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Projected impacts of climate change and ocean acidification on the global biogeography of planktonic foraminifera

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Abstract

Planktonic foraminifera are a major contributor to the deep carbonate-flux and the planktonic biomass of the global ocean. Their microfossil deposits form one of the richest databases for reconstructing paleoenvironments, particularly through changes in their taxonomic and shell composition. Using an empirically-based foraminifer model that incorporates three known major physiological drivers of foraminifer biogeography – temperature, food and light – we investigate (i) the global redistribution of planktonic foraminifera under anthropogenic climate change, and (ii) the alteration of the carbonate chemistry of foraminifer habitat with ocean acidification. The present-day and future (2090–2100) 3-D distributions of foraminifera are simulated using temperature, plankton biomass, and light from an Earth system model forced with historical and a future (IPCC A2) high CO_2 emission scenario. The broadscale patterns of present day foraminifer biogeography are well reproduced. Foraminifer abundance and diversity are projected to decrease in the tropics and subpolar regions and increase in the subtropics and around the poles. In the tropics, the geographical shifts are driven by temperature, while the vertical shifts are driven by both temperature and food availability. In the high-latitudes, vertical shifts are driven by food availability, while geographical shifts are driven by both food availability and temperature. Changes in the marine carbon cycle would be expected in response to (i) the large-scale rearrangements in foraminifer abundance, and (ii) the reduction of the carbonate concentration in the habitat range of planktonic foraminifers: from 10–30 µmol kg^{-1} in the polar/subpolar regions to 30–70 µmol kg^{-1} in the subtropical/tropical regions. High-latitude species are most vulnerable to anthropogenic change: their abundance and available habitat decrease and up to 10 % of their habitat drops below the calcite saturation horizon.

1   Introduction

We are interested in projecting the response of planktonic foraminifera to anthropogenic change. First, large-scale changes to their biogeography and shell chemistry have the potential to alter the marine carbon cycle and the concentration of carbon dioxide in the atmosphere. Second, understanding the processes driving present-day changes in foraminifer biogeography will help us interpret the climate signals preserved in the sedimentary fossil record.

Foraminifer are expected to be useful biological indicators of anthropogenic climate change in the marine environment because:

- foraminifera are established proxies of past climatic change and, by corollary, should "record" future climate change,

- the present day global distribution of foraminifera is one of the most well known of all oceanic taxa and provides a useful baseline for measuring change,

- there are no known specific predators of foraminifera, so, changes in foraminifer distributions are more likely to reflect environmental rather than ecological changes,

- the spatial distributions of pelagic organisms are expected to shift faster to climate change than demersal species (Pereira et al., 2010),

- the growth rates and abundances of foraminifera are very responsive to changes in temperature, particularly at the limit of their temperature range (Rutherford et al., 1999),

- historical changes in foraminifer abundance have been shown to reflect anthropogenic climate change (Field et al., 2006), and

- changes in the abundance and distribution of foraminifera are well preserved in ocean sediments, and can be measured from plankton tows and sediment traps.

Present-day responses of planktonic foraminifera to anthropogenic change should provide a "living laboratory" for interpreting past responses that have been recorded in the sediments over geological times-scales. Understanding the drivers of the changes in foraminifer species assemblages, abundances, distributions and shell chemistry should
5 lead to improved reconstructions of past climates.

Planktonic foraminifera contribute as much as 32 %–80 % to the global flux of calcium carbonate that reaches the seafloor (Schiebel, 2002), despite their relatively sparse distribution throughout the World's oceans. Thus, they represent one of the three planktonic groups that dominate the oceanic carbonate flux alongside coccolithophores and
10 pteropods. Indeed, much of the seafloor is covered by foraminifer tests. The efficient transport of foraminifera to the ocean floor is due partly to their comparatively large size (mostly between 0.01 to 1 mm) and their rapid sinking speeds (Berger and Piper, 1972). Also, the tests of foraminifera are composed of calcite: the less soluble of the two biogenic forms of calcium carbonate.

15 Foraminifera were recently also found to be one of the functional types that dominate the total planktonic biomass of the ocean (Buitenhuis et al., 2012; Schiebel and Movellan, 2012) and they contribute to the mineral ballast that facilitates the vertical transport of organic matter in the ocean (De La Rocha and Passow, 2007). Thus, foraminifera are also expected to play a central role in the organic carbon cycle.

20 Under future scenarios of climate change, ocean acidification is predicted to reduce the global carbonate production by planktonic calcifiers by the end of the century and drive a small reduction in the atmospheric CO_2 concentration (Schmittner et al., 2008; Gangsto et al., 2011). The impacts of both climate change and ocean acidification on planktonic calcifiers are projected to drive a decrease in the fossil-fuel burden of
25 the atmosphere (Ridgwell et al., 2007; Pinsonneault et al., 2012). The strength of this future CO_2-calcification feedback is sensitive to which calcifying species are assumed to contribute to the carbonate production of the open ocean (Ridgwell et al., 2007).

Given the key role played by foraminifera in the marine carbon cycle, and their impact on atmospheric CO_2 concentrations over seasonal to geological time scales (Barker

et al., 2003), it is timely to address how their abundances, distributions and carbonate tests are expected to respond to anthropogenic change. Towards this end, in this study we investigate present and future changes in the 3-D distributions of foraminifer diversity based on their physiological sensitivities to environmental conditions – temperature, food and light (Fairbanks et al., 1982; Bijma et al., 1990; Caron and Swanberg, 1990). These traits demarcate much of the foraminifer distribution throughout the global ocean (Hemleben et al., 1989). Temperature exerts a first order control on the distribution of foraminifera (Bijma et al., 1990; Rutherford et al., 1999). Each species has a unique optimum temperature range and there is generally a fairly sharp drop in their growth rates at either extreme (Fig. S1 in the Supplement). Light also plays an important role in the distribution of many foraminifera species, both directly through providing energy to the algal symbionts hosted by some species of foraminifera (Spero and Lea, 1993), and indirectly by controlling the distribution of the foraminifer prey (Bijma et al., 1992). There are some generalizations that can be made about the broadscale biogeography of foraminifera based on light availability. Many of the spinose species host algal symbionts that can contribute to the growth of the foraminifera. Species with algal symbionts are generally optimized for shallow, high-light, low-nutrient environments, so occur most frequently in the oligotrophic gyres. Some nonspinose species, such as *G. bulloides* and *N. pachyderma*, are optimized for survival in regions with high productivity. Prey availability has also been shown to have a significant impact of the distribution of foraminifera (Ortiz et al., 1995; Watkins et al., 1996, 1998). The spinose species have calcareous spines that assist in prey capture and tend to be carnivorous or omnivorous, feeding on copepods and other zooplankton; while the nonspinose species tend to prefer phytoplankton (Spindler et al., 1984).

