

Use of Foraminifera in Climate Science

Gerhard Schmiedl

Subject: Past Climates Online Publication Date: Apr 2019

DOI: 10.1093/acrefore/9780190228620.013.735

Summary and Keywords

The understanding of past changes in climate and ocean circulation is to a large extent based on information from marine sediments. Marine deposits contain a variety of microfossils, which archive (paleo)-environmental information, both in their floral and faunal assemblages and in their stable isotope and trace element compositions. Sampling campaigns in the late 19th and early 20th centuries were dedicated to the inventory of sediment types and microfossil taxa. With the initiation of various national and international drilling programs in the second half of the 20th century, sediment cores were systematically recovered from all ocean basins and since then have shaped our knowledge of the oceans and climate history. The stable oxygen isotope composition of foraminiferal tests from the sediment cores delivered a continuous record of late Cretaceous–Cenozoic glaciation history. This record impressively proved the effects of periodic changes in the orbital configuration of the Earth on climate on timescales of tens to hundreds of thousands of years, described as Milankovitch cycles. Based on the origination and extinction patterns of marine microfossil groups, biostratigraphic schemes have been established, which are readily used for the dating of sediment successions. The species composition of assemblages of planktic microfossils, such as planktic foraminifera, radiolarians, dinoflagellates, coccolithophorids, and diatoms, is mainly related to sea-surface temperature and salinity but also to the distribution of nutrients and sea ice. Benthic microfossil groups, in particular benthic foraminifera but also ostracods, respond to changes in water depth, oxygen, and food availability at the sea floor, and provide information on sea-level changes and benthic-pelagic coupling in the ocean. The establishment and application of transfer functions delivers quantitative environmental data, which can be used in the validation of results from ocean and climate modeling experiments. Progress in analytical facilities and procedures allows for the development of new proxies based on the stable isotope and trace element composition of calcareous, siliceous, and organic microfossils. The combination of faunal and geochemical data delivers information on both environmental and biotic changes from the same sample set. Knowledge of the response of marine microorganisms to past climate changes at various amplitudes and pacing serves as a basis for the assessment of future resilience of marine ecosystems to the anticipated impacts of global warming.

Use of Foraminifera in Climate Science

Keywords: marine micropaleontology, marine ecology, paleoceanography, paleoclimate, foraminifera, biostratigraphy, plankton evolution, benthic-pelagic coupling, microhabitats, transfer functions

Introduction

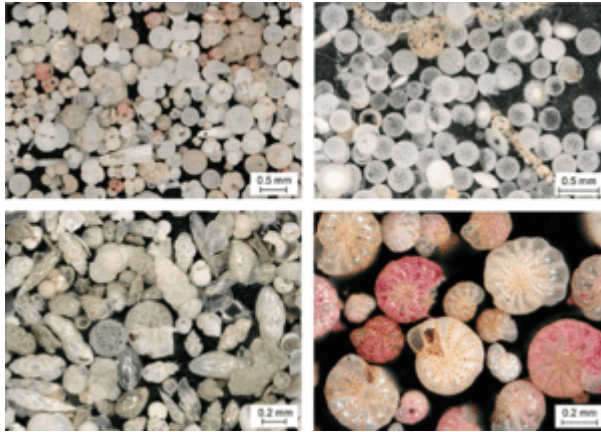


Figure 1. Microscopic images of the sand size fraction ($>63\ \mu\text{m}$) from various marine sediment samples. Upper left: Foraminiferal ooze from the deep-sea of the Caribbean Sea representing a diverse tropical assemblage of planktic foraminifera and a few cone-shaped pteropods. Upper right: Radiolarians and agglutinating benthic foraminifera from the abyssal Southern Ocean. The sample was deposited below the calcite compensation depth. Lower left: Benthic and planktic foraminifera, and radiolarians from the lower part of the oxygen minimum zone on the southwest African continental slope. The foraminiferal fauna is dominated by infaunal benthic foraminifera adapted to eutrophic and dysoxic conditions. Lower right: Low-diverse benthic foraminiferal fauna from intertidal environments of the southeastern North Sea. All images from author.

Microfossils are common constituents of marine deposits and may dominate the lithology of the sediment. Examples are the widely distributed calcareous nannofossil-dominated chinks of the late Cretaceous, the Cenozoic foraminiferal oozes at low to intermediate latitudes, and the Cenozoic diatom oozes of the Southern Ocean (Kennett, 1982). In the modern oceans, vast areas are covered by pelagic sediments, which primarily consist of microfossil remains from single-celled planktic organisms (Dutkiewicz, Müller, O'Callaghan, & Jónasson, 2015). A few examples of typical microfossil associations in the sand fraction of marine sediments are shown in Figure 1. In tropical to temperate regions, the deep-sea floor above the calcite compensation depth (CCD) is commonly covered by calcareous nannofossil-foraminiferal ooze, while siliceous microfossils (diatoms and radiolarians) are dominant below the CCD, and in high-productivity areas (Berger & Herguera, 1992; Dutkiewicz et al., 2015). Benthic organisms are more abundant in continental slope and shelf ecosystems, and in marginal marine settings, where their remains can represent the dominant microfossil group (Fig. 1). Under suitable preservation condi-

Use of Foraminifera in Climate Science

tions, such as hypoxia, neritic marine sediments commonly contain a significant amount of organic microfossils, particularly the cysts of dinoflagellates (dinocysts), which provide complementary environmental information on near-coastal oceanography and oxygenation (Sluijs, Pross, & Brinkhuis, 2005).

Even a small deep-sea sediment sample commonly contains a large number of microfossils. The diversity, morphology, species composition, and geochemistry of their skeletal remains from ocean sediment cores has delivered a wealth of information on changes of oceanic climate and circulation during the Mesozoic and Cenozoic time periods. Older marine sediments from land sections commonly also contain a variety of microfossils. Important Paleozoic microfossil groups include acritarchs and radiolarians (Riegel, 2008; Servais et al., 2016), larger foraminifera (e.g., fusulinids: BouDagher-Fadel, 2018), and ostracods (Crasquin & Forel, 2013). The evolution of the different groups is closely linked to climate and sea-level changes, and is punctuated by the impact of mass extinctions and subsequent radiation phases (Falkowski et al., 2004). Stable isotope records of foraminifera document the Cretaceous and Cenozoic climate evolution in detail (Zachos, Pagani, Sloan, Thomas, & Billups, 2001; Friedrich, Norris, & Erbacher, 2012; Holbourn et al., 2018). The close reflection of orbital changes in the data series provides a powerful tool for cyclostratigraphic age control of marine sediments (Imbrie et al., 1984; Lisiecki & Raymo, 2005; Hinnov & Hilgen, 2012).

Marine micropaleontological research in the 21st century is commonly conducted in interdisciplinary teams and delivers quantitative information on the physical and biogeochemical properties of past oceans (e.g., Kucera, Schneider, & Weinelt, 2006). These studies are accompanied by and integrated with research on the biodiversity, molecular phylogeny, biomineralization and biology of the different microfossil groups (e.g., Armbrust, 2009; De Nooijer, Spero, Erez, Bijma, & Reichart, 2014; Morard et al., 2016; Bernhard, Geslin, & Jordan 2018). In the early 21st century, a new tradition of communication skills is developing for the realization of joint transdisciplinary projects between proxy- and model-based research and research placed within a societal context.

This article aims at providing a concise overview on the use of marine micropaleontology in climate science. Emphasis is laid on applications of foraminifera and their geochemical test composition with reference to other microfossil groups from the late Mesozoic and Cenozoic eras. Benthic and planktic foraminifera are common constituents in marine sediments representing a wide range of shallow to deep marine ecosystems. Due to their comparably large size, foraminifera are easy to study and probably represent the prime group of microfossil applications in climate science. The various topics addressed reflect a personal choice of the author and do not provide an adequate representation of other microfossil groups and applications for the Paleozoic and early Mesozoic eras.

Development of Marine Micropaleontology in Climate Science

Historical Milestones in Marine Micropaleontology

The historical development of marine micropaleontology is closely connected to technical innovations and the systematic exploration of the oceans. The invention of the first compound microscope by the Dutch optician Zacharias Janssen in the year 1590 and subsequent advancement of optical microscopes allowed for the study of sand-sized and smaller objects in great detail.

