

Modern planktonic Foraminifera: migrating is not enough

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Biological Sciences - Article

Keywords: Planktonic Foraminifera, Ocean acidification, Ocean warming, Vertical and spatial migrations, ecosystem collapse, biodiversity shifts, Ecological niche adaptation

Posted Date: October 27th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-3485983/v1>

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Additional Declarations: There is **NO** Competing Interest.

Abstract

Anthropogenic activities, in particular rising CO₂ emissions, provoke ocean warming and acidification^{1,2}, altering plankton habitats and threatening calcifying species^{3,4} such as planktonic Foraminifera (PF). Whether they can cope with these unprecedented rates of environmental change, through lateral migrations and vertical displacements, is unresolved. Here we show, using over a century of data from the FORCIS⁵ global census counts, that PF display evident poleward migratory behaviours, increasing their diversity at mid to high latitudes, and for some symbiont-barren species descending in the water column. Global PF abundance decreased by 24.24±0.11% over the last decades. Beyond lateral migrations⁶, our study uncovers intricate vertical migration patterns among PF species, presenting a nuanced understanding of their adaptive strategies. In projected temperature and carbonate saturation states for 2050 and 2100, low-latitude PF species will face physico-chemical environments that surpass their current tolerance. While these species might replace high-latitude ones through poleward shifts, this would radically alter low-latitude ecosystems. Our insights of PF adaptation during the Anthropocene reveals that 'migration is not enough', and has broader implications for the evolution of marine biodiversity under multiple stressors.

Introduction

Ongoing anthropogenic carbon dioxide (CO₂) emissions are warming and acidifying the oceans^{1,2}, increasing marine temperature, water stratification, and altering ecological niches⁷. Ocean warming has already induced changes in planktonic habitats due to the inability of plankton to adapt fast-enough to physiological stress^{6,8,9}. These effects are exacerbated for organisms producing a calcium carbonate shell, as acidification impedes calcification faster than warming favours it^{4,10}. Similar environmental crises occurred in the geological past, albeit at much slower rates, e.g. during the last deglaciation and the onset of the Holocene, with marked surface waters acidification¹¹. Predictive models suggest that future warming and acidification will escalate, with negative ecological consequences for calcifying plankton¹²⁻¹⁴, with plankton communities shifting polewards^{15,16}. However, the capacity of plankton to acclimate to ongoing (i.e. on decadal timescales) changes, and to migrate in three dimensions, is until now untested, due to the previous lack of spatially and vertically resolved time series.

Among zooplanktonic groups, planktonic Foraminifera (PF) are ubiquitous calcifying micro-organisms, whose global distribution and fossil record make them an ideal model to bridge the geological and historical records of biodiversity. The displacement of PF over the last deglaciation (20-12 kyr ago) shows a spatially heterogeneous pattern, highlighting the complex response of PF communities, and rendering straightforward prediction of future changes difficult¹⁷. The adaptation of PF eco-groups during the climate transition from the Last Glacial Maximum to the pre-industrial period is shown plausible through modeling and the fossil record, but the current rate of change exceeds that of the deglacial by orders of magnitude¹⁸.

To investigate historical changes at the global scale, we make use of a census and synthesis of different biodiversity metrics of PF since the 1910s^{5,19}. We aim to elucidate the responses of PF communities to direct anthropogenic impacts by assessing interdecadal behavioral changes under ongoing environmental change. Specifically, we evaluate diversity changes and PF migrations, in three dimensions. By exploring these migrations together with environmental stressors, temperature and ocean acidity, we provide a comprehensive overview of PF adaptive strategies in an evolving ocean. Furthermore, through simulations of future environments, we probe the potential trajectories and adaptive capacities of these species, and more broadly, for marine ecosystems.

Results And Discussion

Shift in latitudinal diversity gradient

The effects of anthropogenic changes on plankton can be investigated through the analysis of long-term time series of observations^{20,21}. The FORCIS database comprises approximately 188,000 PF subsamples drawn from oceans across the globe since 1910^{5,19}. Specifically, regional data from the North Atlantic Ocean stands out for its remarkable temporal and spatial resolution, boasting PF time series that extend, locally, over half a century (Extended Data Fig. 1).

Atlantic mid-latitudes (30°N to 50°N) emerge as a key biodiversity hotspot, containing a wide spectrum of subtropical and temperate species (Fig. 1A), although reported measured abundances are not particularly high (Extended Data Fig. 2). When comparing the species diversity of modern PF samples taken from the water column in the FORCIS database with the species diversity of PF samples from surface sediments (ForCenS database²²), an evolution in the latitudinal diversity gradient during the early Anthropocene is revealed (Fig. 1B and Extended Data Fig. 3). Over the last century, species diversity in the mid to high latitudes has slightly exceeded pre-industrial levels, with 3 to 24 species (between 48° to 80°N), compared to 4 to 18 species in pre-industrial times (Fig. 1B). Excluding samples with only a single adult specimen, which may be artifacts resulting from the transport of dead individuals from elsewhere, modern diversity surpasses pre-industrial levels by up to 10 species in the modern North Atlantic and Pacific regions (Extended Data Fig. 3).

Several PF species show a poleward shift between the preindustrial (ForCenS database) and the modern era (FORCIS) (Extended Data Fig. 4), implying a change between Holocene and modern distribution patterns. Notably, *G. scitula*, a mixed-layer dweller in the temperate oceans, has expanded its modern ecological niche in FORCIS, now appearing at high latitudes (80°N) (Extended Data Figs. 4 and 5). In addition, post-1995, many low-latitude species began to decline, likely due to higher temperatures, leading to reduced diversity and a shift in the assemblage (Extended Data Fig. 6).