Changes in the characteristics of planktonic foraminifer assemblages preserved in microfossil sediments, and knowledge of the ecophysiological traits of foraminifer species, has helped reconstruct past environmental conditions to as far back as 120 million years ago. Here, we reverse the problem and use an ecophysiological foraminifer model and an Earth-system model to simulate future changes in oceanic

conditions and project how climate change and ocean acidification may be expected to impact foraminifera by the end of the century.

2 Materials and methods

2.1 Earth system model and simulations

To simulate the present-day and future global ocean environments we used the Institut Pierre-Simon Laplace Coupled Model 4 (IPSL-CM4) model. The IPSL model couples the Laboratoire de Météorologie Dynamique atmospheric model (LMDZ-4), with a horizontal resolution of about $3° \times 2.5°$ and 19 vertical levels (Hourdin et al., 2006) to the OPA-8 ocean model, with a horizontal resolution of $2° \times 2° \cdot \cos\phi$ and 31 vertical levels, and the LIM sea-ice model (Madec et al., 1998). The terrestrial biosphere is represented by the global vegetation model ORCHIDEE (Krinner et al., 2005) and the marine biogeochemical cycles by the PISCES model (Aumont et al., 2003).

PISCES simulates the cycling of carbon, oxygen, and the major nutrients determining phytoplankton growth (PO_4^{3-}, NO_3^-, NH_4^+, Si, Fe). Phytoplankton growth is limited by the availability of nutrients, temperature, and light. The model has two phytoplankton size classes (small and large), representing nanophytoplankton and diatoms, as well as two zooplankton size classes (small and large), representing microzooplankton and mesozooplankton. The C : N : P ratios are assumed constant 122 : 16 : 1; (Anderson and Sarmiento, 1994), while the internal ratios of Fe : C, Chl : C, and Si : C of phytoplankton are predicted by the model. For more details on PISCES see Aumont and Bopp (2006), Gehlen et al. (2006) and Schneider et al. (2008).

The IPSL model is forced using historical emissions and the IPCC AR4 A2 high-emission scenario (1860–2100). To calculate the input fields for the FORAMCLIM model (ocean temperature, T, total phytoplankton concentration, PHY, photosynthetically active radiation, PAR, and the carbonate ion concentration. CO_3^{2-}) a monthly cli-

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matology is calculated by averaging the drift-corrected fields over the ten-year periods: present (2000–2009) and future (2090–2099).

2.2 Foraminifer model (FORAMCLIM)

We use the FORAMCLIM model (Lombard et al., 2011) to simulate the growth rates and the abundances of eight common and widely-studied foraminifer species. Five of the simulated species are spinose (*Orbulina universa, Globigerinoides sacculifer, Globigerinoides ruber, Globigerinella siphonifera, Globigerina bulloides*) and three species are nonspinose (*Neogloboquadrina dutertrei, Neogloboquadrina incompta, Neogloboquadrina pachyderma*). For a complete description of the model see Lombard et al. (2011) and references therein.

The growth-rate relationships in FORAMCLIM were based on the observed physiological responses of live specimens under controlled laboratory conditions. In FORAMCLIM, species-specific foraminifer growth (μ, d^{-1}) is simulated based on three main physiological rates: nutrition (N), respiration (R) and photosynthesis by the algal symbionts (P).

$$\mu(T, F, \mathrm{PAR}) = N(T, F) + P(T, \mathrm{PAR}) - R(T) \tag{1}$$

These physiological rates are a function of ocean temperature (T), light (PAR, photosynthetically active radiation) and food concentration (F), Here, the total phytoplankton concentration, PHY, is used as a proxy for F, according to Lombard et al. (2011). We use the 3-D decadal-mean climatologies of T, F, and PAR for present and future time slices of the IPSL model simulations.

The relationships between growth rates and abundances were calibrated against abundances observed in multinet plankton tows (Lombard et al., 2011). Based on the strong relationship between physiological rates and abundances observed in multinet plankton tows, an exponential relationship between abundance (Abund, individuals m^{-3}) and μ was assumed (Lombard et al., 2011), where

$$\mathrm{Abund} = a\mu^b - a + 0.1 \tag{2}$$

Generally, the abundance, or standing stock in the water column, is given by the annual mean $\sum\limits_{t=1:12} \frac{\mathrm{Abund}_i(t)}{12}\mathrm{d}t$. In the cases where we estimate the maximum abundance that could potentially reach the ocean sediments, the monthly-mean depth-integrated abundances are integrated over the seasonal cycle $\sum\limits_{t=1:12} \mathrm{Abund}_i(t)\mathrm{d}t$. The relative abundances, Rabund, for each species is

$$\mathrm{Rabund}_i = \frac{\mathrm{Abund}_i}{\sum\limits_{i=1:8} \mathrm{Abund}_i} \cdot 100\,\%.$$

All the physiological parameters are species-specific. The most relevant parameters to this study are listed in Table 1. The contribution of photosynthetically-derived organic matter to the nutrition rate is set by both $\%P$, the fraction of the symbiont photosynthesis that is utilized in foraminifer growth, and s_{nb}, the number of algal symbionts per 250 μm individual (Table 1). Photosynthesis only contributes to the growth rate in species that bear algal symbionts. The food-driven component to the foraminifer nutrition rate is largely dependent on the half-saturation constant for the Michaelis–Menten relationship, k_n. Species with lower k_n, tend to be more adapted to oligotrophic waters, while species with high k_n tend to require higher food concentrations for growth.

2.3 Foraminifer assemblage and calcite saturation data

For model evaluation we use two independent data sets: (i) the surface abundances from global plankton tows (Bé and Tolderlund, 1971), and (ii) the relative abundances from sediment top cores. The observed relative abundances of foraminifera in sediment cores (Fig. S2a in the Supplement) are compiled from the MARGO database (Barrows and Juggins, 2005; Hayes et al., 2005; Kucera et al., 2005b). We compiled all the available relative abundances in the MARGO database from the top cores and recalculated the relative abundances based on only the eight species used in this study.

The empirical relationships between foraminifer growth rates and abundances in the FORAMCLIM model were originally calibrated against a compilation of multinet plankton tow data (Watkins et al., 1996, 1998; Schiebel et al., 2001, 2004; Field, 2004; Kuroyanagi and Kawahata, 2004), which is why we can not use this comprehensive database to evaluate the model. We use the samping sites from this same data set to characterize the carbonate chemistry of the present day potential habitat of foraminifer species. We "sample" the GLODAP calcite saturation, Ω_C, (Key et al., 2004) at the same locations (latitude, longitude, depth; Fig. S2b in the Supplement) where foraminifera have been collected in multinet plankton tows (Watkins et al., 1996, 1998; Schiebel et al., 2001, 2004; Field, 2004; Kuroyanagi and Kawahata, 2004) and calculate the percentage of the total abundance of each species residing in waters with different Ω_C ranges.