Among the first images of marine microfossils is a foraminifer depicted in a letter of Antoni van Leeuwenhoek from the year 1700, which can be clearly assigned to *Elphidium*, a widespread genus of intertidal and inner-neritic ecosystems. More systematic studies on microfossils followed, including the work of Bianchi (1739), Soldani (1780, 1791) and Fichtel and Moll (1803), in which foraminifera were considered as “micro-mollusks,” specifically, microscopic ammonites (Romano, 2015). The class foraminifera was finally introduced by d’Orbigny (1826).

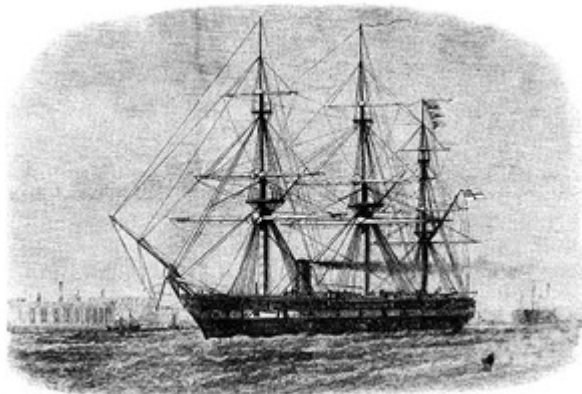


Figure 2. H.M.S. *Challenger* launched in 1858. The Challenger expedition from 1872 to 1876 was the first global scientific cruise and delivered important data on the oceanography, biology, and sediment composition of all major ocean basins. The research included the documentation of microfossils in sediment samples. From the “Report on the scientific results of the voyage of H.M.S. *Challenger* during the years 1873–1876.” Unknown artist, between 1885 and 1895, retrieved from Wikipedia.

A great advancement in the study of marine microfossils came with the scientific exploration of the oceans during numerous ship-based expeditions. Sampling campaigns in the late 19th and early 20th centuries were dedicated to the inventory of life in the oceans, sediment types, and microfossil taxa. The documented results of campaigns such as the expedition of the H.M.S. *Challenger* (Fig. 2) in the years 1872 to 1876 still provide the systematic basis for many modern micropaleontological studies. The scientific results of

Use of Foraminifera in Climate Science

this expedition were published in no fewer than 50 volumes. One volume was dedicated to the description and illustration of radiolarians by Ernst Haeckel (1887), another volume to the documentation of foraminifera by Henry B. Brady (1884). The microfossil collections of Ernst Haeckel (radiolarians) and Christian G. Ehrenberg (a micropaleontologist of the 19th century who studied diatoms) are still matter of reexamination (Tanimura & Aita, 2009). The foraminiferal taxonomy of Brady (1884) was revised twice, by Barker (1960) and Jones (1994), who updated the taxonomy to modern standard and added valuable historical information on the Challenger expedition, collections, and the activities of contemporary scientists. Various other expeditions followed and over the years accumulated information on the taxonomy and distribution patterns of marine microfossils. These expeditions included the Gauss expedition (1901–1903), the British Terra Nova expedition (1910), the German Meteor expedition (1925–1927), and the Swedish Albatross expedition (1947–1948), just to mention a few examples.

With the initiation of the Deep-Sea Drilling Project (1968–1983; international phase from 1975) and subsequent international ocean drilling programs (ODP 1985–2003, IODP since 2003), sediment cores were systematically drilled in all ocean basins and the recovered materials were used to boost the understanding on Cretaceous and Cenozoic climatic, environmental, evolutionary, and ocean circulation changes. Among many others, micropaleontological highlights include the documentation of extinction and recovery dynamics of the ecosystem across the Cretaceous–Paleogene boundary interval (Culver, 2003; Coxall, D’Hondt, & Zachos, 2006; Alegret, Thomas, & Lohmann, 2012; Lowery et al., 2018), and evidence of the impact of hyper-thermal conditions, ocean acidification, and deoxygenation during the Paleocene–Eocene thermal maximum (and other hyperthermal events) on planktic and deep-sea ecosystems (Thomas, 1989; Gibbs, Bown, Sessa, Bralower, & Wilson, 2006; Thomas, 2007; Jennions, Thomas, Schmidt, Lunt, & Ridgwell, 2015; Schmidt, Thomas, Authier, Saunders, & Ridgwell, 2018) (see “RESILIENCE AND RECOVERY POTENTIAL OF MARINE ECOSYSTEMS WITH RESPECT TO PERTURBATIONS”).

Modern marine micropaleontology relies to a large extent on field studies but increasingly involves laboratory experiments, such as cultivation of plankton and benthic microfossil groups under controlled conditions (e.g., Hemleben & Kitazato, 1995; Spero, Bijma, Lea, & Bemis, 1997; Kitazato & Bernhard, 2014; Schlüter et al., 2014), applications of high-resolution computer tomography (e.g., Caromel, Schmidt, & Rayfield, 2017), and the modeling of population dynamics and biogeographic patterns (e.g., Weinmann, Rödder, Lötters, & Langer, 2013).

Plankton Evolution, Biostratigraphy, and Ecology

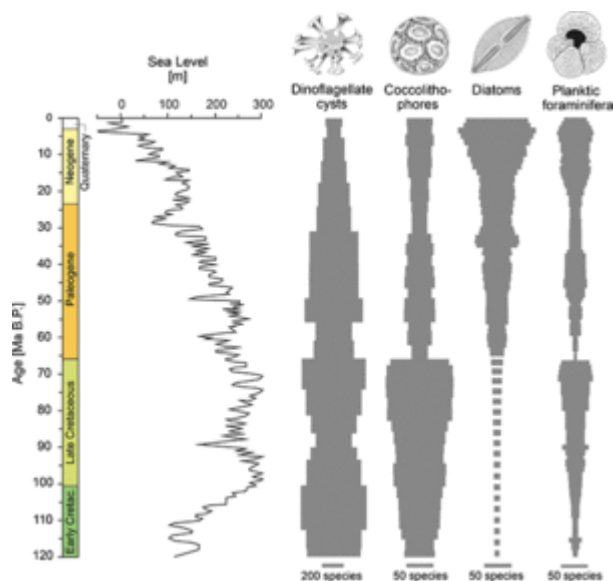


Figure 3. Species diversity of selected plankton groups in relation to sea-level evolution of the past 120 million years. The radiations of calcareous plankton groups correspond to major sea-level cycles. Sea-level record is from Haq and Al-Quahtani (2005); diversity patterns of plankton groups are from Stover et al. (1996, dinoflagellates), Bown et al. (2004, coccolithophores), Spencer-Cervato (1999, diatoms), and McGowran (2012, planktic foraminifera).

The biogeochemical cycling of organic and inorganic carbon in the oceans and the functioning of marine ecosystems on different trophic levels are fundamentally dependent on photosynthesizing prokaryotes and eukaryotic phyto- and zooplankton (Longhurst, 1991; Falkowski & Knoll, 2007). Important phytoplankton groups such as calcareous nannofossils, autotrophic dinoflagellates, and diatoms, first originated in the Mesozoic, and—in spite of several extinction events—experienced marked radiation phases during the late Cretaceous, Paleogene, and Neogene (Knoll & Follows, 2016; Wiggan, Riding, Fensome, & Mattioli, 2018) (Fig. 3). Evolutionary turnover and productivity pulses of radiolarians exhibit a complex pattern and induced a stepwise decrease of dissolved silica levels during the Phanerozoic (Racki & Cordey, 2000). As a first approximation, the evolution of planktic foraminifera parallels that of phytoplankton and reveals particularly high diversities during the late Cretaceous, Eocene, and middle Miocene (McGowran, 2012). The appearance and dispersal of planktic calcifiers profoundly changed the CaCO_3 saturation state of the ocean, leading to the establishment of a calcite compensation depth in the deep ocean (Zeebe & Westbroek, 2003). Changes in plankton diversity retrace the long-term sea-level development, suggesting a close relationship between planktic ecosystems, sea-surface temperature (SST) and the area of flooded continental shelves (e.g., Bown, Lees, & Young, 2004; Falkowski et al., 2004) (Fig. 3). The complex interplay between evolutionary and ecological processes also influences the body size and morpholo-

Use of Foraminifera in Climate Science

gy of marine plankton, although the relations are not fully understood (Gibbs et al., 2006; Schmidt, Lazarus, Young, & Kucera, 2006).

