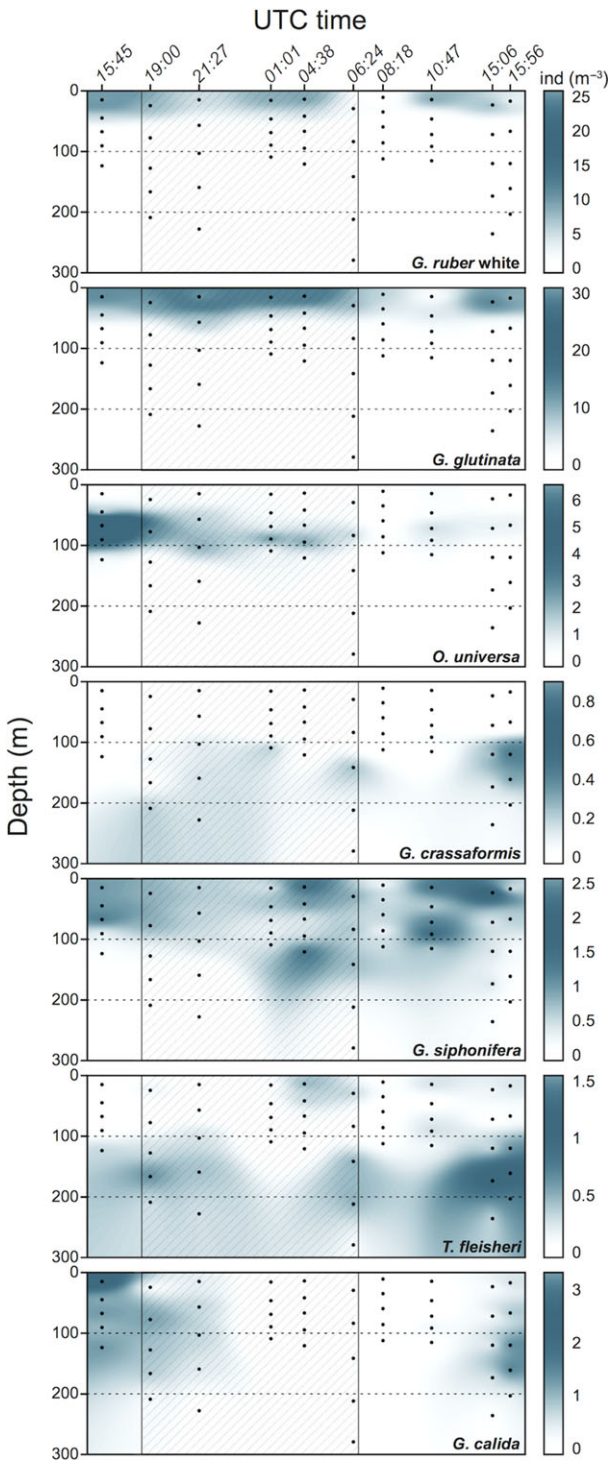

Fig. 6. Vertical distribution of planktonic foraminifera concentration (color scale) per species from 15 August 2017 15:45 to 16 August 2017 17:45 UTC (black dots = average depth of each sample's net). The hatched area highlights the hours of night.

A similar behavior is observed in *T. fleisheri*, whose distribution is also only correlated with time (*t*) (Table III, FD_6) and for which no significant differences could be observed for their concentration and depth of maximum abundances between day and night (Fig. 7, Table II). While the "patchy" distribution of *G. calida* is clearly visible (Fig. 6), it is less obvious for *T. fleisheri* which occurred almost continuously throughout the sampling period and remained concentrated at depths around 200 m albeit with small changes in abundance at shallower depths. Since we can exclude the possibility that specimens of these species migrated below the depth range of our sampling (because concentrations did not differ between day and night), we must conclude that these species track essentially the same vertical habitat but show a variability in their horizontal distribution.

The most variable distribution pattern is shown by *G. siphonifera* (Fig. 6). This species displays a wide total depth range and highly variable concentrations with five abundance maxima peaking at 2.5 ind. m^{-3} in subsurface on 16 August at 10:47. However, neither its concentration nor depth of maximum abundance differed significantly between stations sampled during day and night (Table II, Fig. 7). Its concentration distribution is best explained by the FD_5 model, suggesting that it is best predicted by depth irrespective of day/night time. Therefore, despite the variable distribution, there is no evidence that *G. siphonifera* participated in any kind of DVM either. We note, however, that the variable distribution resulted in a smaller portion of the variance being explained by the best GLMM model (32%, Table III) and indicating that this species has a broader depth range.