2.4 Modelling foraminifera: strengths and limitations

The two most established approaches currently used to simulate the biodiversity of foraminifera are the ecophysiological approach used in this study, FORAMCLIM (Lombard et al., 2011), and the ecosystem approach which captures dynamical changes in planktonic foraminifer populations, PLAFOM Fraile et al. (2008). All approaches used for projecting climate impacts on marine biogeography have their unique set of strengths and weaknesses (Pereira et al., 2010). One of the drawbacks of the dynamic ecosystem approach is that many processes (i.e. mortality, competition, and predation) are not well known (Hemleben et al., 1989), and the parameters that describe these processes can not be optimized independently with the available data. Another limitation of the Fraile et al. (2008) approach is the depth profiles of foraminifer abundance are not simulated. Capturing vertical changes is essential if we want to estimate the impact of shifts in habitat preference on both the net foraminifer abundance and the climate signals recorded by foraminifer paleoproxies. Yet, the dynamical approach could be better adapted to simulate events controlled by population biology and hydrodynamics, which are known to be important in controlling foraminifera abundance and their flux to the deep ocean (De La Rocha and Passow, 2007), such as the pulsed

fluxes of foraminifer tests that can occur sporadically (Sautter and Thunell, 1991) or in short bursts in response to storms (Schiebel et al., 2005), and the advection of empty test from their production sites (Siegel and Deuser, 1997; von Gyldenfeldt et al., 2002).

One of the attractive aspects of the FORAMCLIM model is that it is empirically-based. The relationships between environmental conditions (i.e. light, temperature) and foraminifer growth rates are derived under controlled laboratory conditions. And, the empirical relationships between growth rates and abundances are calibrated against the standing stock of foraminifer observed in plankton tows. Essentially, using the model we are projecting these observation-based relationships into the future. Critical to reliable model performance is that these model relationships are realistic. Here we elaborate on a previous discussion of the strengths and limitations of the FORAMCLIM model (Lombard et al., 2011).

The laboratory-based growth rate relationships may not hold for the real ocean. First, the laboratory experiments were conducted on specific specimens that could have eco-logical adaptations (i.e. ecotypes) that may not be representative of the global popula-tion (Riebesell et al., 2000; Ridgwell et al., 2009). Second, foraminifera in the laboratory could be more sensitive to perturbations in environmental conditions than in their wild habitat. It hasn't been possible to reproduce foraminifera in the laboratory, indicating that foraminifera in the laboratory are not behaving as they would in their natural envi-ronment. Third, the physiological responses of foraminifera in the laboratory could be more related to stress than to environmental perturbations.

Another potential weakness is that the relationships between the abundances and the growth rates are weakly correlated (Lombard et al., 2011). This could partly be due to each morphological species actually being a combination of cryptic species, each with distinct habitat preferences and responses to environmental change (de Vargas et al., 2002). Another explanation could be that the model does not resolve variations in shell size, while foraminifer abundance is highly sensitive to how the total biomass is structured over size classes.

Finally, the FORAMCLIM model is currently limited to the species on which sufficient physiological laboratory experiments have been conducted. That is, 8 of the approximately 50 species of morphologically-distinct planktonic foraminifera. Therefore, we can not use the model to estimate the total (i.e. all species) foraminifer abundance, diversity or carbonate production.

2.5 Model performance

The FORAMCLIM model captures the broadscale patterns of abundance and species dominance. The distributions of surface abundance from plankton tows (Bé and Tolderlund, 1971) are well captured by the model with the highest abundances in the tropics and subpolar regions and the lowest in the subtropics (Fig. S3a in the Supplement). Yet, surface abundances tend to be overestimated, particularly in the subtropics. This is most likely due to that the model is calibrated against multinet plankton tow data, which uses smaller mesh sizes (63–100 μm) relative to the 200 μm used by Bé and Tolderlund (1971).

Qualitatively, the dominant species (the species with the highest abundance) were also simulated well by the model with *G. bulloides* in the more productive upwelling areas, *G. ruber* in the subtropical gyres, *N. pachyderma* in the high-latitudes and *G. sacculifer* dominating in the regions in between (Fig. S3 in the Supplement). The model reproduced 43 % of the observed species dominance from surface plankton tow data (Table 2). This level of agreement is lower than the model-based and satellite-based estimates of Lombard et al. (2011) (Table 2) and is most likely due to the displacement of the simulated water masses and ocean fronts relative to their real world counterparts, as is typical of Earth system models (Seferian et al., 2013). Also some species have quite similar abundances locally, so small errors in abundance can lead to significant errors in species dominance.

The relative abundances and diversity are well captured by the model with the relative abundance RMSE errors ranging between 3 % and 25 % and the diversity RMSE ranging between 0.48 and 0.56 (Table 2). For all species, expect *N. pachyderma*, the

relative abundance RMSEs are slightly larger than in Lombard et al. (2011), but smaller than in Fraile et al. (2008).

In summary, there is a tendency to slightly overestimate the standing stock of foraminifera relative to the sparse surface plankton data, and to underestimate the changes in abundance in response to changing environmental conditions relative to observed abundances from sediment cores (Kageyama et al., 2012).

The challenge remains to observationally evaluate how well foraminifer models capture changes in abundance in response to environmental change. There is little large-scale observational evidence for historical trends in foraminifer abundance and diversity (i.e. over the period of anthropogenic climate change). Large-scale changes in foraminifer abundance have been observed in continuous plankton records over the last 5 decades in the North Atlantic that are intriguingly similar to our simulations (McQuatters-Gollop et al., 2010), but further analysis of this data set is required before a quantitative assessment can be made. Changes in species composition in response to anthropogenic climate change have been observed in the sediment record of the Santa Barbara basin (Field et al., 2006). It was shown that historical warming trends were associated with an increase in the abundance of tropical/subtropical species, and a decrease in subpolar/polar species (i.e. *N. pachyderma*) over the 20th century.

Ideally, the FORAMCLIM simulations should be tested against present-day time series of planktonic abundance and the key environmental variables such as temperature, phytoplankton concentration and light. For future studies, there are several instrumental records that should become available and provide an invaluable resource to improve our understanding of the environmental controls on the biogeography of foraminifera, including data collected with: (i) plankton tows, (ii) sediment traps (Zaric et al., 2005), (iii) sediment cores, and (iv) continuous plankton recorders (CPR).