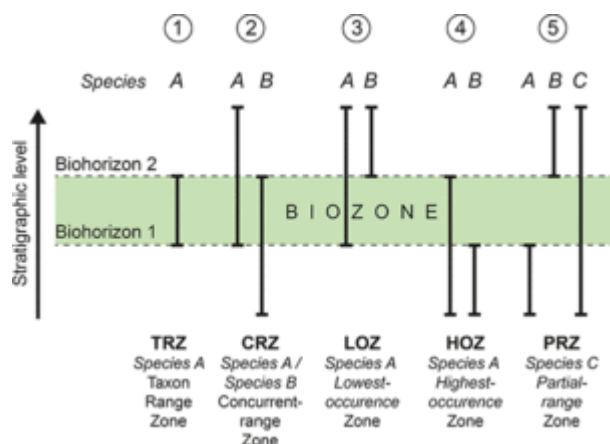


Figure 4. Concept of biostratigraphical zones based on the nomenclature proposed by Wade et al. (2011). Note that at least one of the biostratigraphic maker species must occur within the biozone.

The rapid floral and faunal turnover of phyto- and zooplankton and its wide distribution in marine sediments are the basis for manifold biostratigraphic and paleo-biogeographic applications. The origination and extinction patterns of marker taxa are used to define biostratigraphical zones. These biozones are specified by the International Commission on Stratigraphy, based on the temporal range of a single taxon or the combination of first and last appearance data (FAD, LAD) of several taxa (Wade, Pearson, Berggren, & Pälike, 2011; Gradstein, 2012) (Fig. 4). Regional biostratigraphic schemes were originally established in cooperation with oil and gas exploration in the early 20th century, and in the following decades reached a high level of sophistication with the generation of global biostratigraphic and chronological schemes in the frame of the international drilling campaigns (summary in Wade et al., 2011). Since the late 20th century, the application of astrochronological approaches has allowed for the refinement of biochrons and has greatly improved the applicability of marine proxy records for accurately dated paleoclimate reconstructions (e.g., Raffi et al., 2006; Hinnov & Hilgen, 2012). Useful ecobiostratigraphic information can also be retrieved from temporal changes in the abundance patterns of certain microfossil taxa during the Quaternary, such as the planktic foraminifer *Globorotalia menardii* in the Atlantic Ocean (Ericson, Ewing, Wollin, & Heezen, 1961), or the radiolarian *Cycladophora davisiana* in the Southern Ocean (Brathauer, Abelman, Gersonde, Niebler, & Fütterer, 2001).

Use of Foraminifera in Climate Science

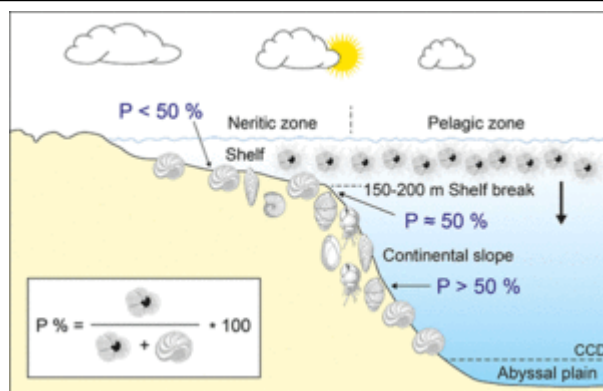


Figure 5. General proportion of planktic foraminiferal tests (P %) in shelf and deep-sea sediments. Planktic foraminifera are less common in shallow-water settings but increase in abundance with distance from shore. By contrast, the benthic foraminiferal number decreases with increasing water depth due to the depth-related decrease in food availability. P % values according to Gibson (1989) and Van der Zwaan et al. (1990). CCD = calcite compensation depth.

Field studies using plankton tows, filtering of water samples from various depth levels, and sediment traps yielded manifold insights into the distribution and ecology of different systematic groups and provide the basis for the paleo-ecological interpretation of planktic microfossils (e.g., Bork et al., 2015). The majority of phytoplankton species inhabit the mixed layer of the oceans, as long as sufficient light and nutrients are available, and account for almost half of the net primary production on Earth (Field, Behrenfeld, Rander-son, & Falkowski, 1998; Falkowski & Knoll, 2007). Some zooplankton groups, such as planktic foraminifera and radiolarians, live in parts in the mixed layer, but also inhabit deeper water levels. These groups avoid turbid coastal conditions, because they pass through vertical habitat changes during their life cycle and are commonly confined to narrow salinity ranges (Lazarus, 2005; Schiebel & Hemleben, 2017). Accordingly, the proportion of planktic foraminifera to the total number of foraminifera in the sediment, often also referred to as plankton/benthos ratio, reflects the depositional water depth or distance to the coast (or both). This proxy can be applied as a simple but powerful tool to the approximation of paleo-water depth at the time of deposition (Gibson, 1989; Van der Zwaan, Jorissen, & de Stigter, 1990) (Fig. 5). As a rule of thumb, planktic foraminiferal tests account for approximately 50% of the total foraminiferal tests in sediments from the shelf break, and their proportion decreases above and increases below that level (Fig. 5). This relation is also affected by changes in shelf and slope geometry, and changes in productivity and oxygen content (Berger & Diester-Haass, 1988; Van Hinsbergen, Kouwenhoven, & van der Zwaan, 2005) (see “QUANTITATIVE RECONSTRUCTION OF RELATIVE SEA-LEVEL CHANGE”).

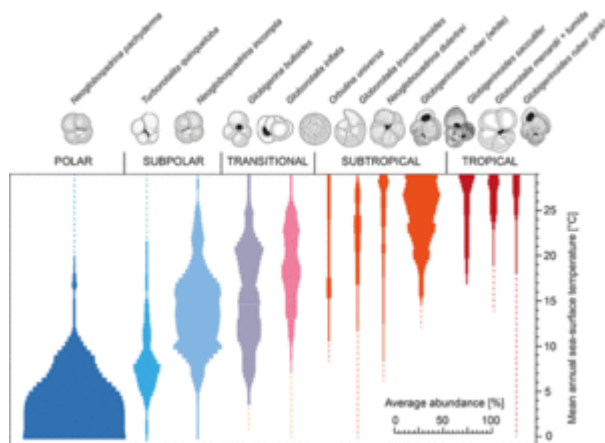


Figure 6. Abundance plots of selected modern planktic foraminiferal species in relation to sea surface temperature (SST). The plots are based on data from surface sediments of the Atlantic Ocean (Kucera et al., 2005) and reflect the strong relationship between species abundance and SST.

Figure modified and complemented after Kucera (2007).

Most modern plankton taxa and assemblages are closely associated with SST resulting in zonal distribution patterns of coccolithophorids (McIntyre & Bé, 1967; Ziveri, Baumann, Böckel, Bollmann, & Young, 2004), diatoms (Cermeño & Falkowski, 2009), radiolarians (Moore, 1978; Lazarus, 2005), and planktic foraminifera (Bé, 1977; Schiebel & Hemleben, 2017). Similar biogeographic patterns have been reconstructed for past oceans (e.g., Mutterlose, Bornemann, & Herrle, 2005; Woods et al., 2014). Species–SST relationships are particularly well expressed in planktic foraminifera (Fig. 6), for which reason this group provided the most accurate and widely applicable transfer functions for late Quaternary SST reconstructions (Kucera et al., 2005) (see “QUANTITATIVE RECONSTRUCTION OF SURFACE-WATER TEMPERATURE AND SALINITY”).

The distribution of phytoplankton also responds to nutrient availability, as impressively illustrated by the distribution of chlorophyll in the surface ocean, based on satellite remote sensing (NASA Earth Observatory). In high-productivity regimes, plankton communities are typically dominated by diatoms and other siliceous microfossils (e.g., Gersonde, Crosta, Abelmann, & Armand, 2005). In low-latitude upwelling regions, such as the Arabian Sea, diatoms seem to compete with coccolithophorids for nutrients, resulting in seasonal and spatial plankton successions (Schiebel et al., 2004).