DISCUSSION

Analysis of vertical profiles of cell densities in the hyper-replicated sampling scheme (Fig. 1, Table III) allowed us to robustly reject the existence of DVM or any other time-related (e.g. tidal) migration pattern in planktonic foraminifera at the examined location. This conclusion, though based on low numbers of individuals for some species (cf. 3.2, Table S2), not only applies to the group as a whole but also to individual species that include symbiont-bearing species with different depth habitats, subsurface and deep-dwelling species, and DVM is also rejected for large spherical *O. universa*. Thus, we confirm the conclusions of Boltovskoy (1973), who did not observe

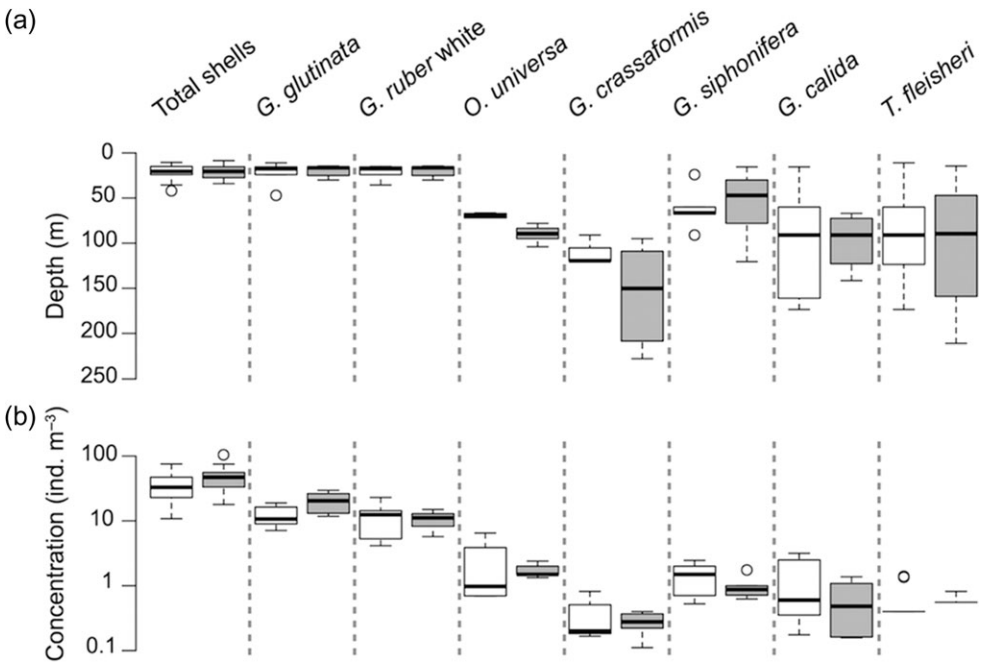

Fig. 7. Boxplots of planktonic foraminifera showing (**a**) depth of maximum abundance and (**b**) total concentrations over entire sampled depth, between day (white boxes) and night hours (gray boxes). Thick lines indicates median, boxes extend to interquartile range (IQR), whiskers indicate 1.5*IQR, circles marl outliers.

Table II: Results of Mann and Whitney U *test (*P*-values have Bonferroni correction) for the comparison of living planktonic foraminifera depth of maximum abundances (*d*) and total concentration over entire sampled depth interval (*c*) between day and night.*

	Adjusted *P*-value	
	Depth *d*	Concentration *c*
Total Shells	1.000	0.130
G. siphonifera	1.000	1.000
G. calida	1.000	0.825
G. glutinata	1.000	0.190
G. ruber white	1.000	1.000
G. crassaformis	0.523	1.000
O. universa	0.039*	0.536
T. fleisheri	1.000	1.000

The asterisk marks adjusted *P*-values < 0.05.

any DVM pattern during a three-week cruise in the South Atlantic Ocean as well as the recent observations that Manno and Pavlov (2014) made for *Neogloboquadrina pachyderma* and *Turborotalita quinqueloba* in the Arctic during summer. It also agrees with the extensive observational data presented by Hull *et al.* (2011), who demonstrated a consistently mesopelagic habitat for *Hastigerinella digitata*. Consequently, earlier observations that were interpreted as showing DVM in the group (e.g. Rhumbler, 1911; Bé and Hamlin, 1967; Berger, 1969; Holmes, 1982) require another explanation.

The absence of DVM in planktonic foraminifera is in contrast with the consistent presence of DVM in macroplankton as evidenced by the ADCP profiles of echo intensity in the studied region (Fig. 2). It implies that foraminifera remain in their preferred depth habitat during the diurnal cycle and do not hitchhike on migrating macro-plankton.