The plankton tow data used here, for the construction of the empirical relationships between physiological growth rates and abundances, represent only a subsample of what should become available in the future. More studies of historical trends in the assemblage of planktonic foraminifera deposited in sediment cores, such as that of Field

et al. (2006), would be invaluable for evaluating the longer-term responses of species assemblages to climate change. Yet, such studies are restricted to ocean sediment cores from locations with high sedimentation rates and sufficient temporal resolution to determine historical trends. These would not be expected to provide the spatial coverage required for the basin-scale evaluation of global models. CPR records provide long time series of plankton diversity, yet unfortunately, we found that the routine preservation protocol used to store CPR samples did not preserve foraminifera well enough to determine relative abundances or shell weights. Only the most robust individuals were preserved and even their shells were found to be brittle and difficult to speciate. Nevertheless, it should be possible to use the total abundance of foraminifera recorded in the original written records for each CPR sample to evaluate the simulated changes in total foraminifer abundance from the model.

Sedimentary paleorecords over glacial/interglacial timescales may be useful analogs for historical climate change. Yet, it can be difficult to know which combination of species is driving the observed changes in relative abundance. The differential dissolution of foraminifera in the sediments further complicates the interpretation of the signals recorded here. Also, we don't have direct measurements of the key environmental drivers of foraminifer abundance – temperature, light, food availability – back through time, and must draw on proxy-based estimates of these quantities, which are plagued by similar uncertainties, and the proxies themselves are often based on foraminifera.

3   Results

3.1   Future changes in abundance and diversity

Under climate change the simulated total foraminifer abundance (combined abundance of all species, Fig. 1a) shifts polewards from the tropics to the subtropics and decreases in the subpolar regions (Fig. 1b) by the end of the century. The simulated depth-integrated abundance is reduced by up to 40 % in the tropics and subpolar re-

gions and increased by greater than 100 % in the subtropics. Throughout the tropics the total abundance (Fig. 1c) shifted deeper in the water column (Fig. 1d), reducing the total abundance of foraminifera at the ocean surface (Fig. 2a) by more than 50 % ($> 10 \, \mathrm{ind \, m^{-3}}$, Fig. 2b). The pattern of foraminifer diversity (Fig. 2c) behaved similarly to abundance under climate change, with a decrease in the tropics, an increase in the subpolar regions (Fig. 2d) and a shift to depth in the tropics (not shown). Decreases in the diversity in the tropics are primarily due to localised extinctions of *G. siphonifera* and *N. dutertrei*.

Three species dominated the changes in total foraminifer abundance: the two most common warm-water species – *G. ruber* and *G. sacculifer* – drove the reduction in total abundance in the tropics and the increase in the subtropics, while *N. pachyderma* dominated the reduction in the high latitudes and the small increases in abundance around the poles (Fig. 3a and b). In the tropics, the climate-driven reductions in the distribution of *G. ruber* and *G. sacculifer* were similar in magnitude ($5 \, \mathrm{ind \, m^{-3}}$), and each integrated to a more than $100 \, \mathrm{ind \, m^{-2}}$ reduction over the whole water column (Fig. 3b). In the high-latitudes, the poleward shift in abundance of *N. pachyderma* reduces the net abundance in surface waters ($\sim 4 \, \mathrm{ind \, m^{-3}}$) and throughout the water column ($\sim 200 \, \mathrm{ind \, m^{-2}}$, not shown).

The changes in relative abundance are also presented, since this is what can be assumed to be measured in sediment cores. In the tropics, despite the large decreases in the abundances of the two dominant species (*G. ruber* and *G. sacculifer*), their relative abundances at the ocean surface increase (Fig. 3c) and the depth-integrated relative abundances changed very little (Fig. 3d). In the mid latitudes (10–40°) the abundance and relative abundance of *G. bulloides, N. incompta* and *N. dutertrei*, while *G. sacculifer* and *G. ruber* increase. In the higher latitudes the species diversity is low and the reduction in the abundance of the dominant species, *N. pachyderma*, was clearly reflected in the relative abundance, yet was accompanied by small increases in the relative abundances of *G.bulloides*, *N. incompta* and *N. dutertrei*.

3.2 Environmental drivers of foraminifer biogeography

An attractive aspect of the FORAMCLIM model is the ease with which the various drivers of the changes in abundance can be disentangled. By systematically allowing only one parameter to vary, we can partially separate the total change in foraminifer abundance into components driven by each of the environmental drivers – temperature, food (phytoplankton concentration) and light. Future changes in ocean temperature and food availability are the primary drivers of the changes in the basin-scale biogeography of foraminifera (Fig. 4), while changes in light availability have a minor impact (not shown).

Temperature was the dominant driver of the poleward shift of foraminifer abundance from the tropics (Fig. 4a). The 1–3 °C increase in sea surface temperatures in the tropics and subtropics (Fig. 5a) throughout the water column (Fig. 5b) decreased the habitat suitability in the tropical waters – the waters became to warm for optimal foraminifer growth – yet increased the habitat suitability in the subtropics (Fig. 4a) and in the deeper waters of the tropics (Fig. 4b).

In the subpolar and polar regions, where *N. pachyderma* dominates (Fig. 3a and b), the shift in abundance was a combined response to temperature and food-driven changes in nutrition rates (Fig. 4a and c, respectively). The broadscale pattern, the subpolar decrease and polar increase in abundance (Fig. 4a and b), is driven by temperature (Fig. 5a). Yet, increases in phytoplankton concentration in localized patches (Fig. 5c) and in subsurface waters (Fig. 5d) drove increases in abundance (Fig. 4c and d). The food-driven increases in the abundance tended to offset the temperature-driven reductions. Other areas where the impact of phytoplankton on foraminifer abundance offsets the impact of temperature include large patches throughout the North Atlantic and the Equatorial and coastal upwelling regions.

3.3 Species abundance and potential suitable habitat

To assess the species-specific vulnerability of foraminifera to climate change we calculated the percent change in the globally-averaged species abundance and potential suitable habitat (Fig. 6), where the potential habitat is defined as anywhere where the environmental conditions (i.e. temperature, food and light conditions) are sufficient for foraminifer growth. Some species "profited" (*O. universa*, *G. sacculifer*, *G. siphonifera* and *G. ruber*); that is their potential habitat increased by between 5 % and 20 %. While, higher-latitude species were more vulnerable (e.g. *N. incompta*, *N. pachyderma*): their potential habitat and net abundance decreased by between 10 % and 40 %. For *G. siphonifera* the potential habitat increased but the abundance decreased.

3.4 Carbon chemistry of the foraminifer habitat

Although we don't explicitly account for the impact of ocean acidification on either foraminifer calcification or physiological processes in the current version of the FORAM-CLIM model, we can make an assessment of the potential impacts by quantifying the predicted changes in the carbonate concentration and calcite saturation state within the habitat range of each foraminifer species.