Benthic-Pelagic Coupling and Ecology of Benthic Foraminifera

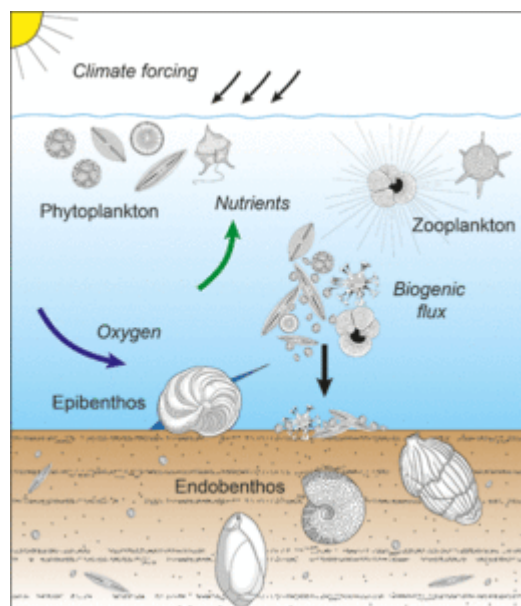


Figure 7. General concept of benthic-pelagic coupling and biogeochemical cycles in the ocean. The different microfossil groups represent various marine ecosystems and trophic levels, and record environmental information through the floral, faunal, and geochemical composition of their fossilized remains. The marine ecosystems are closely linked through the formation of oxygen-rich deep-water masses, upwelling of nutrients, and organic matter fluxes.

Deep-sea benthic ecosystems are linked to the surface ocean via organic matter fluxes serving as the basic food resource for the organisms at the sea floor and within the sediments. This dependence is described as benthic-pelagic coupling (Graf, 1989), in which climate-related productivity changes in the surface ocean are transferred to the deep-sea realm (Cronin & Raymo, 1997) (Fig. 7). In the open ocean, approximately 10–40% of the organic carbon produced by photo- and zooplankton is exported from the photic zone, and only 0.01–1% arrives at the sea floor (Betzer et al., 1984; Berger & Wefer, 1990; Henson, Sanders, & Madsen, 2012). This proportion depends on water depth, settling velocity, and microbial decomposition rate in the water column, thus on the efficiency of the biological pump (Passow & Carlson, 2012). Deep-sea ecosystems are further influenced by oxygen availability, which is controlled by the ventilation of subsurface water masses, water temperature, and the microbial oxygen consumption. In the contemporary oceans, the majority of benthic ecosystems are well ventilated. Strong oxygen minimum zones (OMZ) develop at intermediate depth below high-productivity areas, for example in the Arabian Sea and the western boundary currents off Africa and America (Helly & Levin, 2004).

Oceanographic data document a worldwide OMZ expansion during the late 20th and early 21st centuries responding to global climate warming (Keeling, Körtzinger, & Gruber, 2010; Schmidtko, Stramma, & Visbeck, 2017). The expected changes will likely have sig-

Use of Foraminifera in Climate Science

nificant biological impacts, such as vertical compression of benthic habitats (Stramma, Levin, Schmidtke, & Johnson, 2010).

Changes in benthic-pelagic coupling through time can be monitored through the investigation of microfossils, because various groups represent specific planktic and benthic ecosystems and different trophic levels. In this context, benthic foraminiferal faunas and their stable isotope and trace element signals can serve as proxies for the documentation of past natural oxygen variability and food fluxes (e.g., Zahn, Winn, & Sarnthein, 1986; Van der Zwaan et al., 1999; Murray, 2006; Jorissen, Fontanier, & Thomas, 2007; Hoogakker, Elderfield, Schmiedl, McCave, & Rickaby, 2015, Hoogakker et al., 2018) (see “QUANTITATIVE RECONSTRUCTION OF SURFACE PRIMARY AND EXPORT PRODUCTIVITY, ORGANIC MATTER FLUXES, AND OXYGEN”).

The distribution of deep-sea benthic foraminifera was originally related to specific water depth intervals (Bandy & Chierici, 1966), which appeared to be associated with physical and chemical characteristics of distinct water masses (e.g., Schnitker, 1974). Based on this relationship, shifts of water mass boundaries during glacial and interglacial changes were tentatively reconstructed, although the underlying ecological mechanisms remained elusive (e.g., Streeter & Shackleton, 1979). Subsequent ecological studies revealed that the species composition and microhabitat structure of deep-sea benthic foraminifera respond to changes in food availability and oxygen concentration at the sea floor (summary in Jorissen et al., 2007), and also to near-bottom current strength (Schönfeld, 2002).

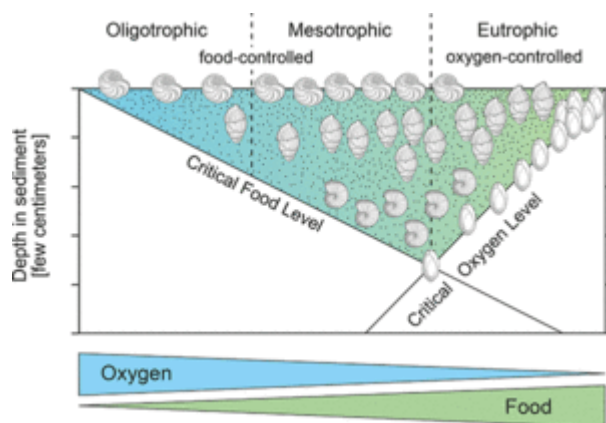


Figure 8. Conceptual model (TROX model) of Jorissen et al. (1995) describing the general dependence of the benthic foraminiferal microhabitat structure on food supply (trophic conditions) and oxygen. Figure modified and complemented after Jorissen et al. (2007).

Different benthic foraminifera inhabit specific microhabitats on and below the sediment surface and are able to change their microhabitat in response to changing biogeochemical conditions (e.g. Corliss, 1985; Mackensen & Douglas, 1989; Linke & Lutze, 1993). The simplified, general ecology of deep-sea foraminifera is best described by the so-called Trophic-Oxygen model (or TROX model), which considers the counteracting influences of food and oxygen, and resulting biogeochemical niches (Jorissen, de Stigter, & Widmark,

Use of Foraminifera in Climate Science

1995; Fontanier et al., 2002) (Fig. 8). In oligotrophic and well-oxygenated environments, the fauna is of low to intermediate diversity and mainly comprises epifaunal (epibenthic) taxa. In mesotrophic environments, faunal diversity is at a maximum and a variety of epifaunal and infaunal (endobenthic) niches are developed. Eutrophic, oxygen-limited ecosystems are inhabited by a low-diversity fauna with high standing stock and dominance of deep-infaunal taxa, which are adapted to dysoxic conditions (Jorissen et al., 1995). Laboratory experiments revealed a diverse metabolic capacity of benthic foraminifera and demonstrated that various species are able to respire nitrate through denitrification in order to sustain their respiration even under anoxic conditions (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010).

Further ecological studies demonstrated that benthic foraminifera have specific requirements concerning the quality of organic matter as food source (Caralp, 1989; Koho et al., 2008), and some taxa respond to seasonal pulses of phytodetritus to the deep sea (Gooday, 1988; Ohga & Kitazato, 1997; Gooday & Rathburn, 1999; Heinz, Kitazato, Schmiedl, & Hemleben, 2001). Most deep-sea benthic foraminiferal taxa have excellent dispersal capacities through the dissemination of propagules (Alve & Goldstein, 2010), accounting for broad distributional ranges. Their biogeography is controlled by the combination of ocean history, such as formation of gateways, the specific evolutionary histories, and various environmental factors (Gooday & Jorissen, 2012). Specifically, zonal patterns in the diversity and species composition of Cenozoic deep-sea benthic foraminifera seem to be mainly linked to surface productivity and related food fluxes (Thomas & Gooday, 1996).

Neritic and littoral environments are more environmentally variable than deep-sea environments, because they are influenced by strong geographic and bathyal gradients in light, temperature, salinity, pH, substrate, and current strengths (Culver, Woo, Oertel, & Buzas, 1996; Sen Gupta 1999; Murray, 2006). These parameters are commonly associated with water depth or elevation and are reflected in the vertical zonation of benthic foraminifera (e.g., Scott & Medioli, 1978; Milker et al., 2009) and ostracods (Cronin, 2015) in shallow-marine and coastal environments. Accordingly, these microfossil groups prove useful in sea-level reconstructions at various timescales, although alteration of fossil assemblages by taphonomic processes has to be considered (Murray & Alve, 1999; Berkeley, Perry, Smithers, Horton, & Taylor, 2007). Coastal ecosystems are susceptible to anthropogenic impacts, such as pollution and eutrophication-induced hypoxia, and benthic foraminifera, ostracods, and dinoflagellates prove useful as biomonitoring tools (Thomas, Gapotchenko, Varekamp, Mecray, & Buchholtz ten Brink, 2000; Ruiz et al., 2005; Gooday et al., 2009; Zonneveld et al., 2012; Alve et al., 2016).