This mirrors a decline in equatorial diversity in the pre-industrial era²³, and diminished diversity in warmer low-latitude waters affecting PF distribution²⁴. This shift is consistent with long-term changes in biological assemblages, as predicted by several modeling studies^{18,25,26}. Such biogeographic shifts are in

line with the spatial changes observed in various other marine and terrestrial species, seemingly influenced by increasing temperatures, particularly in the Northern Hemisphere^{9,13,27–29}. Temperature not only shapes plankton distribution in lower latitudes, but also impacts PF species distribution and diversity via its effect on food supply³⁰.

Spatial and vertical migration and changes in ecological niches

The erosion of biodiversity observed in the low latitudes appears not to be linked to the trophic preferences of PF groups. PF species with or without photo-symbionts (symbiont bearing and symbiont-barren), spinose and non-spinose, tropical and subtropical alike are shifting towards poleward habitats (Extended Data Fig. 7). Only two species (*P. obliquiloculata* and *G. ruber ruber*) have a steady distribution through the last century (Extended Data Fig. 7). Prominent species such as *G. inflata*, *G. rubescens*, *N. dutertrei*, and *G. cultrata* have migrated poleward on average at a pace of about 10.28 km/year. Species such as *G. scitula*, *T. sacculifer*, and *G. ruber* display a poleward shift ranging between 4.11 and 10.28 km/year. Marine species, particularly ectotherms, have been shown to migrate polewards at speeds between 5.92 ± 0.94 km/year³¹ and 7.20 ± 1.35 km/year⁹, outpacing terrestrial species that migrated polewards at about 1.11 ± 0.96 km/year³¹. This migration is consistent with recent modeling work¹⁵, who predicted a median poleward migration speed of 3.5 km/year for all plankton. The upper limit of the PF poleward migration speed (10.28 km/year) corresponds exactly to the pace of thermal shifts of the oceanic isotherms (about 10 km/year)³². This strongly suggests that PF closely tracks warming fronts, outpacing other planktonic groups.

A unique feature of the FORCIS database is the possibility to track vertical changes in the planktonic distribution over time and at the species level. At low latitudes, only 3 species appear to descend to greater depths over the past decades, the most robust signal being the 45 ± 21 m vertical deepening, between samples taken before and after 1997, for the symbiont-barren species *G. crassaformis* (Fig. 2A). In the temperate North Atlantic, there is a statistically significant deepening in the vertical distribution of 5 species, particularly for thermocline-dwelling species such as *N. dutertrei* (20 ± 5 m-deepening before and after 1997), *G. inflata* (30 ± 5 m), and *O. universa* (40 ± 3 m) (Fig. 2B). For mid-latitude symbiont bearing PF species, 6 out of 8 species show no significant vertical migration. Therefore, the trophic regime of PF species appears to constrain the vertical distribution changes of species in the North Atlantic.

Regional and vertical shifts in the PF distribution underscore how symbiont bearing and symbiont-barren species respond to evolving environmental stressors. In the mid-latitudes, tropical and subtropical symbiont bearing species thrive in shallow-water masses, following the latitudinal shift of surface conditions towards low-turbidity waters (Fig. 2B). The vertical descent of certain species, whose habitats align with the deep chlorophyll maximum, matches the anthropogenically driven deepening of the thermocline⁷. While specific cases exhibit notable vertical migrations, a comprehensive analysis of the PF in the FORCIS database indicates limited changes in overall vertical distribution where most of the PF species were not showing a deepening in their depth habitat. This suggests that vertical migration is influenced by the trophic regime of each species, and in any case slower than the deepening of isotherms,

estimated at -6.6 ± 18.8 m/decade between 1980 and 2015, predicted to accelerate to -32 m/decade by the end of the century under a high emission scenario³³, which we speculate will limitate the ability of PF to survive or reproduce in these warmer environments.

Decline in planktonic Foraminifera abundance

The latitudinal shift in diversity, and the restricted vertical descent of PF, shows the limits of their ability to respond to environmental changes. Yet quantitative analysis of abundance should indicate whether their phenotypic plasticity is broad enough to adapt to anthropogenic changes in one location. Our data reveal a gradual decrease in surface and subsurface PF abundance across the different latitudinal bands in the North Atlantic and Arctic Oceans, over the past decades, statistically significant between 0 and 50°N (Fig. 3). This abundance decrease is most pronounced in low to mid latitude regions (5.5 ± 0.05 % for 0 to 30°N, and 24.24 ± 0.11 % for 30 to 50°N, between 1950 and 2018) (Figs. 3A,B; Extended Data Fig. 8), where the decline in abundance is particularly acute for subtropical and temperate species. These trends are even stronger when we include the sparse data prior to 1950 in the low latitudes, (0 to 30°N), with an abundance decline reaching 42.08 ± 0.15 % from 1940 to 2018. Even though early (pre-1960s) census data are rare, the post-1960s data show a decline in abundance statistically significant and robust for 14 out of 26 species (e.g., up to 80 ± 0.3 % decline between 1950 and 2010 for the subtropical species *G. siphonifera*). This general decline in PF abundance resembles the trends observed in other pelagic species³⁴ and, specifically in other zooplanktonic groups, such as copepods²⁵. For example, copepod assemblages have undergone notable biogeographical shifts over the past few decades, including a significant overall reduction in the presence of colder water copepod species²⁵. These findings indicate an overall habitat change of marine plankton, especially in the context of PF abundance variations across latitudinal bands and time.

Whereas the abundance of *G. glutinata*, and *G. ruber ruber* increased in low latitudes since 1940, an increase in *G. uvula* occurred in high latitudes (Figs. 3A and 3C). In contrast, *T. sacculifer* numbers decreased in mid latitudes (Fig. 3B). Two different concurrent processes may explain this: first, the increased calcification cost due to acidification affects predominantly non-spinose species, which provides an advantage to smaller species such as *G. uvula* and *G. glutinata*³⁵; second, this expansion could be attributed to *G. uvula*'s wide range of temperature tolerance^{36,37} (Extended Data Figs. 4 and 5). Overall, the response of PF species to anthropogenic changes shows a muted vertical habitat shift, differentiated on trophic regime, a latitudinal poleward shift tracking the rate of changes of temperature fronts, and a general abundance decline reflecting their limited plasticity to evolving environments.