The lack of DVM in planktonic foraminifera is good news for the interpretation of plankton tow data and for efforts to characterize vertical habitats and calcification depths of individual species to interpret geochemical proxies in paleoceanography. It implies that observations from vertically resolved plankton tows are suited to constrain the depth habitat of species. Furthermore, the observed consistency of species vertical habitats in our study implies that depth habitats can be approximated effectively without significant replication on diurnal time scales. This is not to say that the vertical habitat of a species is the same everywhere or throughout the ontogenetic cycle (Rebotim *et al.*, 2017) or seasonally (Peeters and Brummer, 2002; Lončarić *et al.*, 2006). Rather, we can conclude that our observed variations in species vertical habitats require explanations other than DVM. The existence of well-defined and spatially stable (within our sampling) vertical habitats are also in line with the modeling study by Kretschmer *et al.* (2018), where

Table III: Results from the series of generalized linear mixed effects models (GLMM) on living planktonic foraminifera distribution.

	Best model based on AIC_c	*P*-value			Conditional R^2	Marginal R^2
		Depth *d*	Time *t*	Interaction *d* t*		
Total Shells	FD_3	<0.001*		0.796	1.000	0.696
G. siphonifera	FD_5	0.034			0.323	0.323
G. calida	FD_6		0.001*		0.854	0.446
G. glutinata	FD_3	<0.001*		0.038*	0.716	0.716
G. ruber white	FD_5	<0.001*			0.520	0.520
G. crassaformis	FD_3	0.045*		0.068*	1.000	0.433
O. universa	FD_5	0.007*			0.838	0.084
T. fleisheri	FD_6		0.029*		0.912	0.285

The asterisk marks *P*-values < 0.05. Conditional R^2 shows the percentage of variance explained by the complete model and marginal R^2 shows the percentage of variance explained by the fixed effects only.

differential vertical habitats emerged from the parameterization of species' metabolism, and are consistent with the existence of species-specific calcification depths, inferred from isotopic and trace-elemental compositions of foraminiferal shells (Emiliani, 1966; Fairbanks *et al.*, 1982; Anand *et al.*, 2003).

The one exception to a stable vertical habitat in our sampling was the species *G. siphonifera* (Figs 5 and 6). Weiner *et al.* (2014) labeled this morphological species as being genetically "hyperdiverse", and considering the evidence for vertical segregation of cryptic species in other planktonic foraminifera (Weiner *et al.*, 2012), it is likely that the observed depth habitat range of *G. siphonifera* (Figs 5, 6) results from superposition of more constrained habitats of several cryptic sibling species. This is supported by an observable bimodality in the depth distribution (Fig. 5), which may indicate the presence of two parapatric populations of the morphospecies.

Our observations from the sampling region are characteristic of the (sub)tropical biogeographic province and trophic regimes at large. The assemblage we encountered is typical for (sub)tropical oceans with low productivity, dominated by shallow-dwelling *G. ruber* and *G. glutinata*, and are consistent with previous studies in similar ocean regions (Bé and Hamlin, 1967; Bé and Hudson 1977; Ottens, 1992; Rebotim *et al.*, 2017). Similar to Rebotim *et al.* (2017), the maximum concentrations of planktonic foraminifera densities were recorded in surface waters and in similar numbers (this study: 4 to 331 ind. m^{-3}, Rebotim *et al.*, 2017: > 1 to 486 ind. m^{-3}). Because of the replicated sampling with variable depth intervals, our observations can be used to more precisely constrain the depth habitat of individual species. The observed habitat of *G. ruber* within the mixed layer, a broader habitat of *G. calida* and *G. siphonifera* extending below 100 m (Figs 5 and 6) and a deep habitat of *G. crassaformis* restricted to below 100 m in (sub)tropical regions are in agreement with recent observations from the low-latitude Atlantic Ocean (Rebotim *et al.*, 2017; Jentzen *et al.*, 2018). The observed vertical habitat of *G. glutinata* in the top 50 m is more confined than in the observations by Rebotim *et al.* (2017), but these authors note that the habitat becomes shallower in warmer waters, as in our area and also in the Gulf of Mexico (Jentzen *et al.*, 2018). The observed well-defined depth habitat around 100 m for *O. universa* (Figs 5 and 6) coincides with the DCM (Fig. 3), consistent with earlier observations in the Panama Basin (Fairbanks and Wiebe, 1980), but contrasts with observations in the subtropical-temperate eastern North Atlantic (Rebotim *et al.*, 2017) and in the Gulf of Mexico (Jentzen *et al.*, 2018) where this species was found above the DCM. Such discrepancy may reflect different depth habitats among the three cryptic species of *O. universa*, the state of the population at different times in its ontogeny (assuming synchronized reproduction) or regional differences in the depth habitat because its ecological optimum (e.g. light, temperature, food availability) is reached at different depths for different locations. Thus, our observations cannot be used to infer a consistent relationship between *O. universa* and the DCM.