Stable Isotope Records and Changes in Climate and Ocean Circulation

Stable isotope analyses have been carried out on a variety of calcareous, siliceous, and organic microfossils. In this context, the stable oxygen and carbon isotope signatures of foraminifera, expressed in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, are widely used in paleoceanography and paleoclimatology (Ravelo & Hillaire-Marcel, 2007). The geochemical composition of

Use of Foraminifera in Climate Science

foraminiferal test calcite basically reflects various environmental factors during calcification, although the reasons for species-specific controls on isotope fractionation during biomineralization, so-called “vital effects,” are still not fully understood (e.g., De Nooijer et al., 2014).

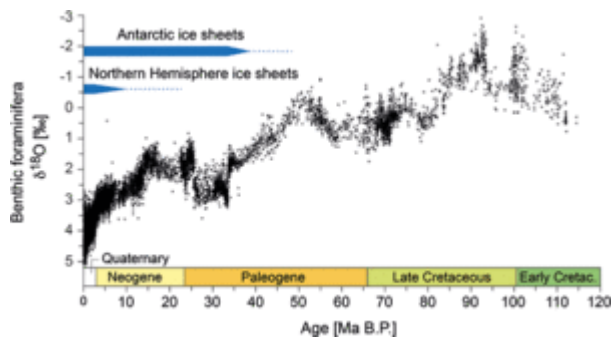


Figure 9. Compilation of stable oxygen isotope data of benthic foraminifera for the past 115 million years reflecting the general climate evolution during the late Mesozoic and Cenozoic eras. Compilation by Friedrich et al. (2012) based on the Cenozoic compilation from Zachos et al. (2008) and various Cretaceous data sets (see Friedrich et al., 2012 for further reference).

The foraminiferal $\delta^{18}\text{O}$ signal primarily reflects the combined influences of ice volume, temperature, and salinity (summaries in Rohling & Cooke, 1999; Pearson, 2012). Accordingly, $\delta^{18}\text{O}$ compilations document the hyper-thermals of the late Cretaceous and early Paleogene and subsequent Antarctic and Arctic glaciation histories in great detail (Zachos et al., 2001; Zachos, Dickens, & Zeebe, 2008; Friedrich et al., 2012; Holbourn et al., 2018) (Fig. 9).

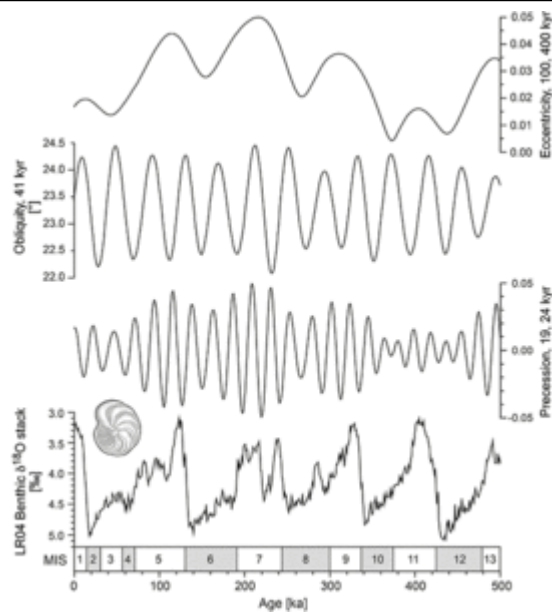


Figure 10. Deep-sea epibenthic foraminiferal stable isotope stack “LR04” for the past 500,000 years (Lisiecki & Raymo, 2005) in comparison with time series of orbital parameters eccentricity (100, 400 kyr), obliquity (41 kyr), and precession (19, 24 kyr). The orbital parameters were calculated with AnalySeries 2.0 (Paillard, Labeyrie, & Yiou, 1996) based on the solution of Laskar et al. (2004). The saw-tooth pattern of the isotope stack reflects ice volume changes driven by the interference of the different orbital parameters. The marine stable isotope stages (MIS) are given according to the boundaries of Lisiecki and Raymo (2005).

Cultivation experiments revealed a strong fractionation of oxygen isotopes during calcification under the influence of variable temperature at constant isotopic composition of water (Epstein, Buchsbaum, Lowenstam, & Urey, 1953). This observation was used to establish equations for temperature reconstructions (summary in Bemis, Spero, Bijma, & Lea, 1998). Foraminiferal $\delta^{18}\text{O}$ records contain significant variability in the orbital bands of eccentricity (100, 400 kyr), obliquity (41 kyr), and precession (19, 24 kyr), demonstrating the impact of orbital forcing on global climate and amplification of these signals within the Earth system (Imbrie et al., 1984) (Fig. 10). The characteristic pattern of stacked $\delta^{18}\text{O}$ records is widely used to evaluate the past dynamics of ice volume, sea level, and temperature (e.g., Shackleton, 1987; Siddall et al., 2003), but also to develop age models for Pliocene and Pleistocene (Imbrie et al., 1984; Lisiecki & Raymo, 2005) and older sediment successions (Grossman, 2012). During the Quaternary, temperature and salinity varied comparatively little in deep and bottom waters, thus deep-sea benthic foraminiferal $\delta^{18}\text{O}$ records for this time interval can be interpreted as a first approximation of continental ice volume (Waelbroeck et al., 2002).

On geological time-scales, $\delta^{13}\text{C}$ records from marine carbonates have been widely used in stratigraphy, because the $\delta^{13}\text{C}$ signature of dissolved inorganic carbon in the ocean reflects the partitioning between organic carbon and carbonate and is therefore directly

Use of Foraminifera in Climate Science

linked to the global carbon cycle and the terrestrial and marine biosphere (Saltzman & Thomas, 2012).

The $\delta^{13}\text{C}$ signal of planktic foraminifera primarily reveals information on the air-sea exchange of CO_2 , the photosynthesis-rem mineralisation cycle, and stratification of the surface water (Rohling & Cooke, 1999). Among other factors, the $\delta^{13}\text{C}$ offsets between different taxa yield insights into species-specific vital effects, symbiont activity (Spero, Lerche, & Williams, 1991), and calcification depths, which characterizes certain depth habitats in the mixed surface layer and thermocline (Mulitza et al., 1999). In marginal basins, $\delta^{13}\text{C}$ -based habitat reconstructions of planktic foraminifera may be biased by input of river run-off leading to decreased $\delta^{13}\text{C}$ values in epipelagic taxa and potential habitat changes (Rohling et al., 2004).

The $\delta^{13}\text{C}$ record of deep-sea epibenthic foraminifera is widely used for the reconstruction of changes in intermediate and deep-water circulation (e.g., Duplessy et al., 1988; Pahnke & Zahn, 2005; Mackensen, 2008). This application is based on the microbial decay of organic matter in the water column, which releases ^{12}C and results in decreasing $\delta^{13}\text{C}$ values of dissolved inorganic carbon in the water mass while spreading in the ocean (Charles & Fairbanks, 1992). Epifaunal and infaunal foraminifera reveal specific $\delta^{13}\text{C}$ offsets, which can be related to metabolic and porewater effects (Grossman, 1987; McCorkle, Keigwin, Corliss, & Emerson, 1990).

The combined analysis of the $\delta^{13}\text{C}$ signals from taxa with different microhabitat preferences (specifically, epifaunal and infaunal) retraces the porewater $\delta^{13}\text{C}$ gradient in the sediment, which depends on the organic matter flux rate and bottom water oxygen content (McCorkle & Emerson, 1988). Accordingly, the evaluation of multispecies $\delta^{13}\text{C}$ records opens applications for a variety of paleoceanographic reconstructions, such as changes in deep-water oxygenation (e.g., Schmiedl & Mackensen, 2006; Hoogakker et al., 2015, 2018) and surface water productivity (e.g., Zahn et al., 1986; Schilman, Almogilabin, Bar-Matthews, & Luz, 2003).

Applications of Foraminifera in Climate Science

Quantitative Reconstruction of Marine Environmental Parameters

One of the prime challenges of marine micropaleontology is the delivery of quantitative information on marine environmental parameters and processes in the past, such as changes in sea-level, sea-surface temperature and salinity, oxygen content and organic matter fluxes, pH, and current velocities. Such data do not only enhance the accuracy of paleoclimate reconstructions but can be also used for the validation of results from earth system model experiments. The discussion will now address a selection of current aspects of marine micropaleontology with a particular focus on foraminifera-based research.