Evolving ecological niches

Species-specific ecological niches of marine biota are undergoing worldwide shifts due to warming and ocean acidification, partly resulting from anthropogenic CO₂ emissions^{6,38}. We use the saturation state of seawater for calcite (Ω_{calcite}), as a metric for ocean acidification. Examining prevalent PF species from three latitudinal North Atlantic range bands, we find their current habitats cover temperature and Ω_{calcite}

spans that largely align with, or exceed, projected mid-to-end-century changes under a realistic, “middle-of-the-road” scenario (SSP 2 - 4.5). These species typically thrive across broad 5–10°C and 1–2 Ω_{calcite} unit ranges, suggesting potential adaptability to future niche shifts (Fig 4A-F). Notably, species like *G. bulloides* exist today even in areas where Ω_{calcite} is below 1. A broader analysis indicates PFs are rather eurytherm and support rather wide temperature ranges, yet with species-specific temperature optima and distribution patterns (Extended Data Fig. 5).

Visualizing ecological niches in a 2-dimensional (Ω_{calcite} and temperature) space (Fig. 4G-I), each species occupies a much narrower niche. The trajectory of these regional niches is predicted for future simulated climatic scenarios, and the temperature and Ω_{calcite} plotted in relation to the current distribution of PF per latitudinal bin (Fig. 4G-I). Our results show that by 2050 most tropical locations will fall outside of current PF-ecological niches. This would be the case for abundant species such as *G. ruber*, *T. sacculifer*, *G. bulloides*, and *G. glutinata* in the tropical and subtropical North Atlantic (0-30°N). Due to the combination of warmer temperatures and lower saturation states, conditions in the tropical Atlantic in 2050 and 2100 will be unlike any inhabited by PF today. It is likely that conditions such as this, with higher SSTs and lower Ω_{calcite} than anywhere present on Earth today, have persisted in the geological past, but with different PF communities. Our knowledge about past analogues is still limited, but (less-)rapid warming has driven whole PF genera to extinction in the past (e.g.,³⁹) (Fig. 4G). By 2050, assuming non-adaptive responses of the PF species, a significant latitudinal migration is projected from low to mid-to-high latitudes, devoid of any known compensatory PF species replacements.

Our observations are in agreement with modeling studies^{14,18}. For instance, Roy et al.¹⁴, using FORAMCLIM model future simulations, showed that PF abundance and diversity are projected to decrease in the tropics and subpolar regions and increase in the subtropics and polar regions. In the mid and high latitudes, key PF species dwell in low temperature and saturation waters, warming and ocean acidification are unlikely, bringing those regions outside of the current zone of PF ecological niches by 2100. More likely, by 2100, mid and high latitude regions may switch from a species niche to another (Fig. 4H,I). There, current PF communities are likely to be replaced by other PF species adapted to warmer environments, as it is already observed through poleward migrations over the last decades.

Such a dramatic extirpation of PF species from the tropics under the predicted, and already observed decline in Ω_{calcite} , particularly evident in high latitudes⁴⁰, does not necessarily imply the total absence of those species. Ultimately, this could lower calcification rates, or limit calcification entirely, leading to the emergence of shell-less PF. Studies by Evans and Erez⁴¹ confirmed that two PF species, *G. ruber* and *G. siphonifera*, can survive, recalcify, and adapt to low pH conditions in culture post-shell dissolution. Shell-less, benthic Foraminifera, or Monothalame, have demonstrated survival and proliferation in sediment, even under low pH conditions^{42,43}. Recalcification of dissolved foraminiferal tests has been validated in both field and laboratory conditions^{44–46}, suggesting that PF could live shell-less in low Ω_{calcite} regions as predicted based on future scenarios (Fig. 4). However, it remains unclear whether they can reproduce under such conditions. Reduced calcification would affect marginally the CaCO_3 cycle, as about 0.1% –

3.8% of the global surface carbonate fluxes in the modern open-ocean originates from PF⁴⁷. Although past large-scale acidification events in Earth history (e.g., the PETM,⁴⁸) have not shown significantly altered long-term calcite fluxes to the seafloor, the exceptional magnitude and pace of the current acidification, combined with other potential stressors, means that PF are entering an uncharted era of environmental changes, and that a global-scale negative impact on calcification is plausible¹⁸.

Our study shows that PF cannot adapt, on decadal timescales, to current anthropogenic environmental changes, and respond largely by declining abundances and latitudinal migration. Notably, their vertical descent is limited in the low to mid latitudes. Projections of future environmental changes on modern PF niches forecast their relative disappearance from low latitudes, raising the question of their adaptability to unprecedented changes. Thus, for modern planktonic Foraminifera, 'migration is not enough'.

Methods

1. Data

The data is sourced from FORCIS^{5,19} and ForCenS²² databases covering the post-industrial and the preindustrial time-periods, respectively. Seasons for both databases were distinguished between the Northern and Southern Hemispheres and follow the meteorological seasons. For the Northern Hemisphere autumn is defined by September, October, November; winter by December, January, February; spring by March, April, May and summer by June, July, August. For the Southern Hemisphere, spring is defined by September, October, November; summer by December, January, February; autumn by March, April, and winter by June, July, August.