Taken together, our observations of habitat depths are consistent with the existence of species-specific vertical habitats that are locally stable but may differ between regions and oceanic basins as well as seasonally. This means that individual species of planktonic foraminifera occupy preferred positions on a regional scale in the water column that remain stable over a day and thus possess some mechanism for buoyancy regulation. This mechanism cannot be such that it provides a species with a given buoyancy, because of the observations of different preferred depths under different environmental conditions irrespective of absolute ambient sea water density values (Rebotim *et al.*, 2017). Also, the buoyancy regulation must to some degree occur actively or else it would not be possible for the foraminifera to

achieve an abundance maximum within an essentially mixed surface layer (Fig. 3).

If planktonic foraminifera do not participate in DVM, then it has to be considered how previous observations suggesting this pattern in the group can be explained. We have no reasons to doubt the validity of observations of higher standing stocks in surface to subsurface waters during the daytime by Rhumbler (1911) or the consistently higher foraminifera concentration in day tows by Bé and Hamlin (1967) or the day-night variability in abundances of some species as reported by Berger (1969). Instead, we believe that the details in these three examples are already hinting at the answer. In each of the three studies, the DVM pattern was different (different timing and direction). This inconsistency could instead of DVM rather hint at the existence of significant lateral variability in species abundance, which has been consequently translated into variability in time during sampling. Indeed, such spatial variability is also present in our observations (Figs 4 and 6).

The high variability of planktonic foraminifera concentrations we observe horizontally in the confined sampling area corroborates the observations by Boltovskoy (1971) who noted a shift in foraminifera concentrations from 2.2 to 198.2 ind. m^{-3} within 1 nautical mile in the South Atlantic, and the observations by Bé and Hutson (1977) made *in situ* while deep diving. Such high variability is consistent with the concept of patchiness in plankton distribution (Mackas *et al.*, 1985). The patchiness we observe occurs on the scale of kilometers is not entirely random in space and the abundance patterns appear coordinated among some species in some casts but not in others (Fig. 6). These observations suggest that foraminifera concentrations depend locally not only on trophic conditions and physical properties of the environment but also reflect other factors that are either unsatisfactorily resolved such as migration during the reproductive cycle, random or yet unknown. Our observations indicate that in planktonic foraminifera, patchiness occurs mainly laterally, not vertically, as manifested by differences in concentration ranging over two orders of magnitude on small spatial scales. This is sufficient to generate variability in repeated vertical casts that is large enough to be mistaken for vertical migration, providing a likely explanation for previous observations that would support DVM in living planktonic foraminifera.

CONCLUSIONS

Using 41 continuous vertically resolved plankton tows taken in a confined area in the subtropical eastern North Atlantic Ocean and sampling the same water column structure we investigated whether planktonic foraminifera participate in DVM. Living planktonic foraminifera abundances were low (median = 31.3 ind. m^{-3}) but highly variable (4–331 ind. m^{-3}). ADCP measurements showed that large zooplankton take part in the DVM and vertically migrate every day. However, analyses of vertical profiles of cell densities indicate that planktonic foraminifera do not participate in DVM and individual species occupy well-defined depth habitats. Our dedicated sampling effort thus brings additional arguments to settle the debate on the occurrence of DVM in planktonic foraminifera in the oligotrophic area of the subtropical eastern North Atlantic we studied. Our observations also indicate that within their stable depth habitats, planktonic foraminifera species abundances may show large horizontal variability, indicating the possible existence of patchiness that could well be the reason DVM has been suspected to occur in planktonic foraminifera for decades.

SUPPLEMENTARY DATA

Supplementary data are available online at the *Journal of Plankton Research* website.

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AUTHOR CONTRIBUTIONS

M. S., M. F. G. W., L. J., R. M., U. B., A. B., J. B., G.-J. B., P. D., T. F.-E., J. G., L. M., P. M., M. C. R., C. S., H. T., G. T., M. K. and J.M. participated in samples collection. M. S. and L. J. conceived the sampling

design and M. F. G. W. and J. M. performed the statistical analyses. J. M. did planktonic foraminifera taxonomy and wrote the manuscript with the help of L. J., R. M., M. S. and M. K. All authors read, commented and approved the final manuscript.

DATA ARCHIVING

Total counts, species concentrations and filtered volumes are available digitally online through supplementary materials. CTD and ADCP data will be made available on request to the main author until their online publication on PANGEA (www.pangea.de).

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