The calcite saturation state is given by $\Omega_C = \dfrac{\left[Ca^{2+}\right]\left[CO_3^{2-}\right]}{K_{sp}^{CaCO_2}}$, where $[Ca^{2+}]$ and $[CO_3^{2-}]$ are the calcium and carbonate ion concentrations and K_{sp} is the stoichiometric solubility product of calcite ($CaCO_3$). When Ω_C is below the threshold of $\Omega_C = 1$, mineral calcite dissolves, while above it calcite remains stable.

Before we analyse the future change in the carbonate chemistry of the foraminifer habitat, we would like to have an indication of the present-day distribution of foraminifer abundance within waters of different Ω_C classes. We find that only a very small proportion of the abundance of all the foraminifer species resides in waters with Ω_C less than 2, even though substantial volumes of water with low Ω_C are sampled, particularly

in the northern high latitudes (Fig. 7). The highest foraminifer abundances from the multinet plankton tows were sampled in waters with $3 < \Omega_C < 6$.

How will the carbonate chemistry of foraminifer habitat change by the end of this century? Calcite saturation states decrease throughout the global ocean and waters with low saturations states ($\Omega_C < 2$) shoal (Fig. 8a and b) and become more widespread across the surface ocean. Most surface waters polewards of 40° are expected to have $\Omega_C < 2$. Virtually none of the simulated present day foraminifer habitat has ambient calcite saturation states of less than 2. Yet, by the end of the century between 10 % and 95 % of the habitat of all foraminifer species, except *G. ruber,* has an Ω_C of less than 2 (Fig. 8c). High latitude species, *N. pachyderma* and *N. incompta*, are most vulnerable, with some of their suitable habitat even becoming undersaturated ($\Omega_C < 1$) with respect to calcite by the end of the century. Also, the carbonate ion concentrations of the potential foraminifer habitat decrease to between 20 and 70 μmol kg^{-1}, with the largest reductions in the equatorial regions (Fig. 8d).

4 Discussion

4.1 Acidification impacts

If net calcification were to scale directly with foraminifer abundance, alone the large-scale rearrangements in abundance with climate change would cause significant changes in regional carbonate production. This potential change could be amplified by ocean acidification, which can reduce foraminifer calcification rates (Lombard et al., 2010), or could be dampened by higher ocean temperatures, which can accelerate calcification rates.

With future increases in atmospheric CO_2, we show that the carbonate concentration of the preferred habitat range of planktonic foraminifera decreases zonally from 10–30 μmol kg^{-1} in the polar/subpolar regions to 30–70 μmol kg^{-1} in the subtropical/tropical regions by the end of this century. Even without dropping below the calcite

saturation state, such changes in carbonate concentration may have significant impacts on foraminifer tests. Evidence exists for shell thinning in foraminifera over recent (de Moel et al., 2009; Moy et al., 2009) and geological timescales (Barker and Elderfield, 2002) and it has been suggested that these changes are a response to higher atmospheric CO_2 concentrations. Like for other calcifying planktonic species (Riebesell et al., 2000; Zondervan et al., 2001; Fabry et al., 2008; Comeau et al., 2010), the calcification of foraminifera is generally reduced at lower carbonate ion concentrations both in their natural environment (Beer et al., 2010) and in laboratory cultures (Spero et al., 1997; Bijma et al., 1999, 2002; Russell et al., 2004; Beer et al., 2010; Lombard et al., 2010; Manno et al., 2012). If wild foraminifera respond in the same way to such reductions in carbonate concentrations as in laboratory experiments (Bijma et al., 2002; Lombard et al., 2010; Manno et al., 2012), ocean acidification could result in up to a 20 % reduction of foraminifer shell weights – depending on the species, size, and the geographical location.

In the polar/subpolar regions *N. pachyderma* dominates the assemblages. The tests of *N. pachyderma* are expected to be most vulnerable to dissolution because the polar regions have lower carbonate concentrations and are, thus, closer to the threshold of calcite saturation ($\Omega = 1$). We show that by the end of the century, most of the habitat of high-latitude species drops below the calcite saturation state of 2 with greater than 10 % of the potential habitat of the dominant high-latitude species, *N. pachyderma*, residing below the saturation horizon, which could result in shell dissolution throughout this range.

Although calcification by foraminifera is directly influenced by CO_3^{2-}, many other environmental factors besides ambient carbonate concentrations influence the shell weight (de Villiers, 2004) including temperature (Hemleben et al., 1989; Lombard et al., 2009; Manno et al., 2012), light (Spero, 1992; Lombard et al., 2010), phosphate and growth potential (Aldridge et al., 2012). Clearly, the environmental controls on calcite production by foraminifera are still poorly understood. A complex intra- and interspecies-specific interplay of factors drive foraminiferal shell weights (Beer et al., 2010). Both the

magnitude and the sign of the slope of the relationships between shell weight and carbonate concentrations are species-specific and they vary widely depending on whether the relationships were based on plankton tows (Beer et al., 2010), core tops (Barker and Elderfield, 2002), or laboratory cultures (Bijma et al., 1999, 2002). A quantitative assessment of the impact of acidification on the foraminiferal carbonate flux can be made with confidence only once these complexities have been taken into account.

To quantify the foraminifer carbonate flux, further model development should be encouraged, particularly the incorporation of enhanced species diversity, shell calcification processes, and empirical relationships between environmental conditions and foraminifer size. Ideally, future models will also incorporate the physiological response of foraminifer calcification to multiple environmental drivers.

4.2 Climate impacts

It is unclear how vulnerable specific foraminifer species may be to anthropogenic climate change. Since the last substantial extinction event in the Pliocene the modern assemblage of species has remained relatively stable under glacial–interglacial fluctuations (Jackson and Sheldon, 1994). Yet, the oceanic environment is fast approaching conditions that are well outside those of glacial–interglacial cycles. Generally it is expected that pelagic species, and in particular planktonic species, will have the potential to escape some climatic changes by shifting their populations to regions with more favorable conditions (Burrows et al., 2011), as predicted here for species such a *G. sacculifer* and *G. ruber*. Yet, we show that the available potential habitat is reduced for high latitude species, such as *N. pachyderma*, and that this reduction is associated with a drop in the net global abundance. For one species, *G. siphonifera*, climate change increases the available suitable habitat range, yet it's net global abundance decreases. This indicates that temperature, light and food availability are perturbed such that some species are forced to live in suboptimal environments.

We have shown that climate change is expected to alter the temperature, food and light conditions required for optimal foraminifer growth and, consequently, shift both the

vertical and geographical distributions of foraminifer abundance/diversity. In the tropics, the changes in abundance are driven by the regionally dominant species: *G. ruber* and *G. sacculifer*. Here, temperature dominates the geographical shifts in foraminifer abundance, while multiple drivers (phytoplankton and temperature) cause the vertical shifts.