Quantitative Reconstruction of Relative Sea-Level Change

Eustatic sea-level changes are ultimately linked to climate variability and have shaped the morphology, sediment facies, and ecosystems of continental shelves and coastal areas on various timescales. During the early 21st century, quantitative reconstructions of past global sea-level changes have been refined utilizing the $\delta^{18}\text{O}$ records of deep-sea benthic foraminifera from the open ocean (e.g., Waelbroeck et al., 2002), but also the $\delta^{18}\text{O}$ records of planktic foraminifera from marginal basins such as the Red Sea and Mediterranean Sea (Siddall et al., 2003; Rohling et al., 2014; Grant et al., 2014). The marginal basins respond to sea-level changes by reduced exchange with the open ocean through narrow gateways, leading to amplified changes in surface water salinity, which in turn affect the foraminiferal $\delta^{18}\text{O}$ values. The generated time series yielded insights into the magnitude of glacial low-stands, contrasts between different interglacial high-stands, and even subtle sea-level changes during millennial-scale climate variability (Grant et al., 2014).

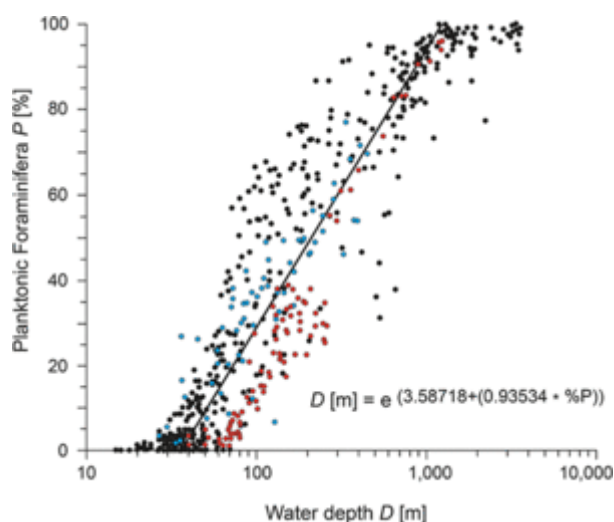


Figure 11. Relative proportion of planktic foraminifera (% P) to the total foraminifera in sediments from various water depths of the Adriatic Sea (red dots), Gulf of Mexico (black dots), and Gulf of California (blue dots), disregarding infaunal benthic foraminifera. The dependence of % P is best described by an exponential function and can be applied to paleobathymetric reconstructions.

Modified from Van der Zwaan et al. (1990).

Quantitative sea-level estimates can also be obtained from the proportion of planktic foraminifera in the total foraminiferal fauna (see also “PLANKTON EVOLUTION, BIOS-TRATIGRAPHY, AND ECOLOGY”). This simple approach was modified by removal of the proportion of infaunal benthic foraminifera, which can vary independently from water depth and instead depend on local organic matter fluxes and oxygen content (Van der Zwaan et al., 1990; Van Hinsbergen et al., 2005). The obtained exponential function fits

Use of Foraminifera in Climate Science

data sets from various oceans (Van der Zwaan et al., 1990) and proves widely applicable, but uncertainties remain relatively high (Fig. 11).

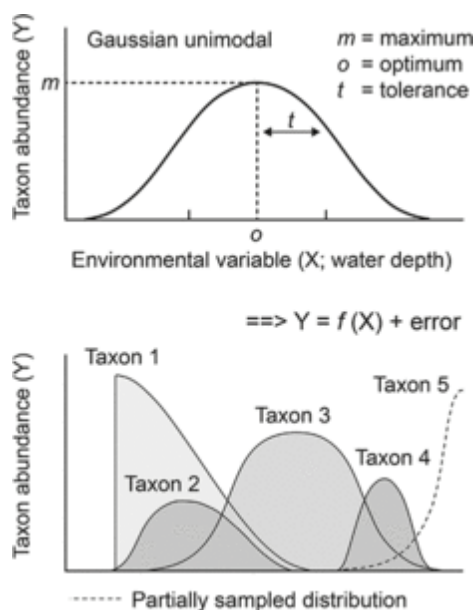


Figure 12. Concept of transfer functions to reconstruct relative sea level based on benthic foraminifera from intertidal and shelf environments. The abundance data of various taxa in a modern training data set are quantitatively related to the environmental parameter (e.g., water depth or elevation) applying numerical techniques.

Modified from Kemp and Telford (2015).

Much of the existing knowledge on late Holocene sea-level change and its coastal impacts is gained from the application of microfossil-based transfer functions on benthic foraminifera, ostracods, benthic diatoms, and testate amoebae from salt marshes (e.g., Scott & Medioli, 1978; Scott, Medioli, & Schafer, 2001; Kemp & Telford, 2015). The transfer function relates the usually unimodal distribution patterns of different taxa in a training data set to the desired environmental parameter (e.g., elevation, water depth, etc.) using regression methods such as Partial Least Squares (PLS), Weighted Averaging (WA), or the combination of both (WA-PLS) (Fig. 12). Application to well-preserved fossil assemblages from sediment cores delivered a wealth of accurate sea-level estimates, which extended the historical tide gauge records significantly back in time (e.g., Nydick, Bidwell, Thomas, & Varekamp, 1995; Horton & Edwards, 2006; Kemp et al., 2011; Zong & Sawai, 2015; Kemp et al., 2017). As one of the main results, the relative sea-level records confirm accelerated sea-level rise since the late 19th century.

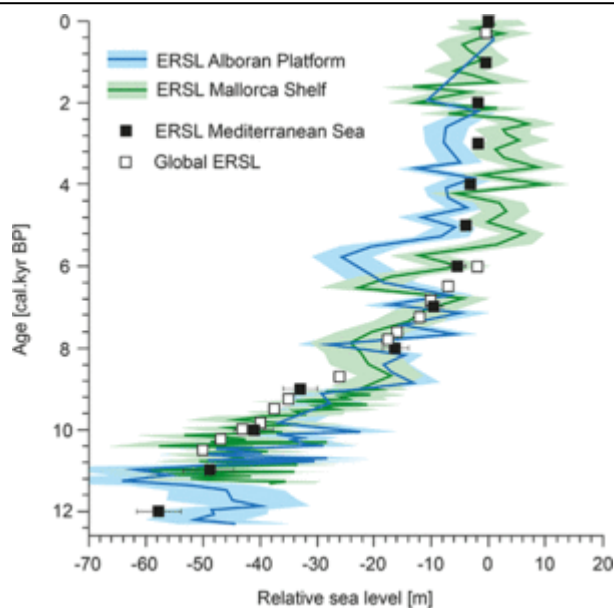


Figure 13. Application of a water depth transfer function to benthic foraminiferal assemblages from sediment cores of the Alboran Platform (blue) and the Mallorca Shelf (green) in the western Mediterranean Sea (Milker et al., 2011). The estimated relative sea-level (ERSL) changes match published global (Bard et al., 1996) and Mediterranean (Lambeck & Bard, 2000) reconstructions and mainly reflect the postglacial eustatic sea-level rise.

Similar statistical approaches have been extended to shelf environments and used for the reconstruction of Holocene sea-level changes in the Mediterranean Sea (Rossi & Horton, 2009; Milker, Schmiedl, & Betzler, 2011). The prediction errors of the established transfer functions were in the order of 5% to 10% of the water depth range considered in the training data set. The reconstructed Holocene sea-level histories for shelf environments in the western Mediterranean Sea match independent reconstructions confirming the good performance of shelf foraminifera-based transfer functions (Fig. 13). Also, transfer functions for water-depth estimates were applied to a range of other geological problems, including the estimation of vertical movements in the course of prehistoric megathrust earthquakes on the Pacific east coast (Milker et al., 2016) and quantification of neotectonic processes in the eastern Mediterranean (Milker et al., 2017).

Quantitative Reconstruction of Surface-Water Temperature and Salinity

Sea-surface temperature (SST) and sea-surface salinity (SSS) represent essential parameters for the understanding of past climate and ocean circulation changes. In the 1970s and 1980s, the first quantitative reconstruction of global SST distribution for the Last Glacial Maximum (LGM) was realized based on regression analyses of planktic microfossils in the framework of the joint international program Climate: Long Range Investigation, Mapping, and Prediction (e.g., CLIMAP project members, 1976). Surprisingly, the CLIMAP results suggested substantial regional contrasts in the glacial cooling pattern (Mix, Bard, & Schneider, 2001). Improved training data sets and transfer functions led to

Use of Foraminifera in Climate Science

amended reconstructions for the Atlantic Ocean in the project Glacial Atlantic Ocean Mapping (GLAMAP; Sarnthein et al., 2003). The accuracy of SST reconstructions was further improved by an interdisciplinary study which combined data from various plankton groups (diatoms, radiolarians, dinoflagellates, and planktic foraminifera) and geochemical proxies in the project Multiproxy Approach for the Reconstruction of the Glacial Ocean Surface (Kucera et al., 2006; MARGO project members, 2009). Based on these efforts, the magnitude of changes is well constrained, suggesting glacial SSTs which were on average 4°C lower than today, and amplified glacial cooling and associated faunal shifts at high latitudes. These results are essentially in agreement with modeling studies, but substantial uncertainties remain in tropical areas and on regional scales (Annan & Hargreaves, 2015).