1.1 FORCIS database (post-industrial)

More than 188 000 subsamples (one single plankton aliquot collected within a depth range, time interval, size fraction range, at a single location) coming from ~163 000 samples collected from different oceanographic environments by plankton nets (~22 000 subsamples from ~6 000 samples), Continuous Plankton Recorders (CPR) (~157 000 subsamples), sediment trap (~9 000 subsamples), and plankton pump (~400 subsamples) from the global ocean (Extended Data Fig. 1), were extracted from the FORCIS database^{5,19}. This data include literature published and unpublished data between 1910 and 2018. Total abundance of the PF and species-specific counts for these samples were extracted from FORCIS.

1.2 ForCenS database (pre-industrial)

Around ~5 000 samples covering the preindustrial period are presented in the ForCenS database²² of PF census counts in marine surface sediment samples. This database only includes samples larger than 150 µm diameter. In our study, species abundances were normalized at 0 and 1 for the species absence and presence, respectively.

2. Data and taxonomy harmonization

To perform data harmonization and address methodological and taxonomic biases, we converted the abundance data extracted from FORCIS into number concentration (individuals/m³). Specifically, where coarse fractions were sampled using a mesh size greater than 100 µm, we employ the approach described in⁴⁹ to standardize them. This allows us to estimate the number concentration of the coarse fractions down to 100 µm to a high degree of accuracy, based on field calibration, and reconstruct the assemblage as it would have appeared if the material had been sampled with a 100 µm net. Predicting the abundance of very small or rare species is still challenging, and those data are not interpreted here.

Moreover, the FORCIS dataset has been assessed and corrected for taxonomic discrepancies over time⁵, and though some species might have been misidentified, it appears quite unlikely as overall mostly large PF, whose taxonomy is easier to identify, were collected in the early part of the record (i.e., due to large net mesh sizes in the 1960s). All species counts were generated based on the different taxonomies (Lumped and validated taxonomies) proposed by the FORCIS group⁵ and based on the analysis requirement. In this study, several morphospecies were grouped together for analysis such as *G. ruber* (*G. ruber albus* and *G. ruber elongatus*), *G. truncatulinoides* (*G. truncatulinoides* left and *G. truncatulinoides* right) and *T. sacculifer* (*T. sacculifer* no sac and *T. sacculifer* sac). Because of species-specific habitat preferences, the species provinces of the PF assemblages are defined for seven different groups (Supplementary Tab. 1) tropical, subtropical, temperate, subpolar, polar and global species³⁰. Additionally, they were also split into 3 groups based on their food preference regime: symbiont bearing, symbiont-barren and facultative following the work of Takagi et al⁵⁰.

3. Data analyses

To correct for the sampling biases, we employ several techniques (1) Some analyses were focused on latitudinal bands to dilute the effect of under-sampled regions through time. Latitudinal bands were selected according to assemblages' provinces and based on Schiebel and Hemleben⁵¹. (2) Sample depth selection was limited for most of the analysis to the depth where most of the individuals are thought to be alive so as to not confuse between depth habitat and post mortem collection. (3) Most of the analyses were limited to the spring to summer blooms in the North Atlantic Oceans where the sampling coverage and number of samples are highest (Extended Data Fig. 1). (4) Number concentrations were standardized from 0 to 1 to correct for the number of samples and enhance the visualization in heatmaps. (5) To analyze the first and second halves of the dataset, cut-offs were defined between 1990 and 2000, with the precise date depending on the number of samples selected. This allows intercomparison of datasets with similar amounts of information. The mean point of all the net derived data is January 1995.

3.1. Environmental data

Temperature and Ω_{calcite} estimates associated with each PF North Atlantic sample (Fig. 4) were taken from the IPSL-CM6A-LR global climate model⁵¹, in its CMIP6 historical simulation, version r22i1p1f1, with a monthly resolution. The model output was converted to the World Ocean Atlas spatial grid, with a 1x1°

resolution. Ω_{calcite} was computed by dividing the modeled in situ carbonate ion concentration (denoted *co3* in the CMIP6 nomenclature) by the carbonate ion concentration at saturation with respect to calcite (denoted *co3satcalc*). Temperature and Ω_{calcite} were then associated with each sample of the FORCIS database by linearly interpolating the model output temperature to the latitude, longitude, depth and time of sampling. For multinet, CPR and pump data, we used the averaged sampled depth. For time series (Fig. 4A-F), we average the data annually, and over the latitudinal ranges in the Atlantic, but only considering values that correspond to locations where a PF sample is present. Then, at the locations and depths corresponding to each PF sample, we extracted from the IPSL-CM6A-LR “SSP 2-4.5” simulation which corresponds to future predictions in response to atmospheric CO₂ growth trajectories corresponding to the SSP2-4.5 “middle-of-the-road” scenario, to calculate how temperature and Ω_{calcite} would change throughout the 21st century.

3.2. Biodiversity change

Species richness was calculated within each 3° latitude by 6° longitude box and time for each profile, considering data from plankton net, pump, CPR, and sediment trap samples in FORCIS (Fig. 1A). The species richness in ForCenS was determined by calculating the number of species present in each sample and latitude, and compared to the ones obtained from FORCIS (Fig. 1B). These analyses focused on 26 species that were found in both ForCenS and FORCIS, using the same taxonomic criteria. Species that were absent in ForCenS, such as *B. variabilis*, *T. fleisheri*, and *T. parkerae*, were not considered as a comparison between the datasets is impossible. In a second step, the assessment aimed to determine any species loss or gain from the preindustrial to the postindustrial period. For this analysis, the diversity in FORCIS and ForCenS was evaluated within each 4.5° latitude by 9° longitude box and time, considering data from plankton net, pump, CPR, and sediment trap samples in FORCIS, as well as each sample in ForCenS. The species richness in FORCIS was subtracted from that in ForCenS within each grid to identify any changes (loss or gain) in species richness. This analysis focused on the major species (26 species) on a presence / absence basis (Extended Data Fig. 3).