To the contrary, in the polar/subpolar regions food availability and temperature drive the geographical shifts in foraminifer abundance, while mostly changes in phytoplankton concentrations drive the vertical shifts. The changes in the abundance of foraminifera are associated with *N. pachyderma* and are in agreement with observational studies (Fairbanks and Wiebe, 1980; Kohfeld et al., 1996; Kuroyanagi and Kawahata, 2004; Bergami et al., 2009) that demonstrate that the geographical distribution was primarily controlled by ocean temperatures, while the vertical distribution was controlled by depth of the chlorophyll maximum and the pycnocline.

Opinions differ on the relative impacts of food availability, temperature or other environmental factors on the geographical distribution of planktonic foraminifera. Although it is generally accepted that at the extremes of a species temperature tolerance, temperature drives the changes in the geographical extent of foraminifera (Rutherford et al., 1999), each species preferred temperature range is broad. Within these temperature ranges it has been shown that regional patterns of abundance are strongly correlated to specific-specific responses to food, light (Ortiz et al., 1995; Watkins et al., 1996; Field, 2004) salinity, and turbidity (Retailleau et al., 2011). Vice-versa, it could be argued that food availability is generally adequate to maintain foraminifer populations and that changes in abundance are primarily temperature-driven. A database of time-series of foraminifer abundance/assemblage data and concomitant environmental measurements of temperature, food and light would be an invaluable resource for the evaluation of the drivers of the simulated changes in the distributions of foraminifer abundance.

The simulated response of foraminifer diversity to climate change may differ significantly if all extant species could be included in the model. For example, tropical species present in low concentrations, but excluded in this analysis, could flourish as temperatures increase. Also, the vertical stratification of large regions of the global

ocean should increase with climate change (Sarmiento et al., 2004), which can increase vertical niche separation thereby allowing a greater diversity of species to subsist (Al-Saboui et al., 2007). By including more species in the FORAMCLIM model, these effects could counteract the simulated decrease in diversity in the tropics. Another important factor that will influence how diversity responds to climate change is that most foraminifer morphospecies have many genotypes that exhibit specific ecology, habitat preferences and biogeography (Aurahs et al., 2009). A potential approach to incorporate more species diversity, and to partially circumvent the lack of information on key ecological and physiological processes for many foraminifer species, would be to apply the self-assembling biodiversity approach (Follows et al., 2007) to simulate more complex foraminifer assemblages.

Based on the FORAMCLIM simulations, it would be expected that anthropogenically-driven shifts in the basin-scale biogeography of foraminifera should be observable. But, in sediment samples, the changes in the relative abundances in some regions, particularly the tropics, may be too small to detect. Furthermore, shifts in the species abundance can cause non-intuitive shifts in the relative abundance, particularly in regions of high species diversity such as the tropics. Yet, in the high latitudes, where the diversity is low, the interpretation of the changes in relative abundance should be simpler. In most regions where climate change results in vertical shifts in foraminifer abundance, both food availability and temperature drive the response. As thermocline waters become too warm or nutrient-poor, foraminifera shift deeper in the water column. Comparable vertical shifts in foraminifer abundance over glacial–interglacial time periods may complicate the reconstruction of sea-surface temperatures from foraminifer microfossil deposits: in paleoclimate reconstructions (Kucera et al., 2005a) the vertical distributions foraminifera are generally assumed to be stationary over time.

Subsequent studies should focus on (i) the continued sampling of foraminifer diversity, abundance, and shell size and concomitant biophysical parameters to quantify changes in their distributions in response to environmental perturbations, and (ii) evaluating the detectability of large-scale biogeographical shifts driven by climate-change

given the natural variability in foraminifer distributions. More skill in representing the responses of foraminifer growth and abundance to climate change in models will increase our confidence in both future projections of foraminifer biogeography and the reconstructions of past climates. Given that i) the distributions of foraminifera are one of the most well known of all the taxa in the pelagic ocean and ii) the feasibility of monitoring the large-scale changes in foraminifera, we have confidence that ongoing model-data syntheses should lead to detection and attribution of anthropogenically-driven changes in large-scale planktonic foraminifer distributions.

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Table 1. Key species-specific parameters used in the FORAMCLIM model. The half saturation constant for the Michaelis–Menten relationship that describes the influence of food availability on the nutrition rate, k_n; the percentage of the phtosynthetically-derived growth by the algal symbionts that contributes to foraminifer growth, *%P*; and the number of symbionts per individual 250 µg foraminifer, s_{nb}.

	k_n (µg C L^{-1})	%P	s_{nb}
O. universa	1.73	0.46	716
G. sacculifer	1.32	0.40	1160
G. siphonifera	1.19	0.30	720
G. ruber	0.51	0.37	1104
N. dutertrei	1.00	–	–
G. bulloides	6.84	–	–
N. incompta	3.33	–	–
N. pachyderma	4.70	–	–

Table 2. The percent agreement of the dominant species are assessed against the plankton tow data of Bé and Tolderlund (1971). The RMSE of diversity and relative abundance are assessed against the MARGO top-core data. Lombard[1] is the model-based (FORAMCLIM) estimate from Lombard et al. (2010); Lombard[2] refers to the satellite-based estimate from Lombard et al. (2010); Fraile[1] refers to the model-based (PLAFOM) estimate from Fraile et al. (2008).

	This study	Other studies		
		Lombard[1]	Lombard[2]	Fraile[1]
Dominant species (%)	43 %	59 %	71 %	
Diversity (RMSE)	0.56	0.48	0.52	
Relative abundance (RMSE)				
O. universa	3.2	3.24	3.28	–
G.sacculifer	12.1	12.38	17.46	23
G. siphonifera	6.1	5.29	6.00	–
G. ruber	24.1	23.14	17.76	25
N. dutertrei	18.3	17.53	17.23	–
G. bulloides	22.0	21.02	18.97	25
N. incompta	16.2	15.85	14.85	22
N. pachyderma	20.6	17.01	12.32	9