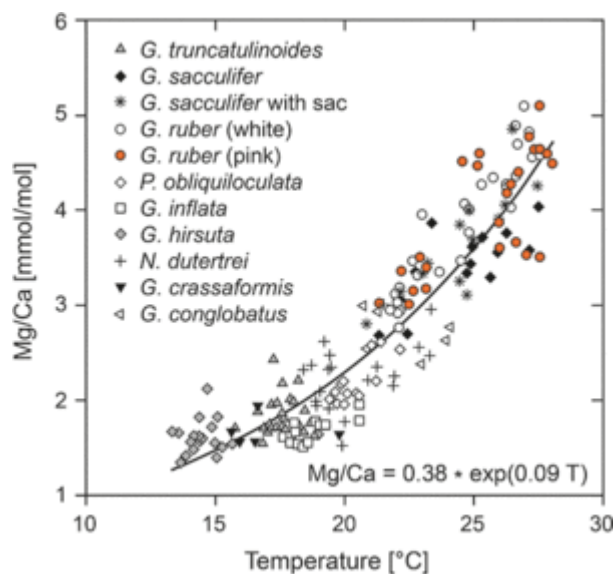


Figure 14. Temperature calibration for the Mg/Ca ratios of various planktic foraminiferal taxa displaying an exponential relationship between Mg/Ca and isotopically derived calcification temperatures (Anand, Elderfield, & Conte, 2003).

Figure modified from Barker et al. (2005).

Microfossil-based temperature reconstructions are increasingly complemented by the application of sophisticated geochemical proxies, biomarkers (e.g., alkenone $U^{K'}_{37}$, TEX 86), and the Mg/Ca value of foraminiferal test calcite (e.g., Rosell-Melé et al., 2004; Barker, Cacho, Benway, & Tachikawa, 2005; de Vernal et al., 2006; Wade et al., 2012). The Mg/Ca proxy is based on the observation that the Mg content in foraminifera test calcite increases proportionally to the calcification temperature (Lea, 2014). Various temperature calibrations have been established for a number of planktic and benthic foraminifera (for an example see Fig. 14). Since Ca and Mg have comparatively long oceanic residence times, late Quaternary Mg/Ca changes can be directly related to temperature changes, although accurate temperature estimates need to consider potential alteration by dissolution (Rosenthal & Lohmann, 2002). Over longer timescales (>1 Ma), the reconstruction of absolute temperatures has to consider changes in seawater Mg/Ca (Lear et al., 2015).

Use of Foraminifera in Climate Science

Changes in sea-surface salinity (SSS) are traditionally estimated by the combination of planktic foraminiferal $\delta^{18}\text{O}$ and independent temperature proxies (e.g., Sarnthein et al., 2004), although the relations between residual $\delta^{18}\text{O}$ values and SSS contain considerable regional uncertainties (Rohling, 2000; Ravelo & Hillaire-Marcel, 2007). Independent SSS estimates can be retrieved from the process length of specific dinoflagellate cysts (Verleye et al., 2012; Mertens et al., 2012). However, these studies suggested that cyst morphology responds to surface water density as a function of SSS and SST rather than to salinity alone. So far the only reliable independent salinity proxy was proposed by Bollmann, Herrle, Cortés, and Fielding (2009), who found a significant linear correlation between the size of placoliths of the cosmopolitan coccolithophorid species *Emiliania huxleyi* from plankton samples and *in-situ* SSS. This function was successfully applied to the reconstruction of the early Holocene water-mass exchange between the Aegean and Black seas (Herrle et al., 2018).

Quantitative Reconstruction of Surface Primary and Export Productivity, Organic Matter Fluxes, and Oxygen

Surface-water productivity, organic matter fluxes, and oxygen concentrations characterize the marine organic carbon pump and are commonly linked to each other, complicating their separation (see “BENTHIC-PELAGIC COUPLING AND ECOLOGY OF BENTHIC FORAMINIFERA”). Qualitative information on export production can be derived from diatom and radiolarian fluxes and the stable Si isotope composition of their skeletal opal (e.g., Crosta & Koç, 2007; Abelman et al., 2015). Export productivity has been quantified on the basis of the accumulation rate of benthic foraminifera in sediments from the western equatorial Pacific Ocean (Herguera & Berger, 1991). However, the transfer of this relation to other regions failed, suggesting a non-linear response of the foraminiferal number to organic matter fluxes and the interference of other parameters, such as oxygen levels (Schmiedl & Mackensen, 1997; Naidu & Malmgren, 1995). Also, minor changes in the transfer efficiency of exported organic matter (e.g., due to temperature changes and related changes in metabolic rates) could significantly change the food fluxes at the seafloor (Laws, Falkowski, Smith, Ducklow, & McCarthy, 2000; John et al., 2013).

A number of semi-quantitative to quantitative approaches have been developed on the benthic foraminiferal fauna, either based on species-specific flux regimes (Schönfeld & Altenbach, 2005) or on multivariate statistics (e.g., Kuhnt, Hess, & Jian, 1999; Wollenburg, Kuhnt, & Mackensen, 2001), but none of these approaches proved widely applicable as a straightforward quantitative paleoproductivity proxy (summary in Jorissen et al., 2007).

The $\delta^{13}\text{C}$ difference between shallow infaunal and epifaunal benthic foraminifera varies proportional to the organic matter flux rate (e.g., Zahn et al., 1986; McCorkle et al., 1990; Schilman et al., 2003). Accordingly, Theodor, Schmiedl, Jorissen, and Mackensen (2016) used the $\delta^{13}\text{C}$ signals of epifaunal taxa and the shallow infaunal *Uvigerina mediterranea* to develop a transfer function for organic carbon flux rate in the Mediterranean Sea. A comprehensive testing of this transfer function is still missing, but its applicability is likely restricted to open-ocean settings since isotope data from marginal settings with sub-

Use of Foraminifera in Climate Science

stantial lateral organic carbon fluxes lead to an overestimation of vertical fluxes and related surface water productivity (Theodor et al., 2016).

Oxygen exerts a strong control on deep-sea benthic diversity and microhabitat partitioning, facilitating the development of oxygen proxies on the basis of the benthic foraminiferal fauna (summary in Jorissen et al., 2007). Semi-quantitative oxygen indices use the ratio of various morphological groups (Kaiho, 1994), or a combination of the ratio between high- and low-oxygen tolerant taxa, and faunal diversity (Schmiedl et al., 2003). The latter approach was applied to the characterization of deep-water oxygen changes across the early Holocene sapropel S1 in the Mediterranean Sea (Schmiedl et al., 2010), illustrating the response of deep-water formation to low- and high-latitude climate forcing (see “RESILIENCE AND RECOVERY POTENTIAL OF MARINE ECOSYSTEMS WITH RESPECT TO PERTURBATIONS”).

Field and laboratory studies demonstrated that various benthic foraminifera taxa increase their pore density and size in response to reduced oxygen and enhanced nitrate concentrations in the bottom water (Perez-Cruz and Machain-Castillo, 1990; Moodley & Hess, 1992; Glock et al., 2011). This morphological adaptation is likely related to the respiration of the foraminifera as demonstrated by the clustering of mitochondria in the vicinity of the pores (Leutenegger & Hansen, 1979). In the meantime, transfer functions exist for a variety of taxa and regions (Glock et al., 2011; Kuhnt et al., 2013; Rathburn, Willingham, Ziebis, Burkett, & Corliss, 2018) and allowed estimating changes in the late glacial and Holocene nitrogen inventory of the Peruvian upwelling region (Glock et al., 2018).