3.3. Number concentration changes

3.3.1. Changes through time

The total number concentration of PF is first determined and normalized from 0 to 1 for each species collected using the plankton net, plankton pump and CPR and from 0 to 200 m depth from the North Atlantic to the Arctic Oceans at each latitudinal band of a resolution from 20 to 40°N (from 0 to 30°N; 30 to 50°N and 50 to 90°N) and per decade, to assess its temporal variation per decade since 1940 (where data density becomes sufficient for valid conclusions to be drawn) (Fig. 3). To investigate whether there were significant changes in the number concentration of different species within each latitudinal band, an analysis of variance (ANOVA) was conducted. The ANOVA calculates a p-value, which indicates the probability of observing the differences in number concentration between species by chance alone. A low p-value (below 0.05) suggests that the observed differences are unlikely due to random variation and are

more likely to represent real change. Then, similarly to the above analysis, number concentration of the different species collected using plankton net and pump only and at a larger depth range between 0 and 300 m from the North Atlantic to the Arctic Oceans and at each latitudinal band of a resolution from 20 to 40°N and for each species was assessed (Extended Data Fig. 8).

3.3.2. Changes through latitude

For the data presented in Figure Extended Data Fig. 2, only studies that provide species counts in the North Atlantic, Antarctic, and/or Arctic Oceans, using data sourced from the FORCIS database were considered as they present the best temporal and spatial data coverage. The selected studies cover the period from 1980 to 2018 (Extended Data Fig. 2). The depth profiles of these data range from 0 to more than 100 meters. To examine the latitudinal abundance trend of PF species over time, the surface data (up to 100 meters) and deep-water samples (beyond 100 meters) from 1980 onwards against latitudes grouped in 10-degree intervals are plotted. This analysis specifically focuses on the spring and summer seasons, which are best documented by data.

3.4. Spatial and vertical migration of planktonic Foraminifera

The species' poleward migration was first assessed within the FORCIS database. Thus, the loss and gain of species in the northernmost limit of the North Atlantic and Arctic Oceans is assessed on the PF living at depth ranges between 0 and 100 m during spring and summer before and after the cut-off year (1990). The maximum latitude of the northernmost 5% samples was calculated for all species before and after 1990e. The difference between the maximum latitude before and after 1990 was evaluated to assess the direction and magnitude of the latitudinal migration of the different species (Extended Data Fig. 7). The selection of various cutoffs for spatial migration is influenced by the quantity of data available both before and after applying specific filters that are sometimes very few between 1910 and 1970.

Analyses were complemented by assessing the vertical migration of the PF through the water column. It was assessed for each latitudinal band of a resolution about 20 °N to 40°N (Fig. 2). Only multinet data sampled across the upper 200 m and at profiles presenting 5 samples and the same sampling resolution (e.g., depth separations) during both spring and summer were selected. The data mainly covers the North Atlantic and Arctic Oceans between 1980 and 2018. The depth at maximum of abundance was calculated at each profile and for each species and then the results were compared for before and after the cut-off year (1997) (Fig. 2). To assess whether there were significant changes in depth at the maximum abundance of different species within each latitudinal band and through time, an ANOVA test was conducted.

Declarations

Data availability

The FORCIS database used for this paper is available on Zenodo through <https://zenodo.org/record/8186736>.

ForCenS database is also available from <https://doi.pangaea.de/10.1594/PANGAEA.873570>.

Code availability

Codes to harmonize the number concentration data were sourced from <https://zenodo.org/record/7437720>.

All codes used for data analysis and generation of figures related to this article can be accessed on Zenodo at <https://doi.org/10.5281/zenodo.8409865>

Acknowledgements

The FORCIS project is supported by the French Foundation for Biodiversity Research (FRB) [<https://www.fondationbiodiversite.fr/>] within the Centre for the Synthesis and Analysis of Biodiversity (CESAB) [<https://www.fondationbiodiversite.fr/la-fondation/le-cesab/>] and co-funded by INSU LEFE program, and the Max Planck Institute for Chemistry (MPIC) in Mainz, Germany.

Author contributions

The study was designed by S.C., T.G., R.S., J.M., O.S., T.C., G.B. and G.M. during the FORCIS project workshops at FRB-CESAB. All authors contributed to the interpretation and discussion of the results. S.C. carried out the data analysis and wrote the paper with contributions from T.G., R.S., J.M., O.S., T.C., G.B., G.M., X.G., H.H., N.C., A.K. and G.B. Figures and statistical analyses were generated by S.C., O.S. and T.C.

Funding

Open access funding provided by CEREGE in Aix-en-Provence, France, and MPIC in Mainz, Germany.

Competing interests

The authors declare that they have no conflict of interest.