Figure 1. The present **(a, c)** and future changes **(b, d)** in the total simulated abundance (all species). **(a, c)** Column-integrated abundance (ind m^{-2}), and **(b, d)** zonal-mean abundance (ind m^{-3}).
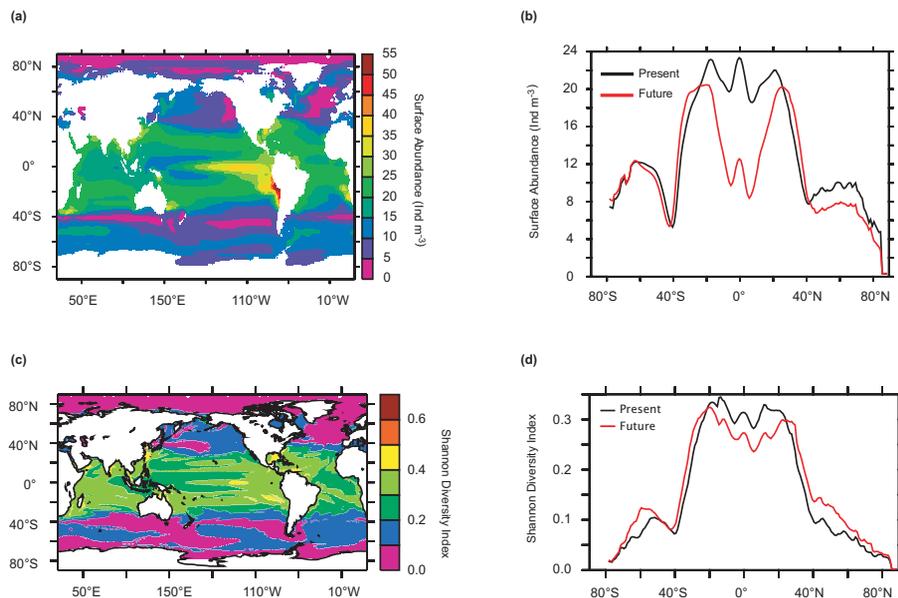
Figure 2. Total surface abundance of foraminifera (ind m^{-3}): **(a)** present-day surface distribution, and **(b)** zonally-averaged surface abundance for the present-day and the future. The Shannon diversity index of the simulated foraminifera: **(c)** surface distribution, and **(d)** zonally-averaged for the present-day and future.

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Interactive Discussion
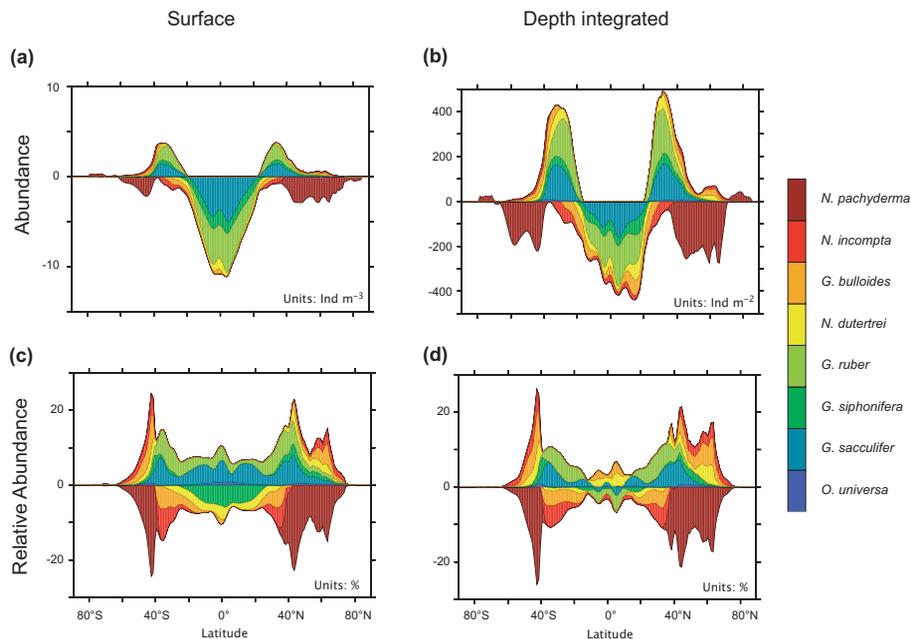
Figure 3. The zonally averaged changes (i.e. present – future) in the abundance, Abund, and the relative abundance, Rabund, of each foraminifer species simulated in FORAMCLIM at **(a, c)** the ocean surface, and **(b, d)** integrated throughout the water column.