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Figures

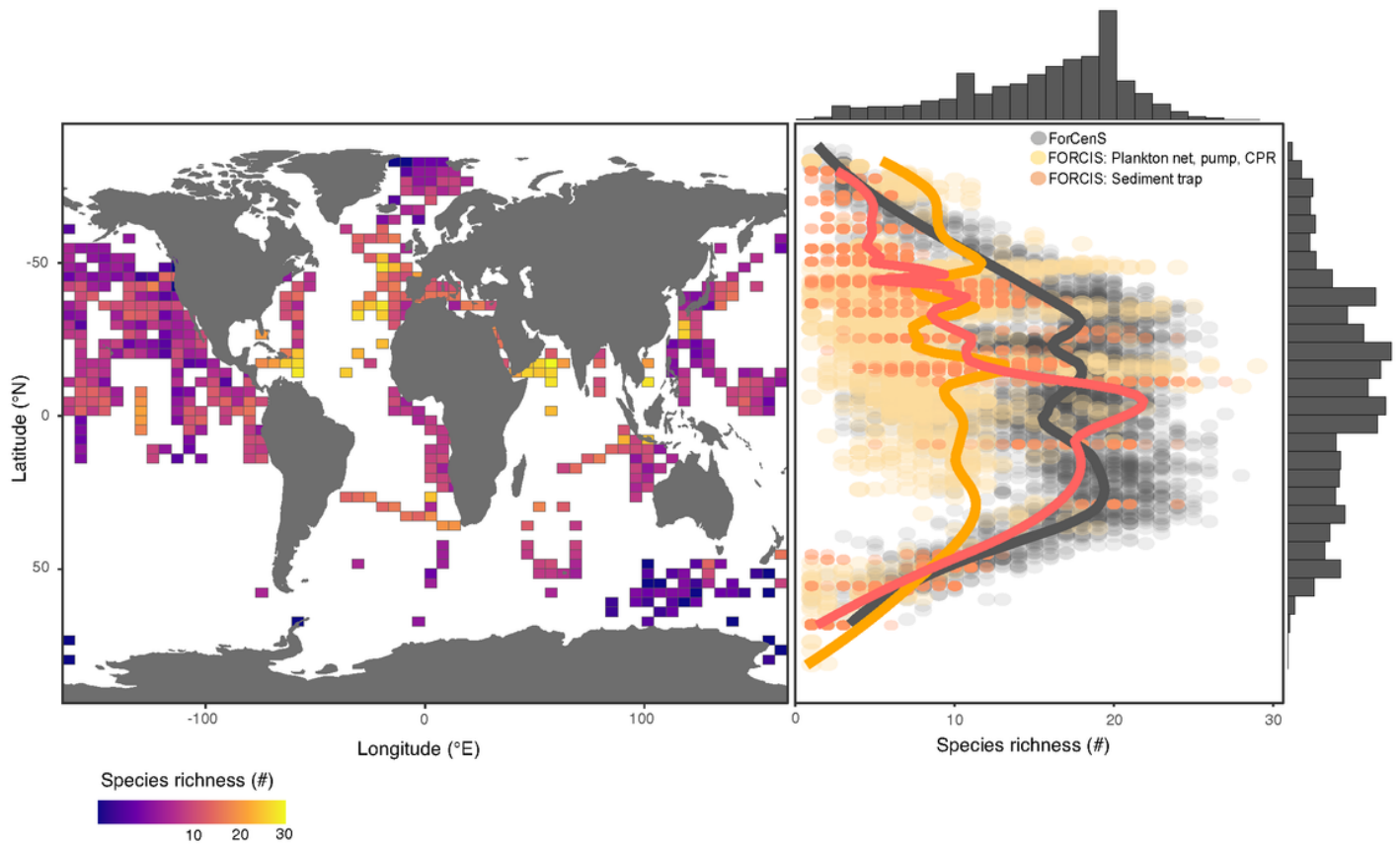


Fig. 1

Figure 1

Diversity Changes in Planktonic Foraminifera: (A) Map of diversity of planktonic Foraminifera (number of species using the compiled taxonomy⁵), and **(B)** Comparison of pre-industrial diversity inferred from surface sediment ForCenS database with living planktonic Foraminifera FORCIS database over the last 100 years fitted by a LOESS smoothing curve (gray line: ForCenS data; orange line: FORCIS sediment trap data; yellow line: FORCIS plankton net, pump and CPR data). The number of total observations in FORCIS and ForCenS together for each latitudinal bin (each 6°) and each species richness level are presented in the histograms.

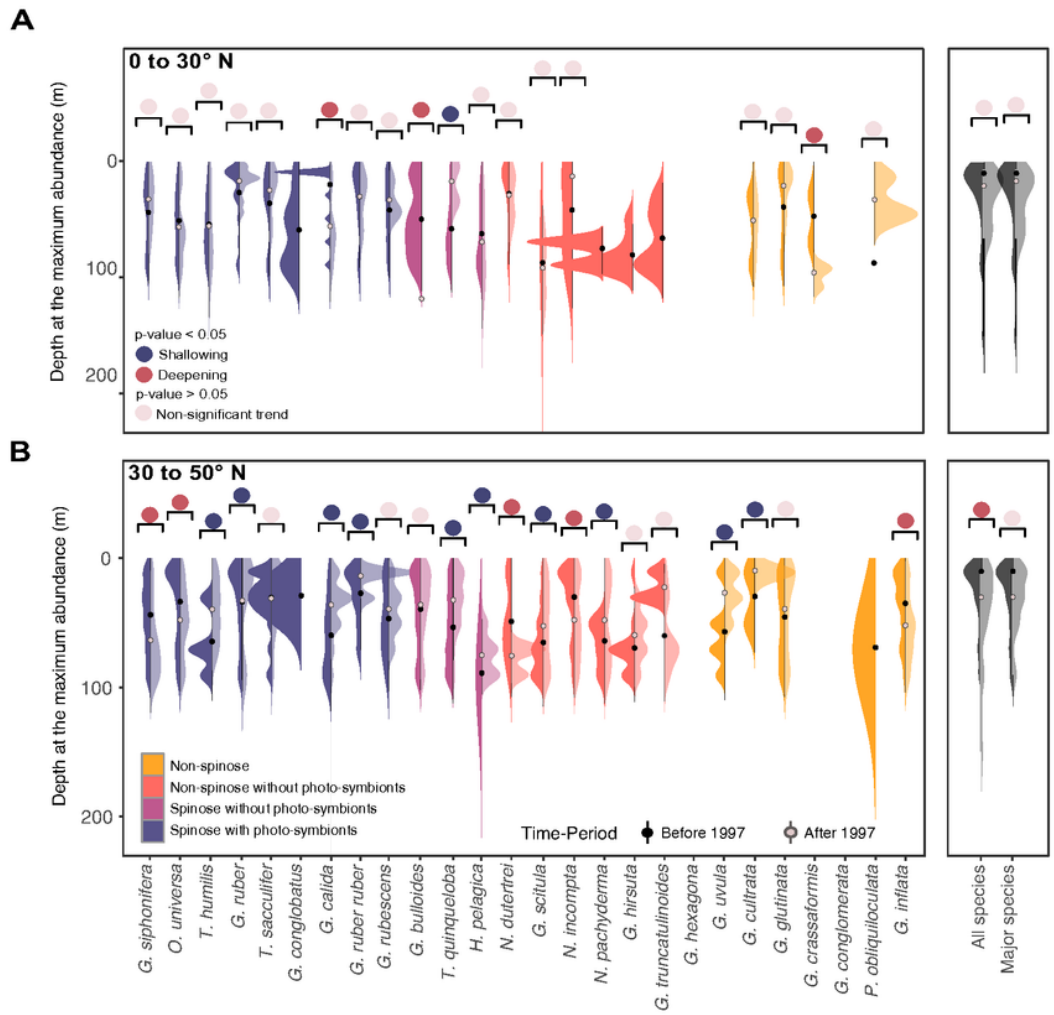


Fig. 2

Figure 2

Vertical Distribution of Planktonic Foraminifera in the surface ocean: Calculated depth of the maximum abundance before (dark colored half violin plot) and after (light colored half violin plot) 1997. Data on the planktonic Foraminifera are from samples collected with plankton nets during spring and summer from the North Atlantic and Arctic Oceans, between 0 to 200 m water depth, from **(A)** 0 to 30°N and **(B)** 30 to 60°N. The black and gray dots show the mean water depths at the maximum abundance for before and after 1997, respectively, and bars give the standard deviation. The p-value obtained from the ANOVA test is reported by coloured circles above each violin plot (light pink: non-significant trend; red: significant deepening; blue: significant shallowing).

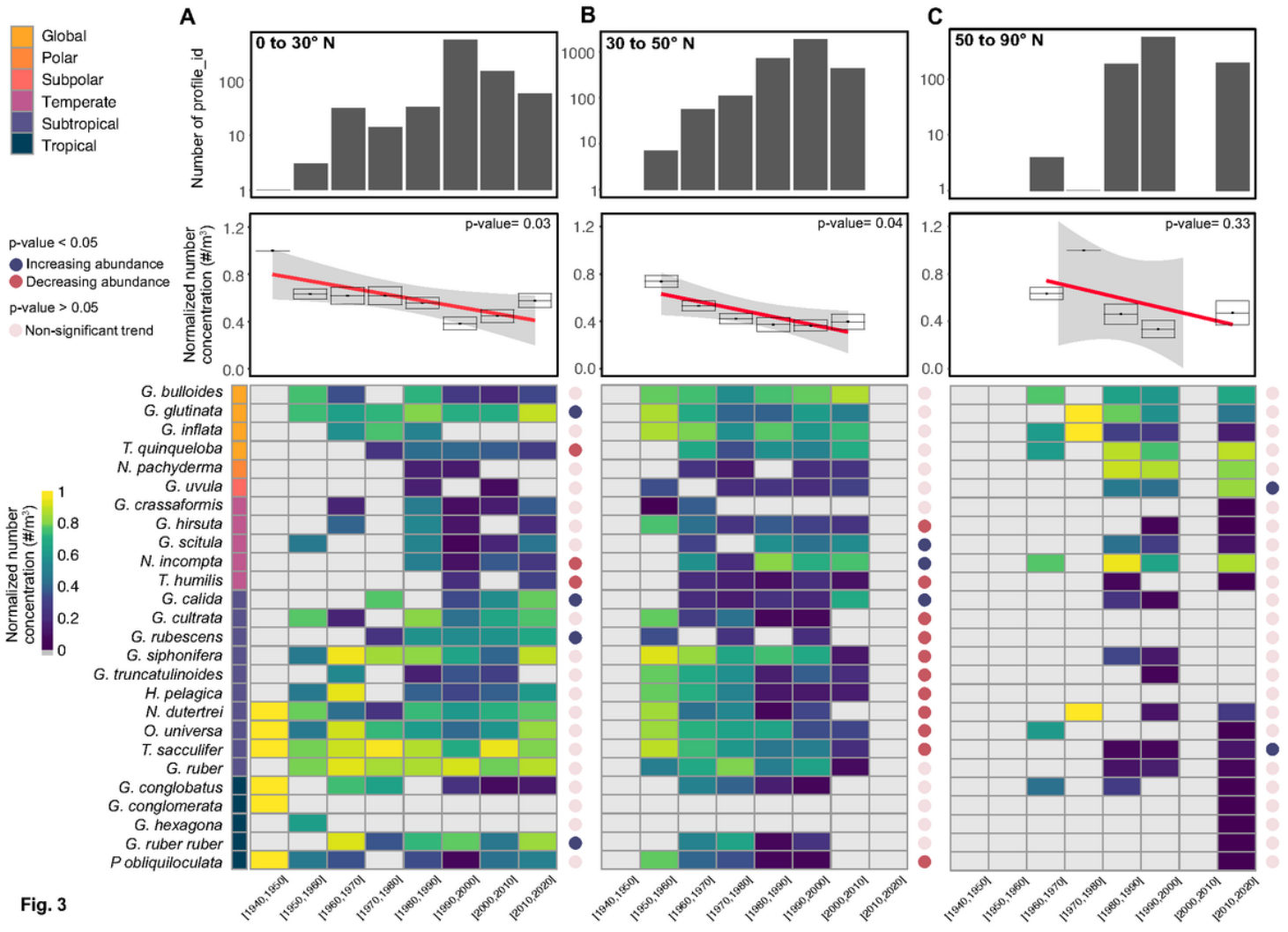


Fig. 3

Figure 3

Temporal Variations in Planktonic Foraminifera Number Concentration: Heatmaps showing the normalized number concentration of the different modern planktonic Foraminifera species in FORCIS collected using the plankton net, plankton pump, and CPR from the Arctic and North Atlantic Ocean, from 0 to 200 m depth, and over the last decades at different latitudinal band from (A) 0 to 30°N, (B) 30 to 50 °N, and (C) 50 to 90°N. The p-value obtained from the ANOVA test is reported by coloured circles for each species per latitudinal band (light pink: non-significant trend; red: significant decrease; blue: significant decrease). Upper panels display the number of observations for each decade and latitudinal band. The regression lines (red) represent the relationship between the mean values of normalized number concentrations and the decades.