Change in foraminifer abundance

Column integrated

Zonal mean
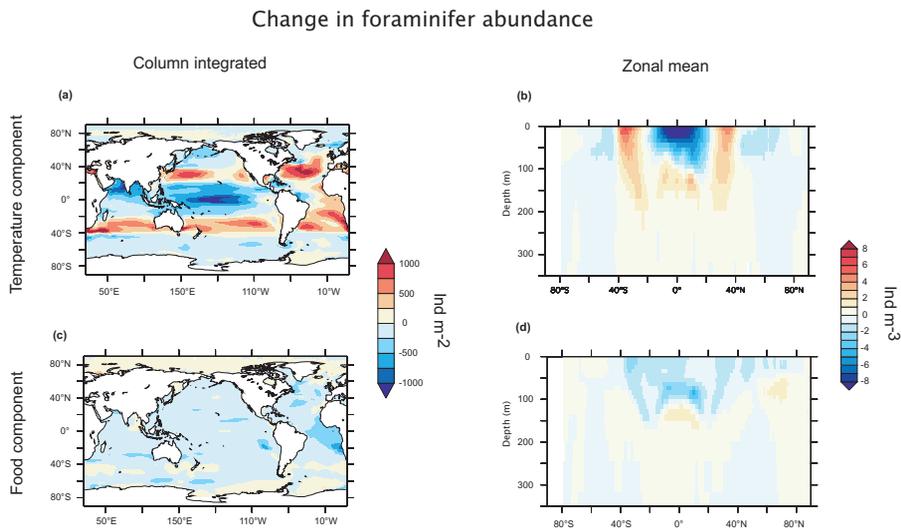
Figure 4. The component of the future change in total foraminifer abundance due to temperature: **(a)** depth integrated (ind m^{-2}), **(b)** zonally-averaged (ind m^{-3}). The component of the future change in total foraminifer abundance due to food availability: **(c)** depth integrated (ind m^{-2}), **(d)** zonally-averaged (ind m^{-3}).
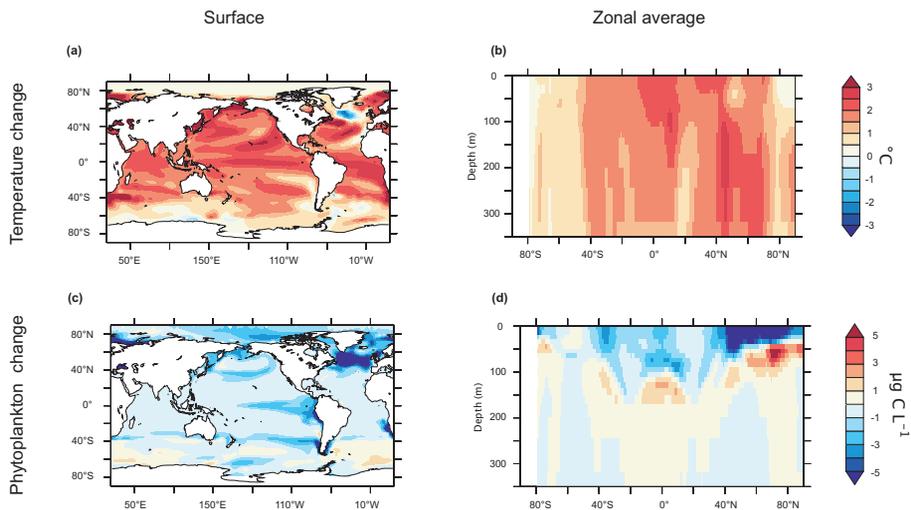
Figure 5. The future changes in the dominant environmental drivers of foraminifer abundance. Ocean temperature (°C): **(a)** at the surface and **(b)** zonally averaged. Phytoplankton concentration ($\mu C\,L^{-1}$): **(c)** at the surface, and **(d)** zonally averaged.
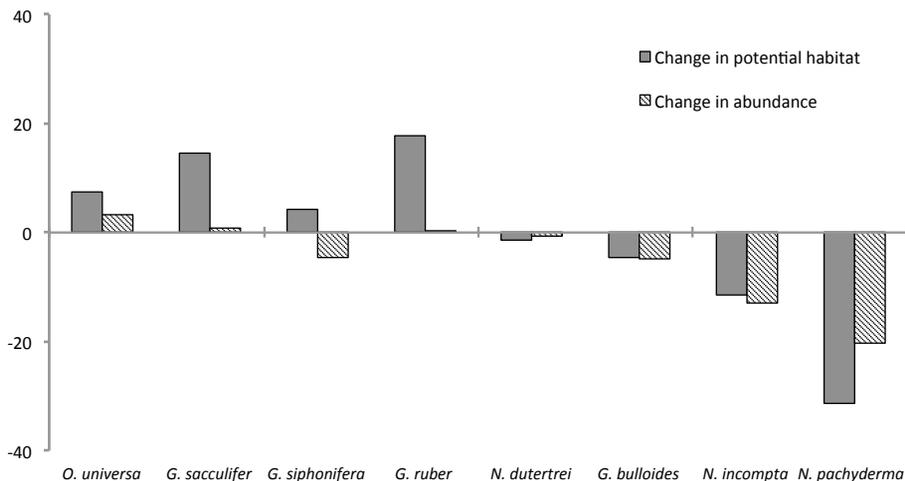
Figure 6. The future change (%) in the potential habitat range (blue) and abundance (red) of each foraminifer species. The potential habitat range is defined as the area where a foraminifer has the potential to grow given the environmental conditions (i.e. temperature, food availability and light).
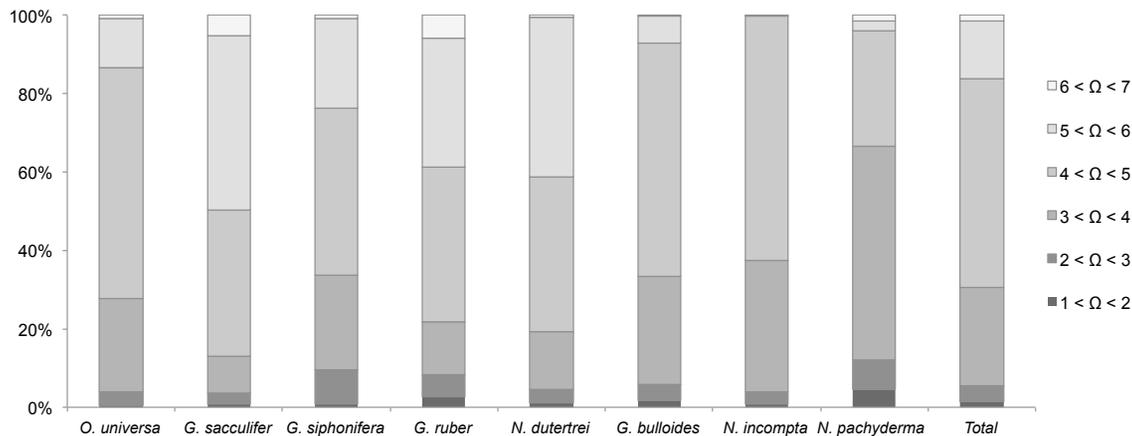
Figure 7. The percentage of the foraminifer species abundance form multinet plankton tows that resides in each Ω_C class.
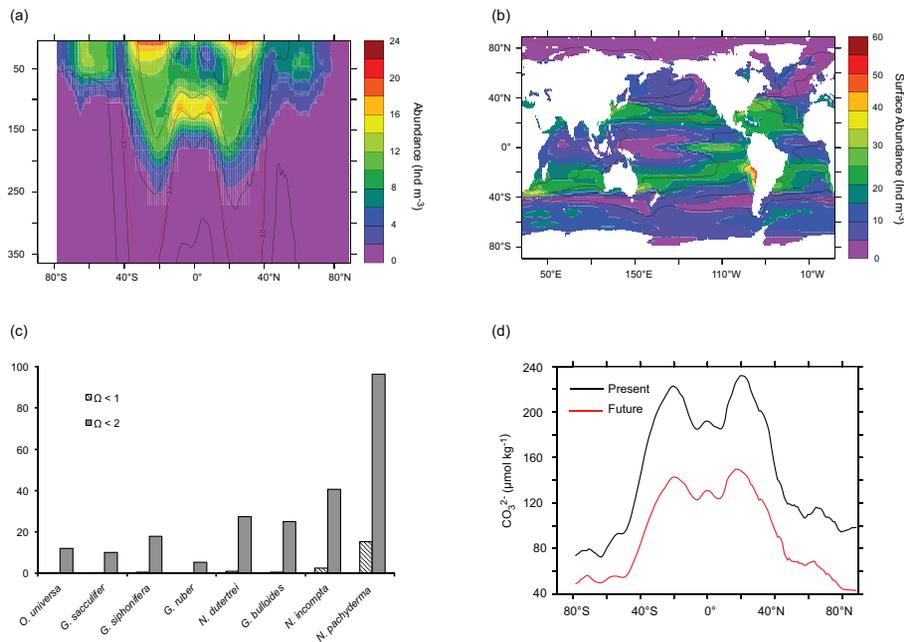
Figure 8. Future changes in carbon chemistry of the potential suitable habitat of foraminifera. Simulated present day total abundance of foraminifera: **(a)** zonal mean (ind m^{-3}), and **(b)** surface (ind m^{-3}). The contours represent the calcite saturation state, Ω_C, for the present day (black) and the future (red). **(c)** The percentage of the potential suitable habitat of foraminifer species with low calcite saturation states, $\Omega_C < 2$. **(d)** The present day and future simulated carbonate ion concentration (µmol kg^{-1}) of the potential suitable habitat of all foraminifer species.