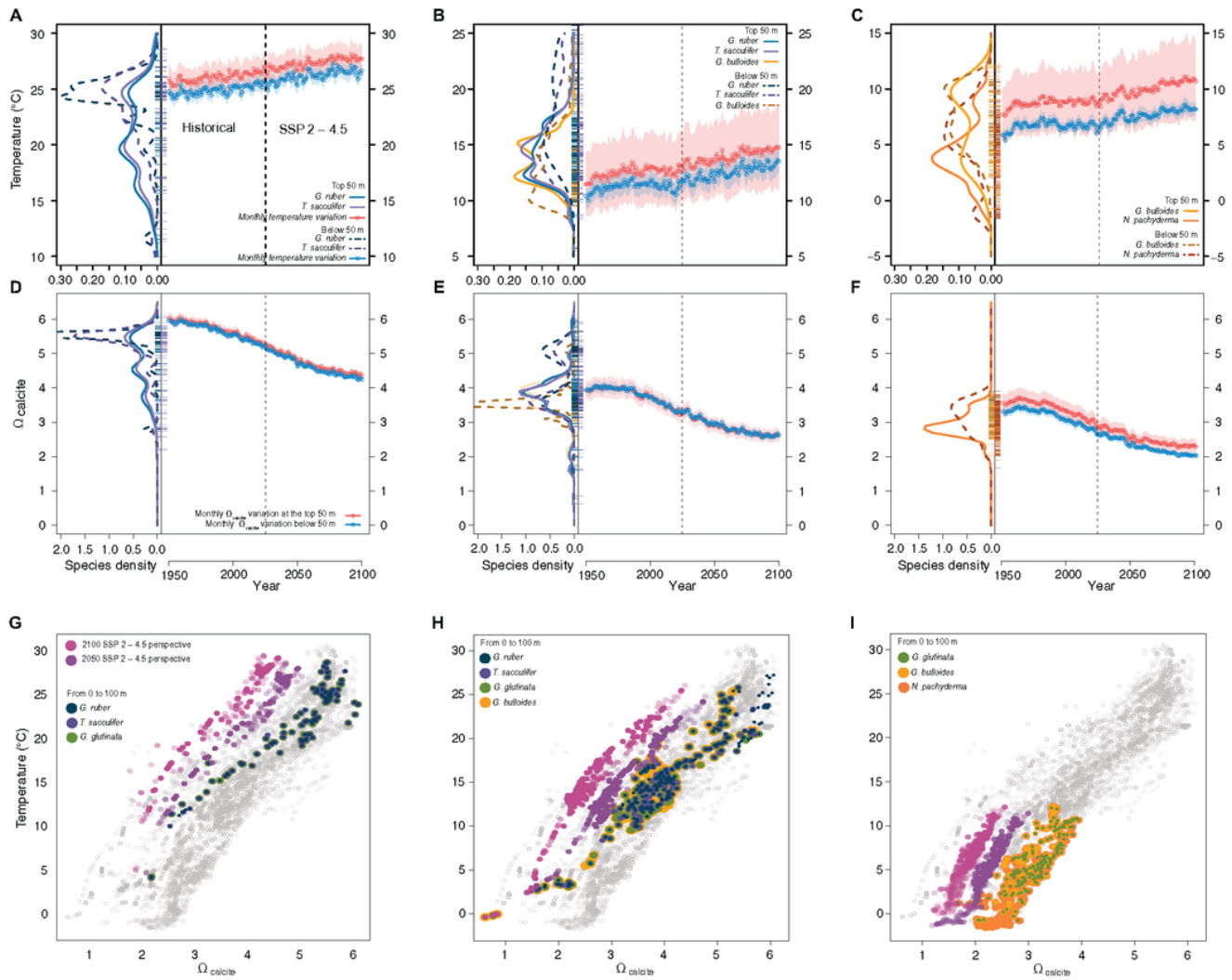


Fig. 4

Figure 4

Planktonic Foraminifera Distribution and Environmental Factors: Atlantic planktonic Foraminifera distribution and occurrence of common species by depth range (solid lines: 0 to 50 m; dashed lines: 50 to 100 m) at 0 to 30°N (**A, D, G**); at 30 to 50°N (**B, E, H**), and at 50 to 90°N (**C, F, I**), plotted vs. temperature and Ω_{calcite} and compared to modeled temperature and Ω_{calcite} variations from 1950 to 2100 (data extracted from World Climate Research Program IPSL IPSL-CM6A-LR model output). Each model output line corresponds to an average temperature across the basin and in the latitudinal bin with 2SD shown in the coloured envelope. Lower panels (**G, H, I**) show temperature and Ω_{calcite} at collection time and water depth of *G. ruber* (blue), *T. sacculifer* (dark purple), *G. glutinata* (green), *G. bulloides* (yellow), and *N. pachyderma* (orange). Also shown are the future conditions of all current niches of Foraminifera species in each basin in 2050 (light blue) and 2100 (pink) based on the model perspective output SSP 2 – 4.5. Gray background dots: all FORCIS data including other ocean basins and showing temperature and Ω_{calcite} at time of collection.

Supplementary Files

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