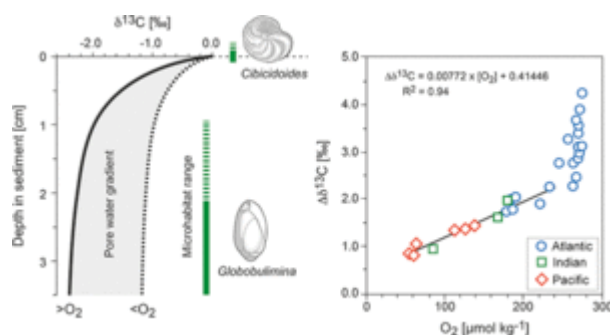


Figure 15. Relationship between bottom water oxygen and the stable carbon isotope difference ($\Delta\delta^{13}\text{C}$) between epifaunal and deep infaunal benthic foraminiferal taxa. Left: Conceptual model describing the pore water $\delta^{13}\text{C}$ gradient under contrasting bottom water oxygen concentrations and the microhabitat range of epifaunal and deep infaunal genera (following Schmiedl & Mackensen, 2006). Right: Oxygen calibration for the $\Delta\delta^{13}\text{C}$ signal between epifaunal and deep infaunal benthic foraminifera (modified from Hoogakker et al., 2015).

Changes in bottom water oxygen concentrations are also recorded in the isotope and trace element geochemistry of benthic foraminiferal test calcite. The $\delta^{13}\text{C}$ of dissolved in-

Use of Foraminifera in Climate Science

organic carbon in the pore water at sediment depth where oxygen approaches zero is directly related to the oxygen concentration of the bottom water (McCorkle & Emerson, 1988) (Fig. 15 left). Accordingly, the $\delta^{13}\text{C}$ difference between epifaunal benthic foraminifera, such as *Cibicidoides wuellerstorfi*, and deep infaunal taxa, such as *Globobulimina affinis*, can be used as proxy for bottom water oxygen (McCorkle et al., 1990). Two calibration data sets were generated on the basis of modern foraminifera and successfully applied to late Quaternary successions from the Arabian Sea, North Atlantic Ocean, and the equatorial Pacific Ocean (Schmiedl & Mackensen, 2006; Hoogakker et al., 2015, 2018). The applicability of this proxy is restricted to oxygen concentrations below $235 \mu\text{mol kg}^{-1}$ and lacks a clear relation above this threshold (Fig. 15 right).

In the 21st century, analytical progress, such as the application of secondary ion mass spectrometry, fostered the development of novel geochemical proxies for the redox state of ambient water. Field studies demonstrated that, in the absence of diagenetic alteration, Mn/Ca and I/Ca ratios of foraminiferal test calcite are highly redox-sensitive and increase proportionally to oxygen concentration (e.g., Glock et al., 2012; Glock, Liebetrau, Eisenhauer, & Rocholl, 2016). Accordingly, the I/Ca ratios in planktic foraminifera from a sediment core of the Southern Ocean were analyzed and used to document glacial decrease in dissolved oxygen concentration in the near-surface ocean (Lu et al., 2016). Similarly, planktic foraminiferal I/Ca gradients indicate lateral expansion of oxygen minimum zones in the Atlantic, Indian and Pacific oceans during the Paleocene-Eocene thermal maximum (Zhou, Thomas, Rockaby, Winguth, & Lu, 2014).

Quantitative Reconstruction of Bottom Current Strength

Bottom currents shape benthic ecosystems because they raise the energy at the benthic boundary layer, modify substrate at the sea floor, and transport suspended food particles. Bottom currents are particularly relevant in shallow-water ecosystems, on submarine elevations, and in areas influenced by oceanic gateways. In the South Atlantic Ocean, benthic foraminiferal faunas with a dominance of *Angulogerina angulosa* were assigned to sandy substrates in high-energy environments on submarine highs, the shelf edge, and upper slope (Mackensen, Schmiedl, Harloff, & Giese, 1995). The first quantitative relation between near-bottom current velocities and abundance of elevated epifaunal benthic foraminifera was established for the pathway of the Mediterranean Outflow Water (MOW) undercurrent in the Gulf of Cadiz, northeastern Atlantic Ocean (Schönfeld, 2002). The applicability of this function to the reconstruction of changes in MOW strength was evaluated based on early Pliocene benthic foraminiferal faunas from a sediment core of the Gulf of Cadiz (García-Gallardo, Grunert, Voelker, Mendes, & Piller, 2017). The reliability of this proxy is biased by the downslope transport of epifaunal foraminifera from the shelf, but appears a suitable indicator for current velocity after removal of allochthonous tests.

Response of Marine Ecosystems to Climate Changes and Abrupt Perturbations

Use of Foraminifera in Climate Science

As outlined in “QUANTITATIVE RECONSTRUCTION OF MARINE ENVIRONMENTAL PARAMETERS,” marine microfossils provide a variety of proxies for quantitative environmental reconstructions. Marine microfossils also prove useful for the evaluation of ecological responses to both long-term and abrupt climate change. Such information is relevant in order to assess the resilience and recovery potential of marine ecosystems with respect to past and future climate perturbations.

Response of Marine Ecosystems to Orbital Climate Changes

The excellent applicability of marine protists in quantitative environmental reconstructions is based on their immediate response to climate forcing on various timescales. Some prominent examples are documented for the marine ecological impacts of glacial-interglacial climate variability during the late Quaternary.

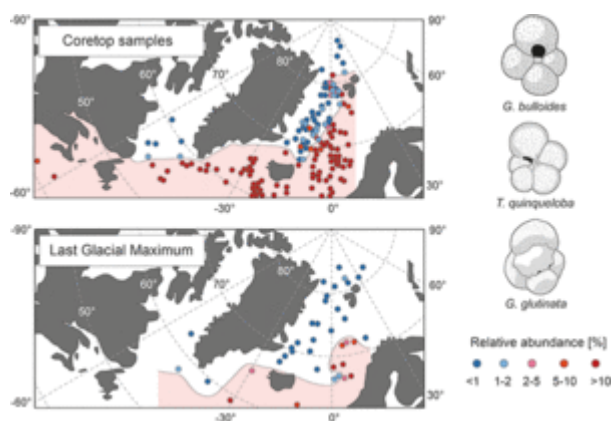


Figure 16. Spatial distribution of selected transitional to subpolar planktic foraminifera (relative proportion of *Globigerina bulloides*, *Turborotalita quinqueloba*, and *Globigerinita glutinata*) in sediments from the modern and last glacial North Atlantic Ocean. The distribution changes mirror the contrasts in surface water temperature and sea-ice distribution.

Modified from Kucera (2007) and based on data from Kucera et al. (2005).

Planktic microfossils document the impact of glacial-interglacial climate changes on sea surface temperature, sea-ice cover and other environmental parameters of the surface ocean. Joint programs dedicated to the reconstruction of the last glacial ocean (see “QUANTITATIVE RECONSTRUCTION OF SURFACE-WATER TEMPERATURE AND SALINITY”) documented changes in the zonal distribution of certain plankton groups. For example, the distribution area of transitional and subpolar planktic foraminifera in the northern North Atlantic and Arctic oceans shifted further south during the last glacial maximum (LGM) (Kucera et al., 2005; Kucera, 2007) (Fig. 16). At high northern latitudes, shifts in the zonation of plankton associations reveal immediate responses to both orbital and suborbital climate variability, which retrace the northward inflow of warm surface waters (e.g., Kandiano, Bauch, & Müller, 2004; Barker et al., 2015). Similarly, the distribution of siliceous microfossils in the Southern Ocean responded to orbital changes in sea-

Use of Foraminifera in Climate Science

ice extent, which was displaced northward by 7–10° during the LGM (e.g., Gersonde et al., 2005; Studer et al., 2015). Shifts of the austral frontal systems during the past five glacial-interglacial cycles also affected the intensity of the Agulhas Current as documented by changes in the abundance of subtropical planktic foraminiferal species in a sediment core off the Cape of Good Hope (Peeters et al., 2004).

At low latitudes and in upwelling areas, the orbital-scale variability of planktic ecosystems is linked to changes in nutrient availability and surface productivity. The temporal variability is strongly coherent on the obliquity and precession bands because the position of the Intertropical Convergence Zone, and the intensity of the monsoon circulation, exhibit substantial seasonal variations (e.g., Clemens, Prell, Murray, Shimmield, & Weedon, 1991; Beaufort et al., 1997). Tropical plankton communities also mirror changes in surface-water stratification and thermocline depth, and respond to climate oscillations, such as the El Niño Southern Oscillation (e.g., Beaufort, de Garidel-Thoron, Mix & Pisias, 2001; Wara, Ravelo, & Delaney, 2005).

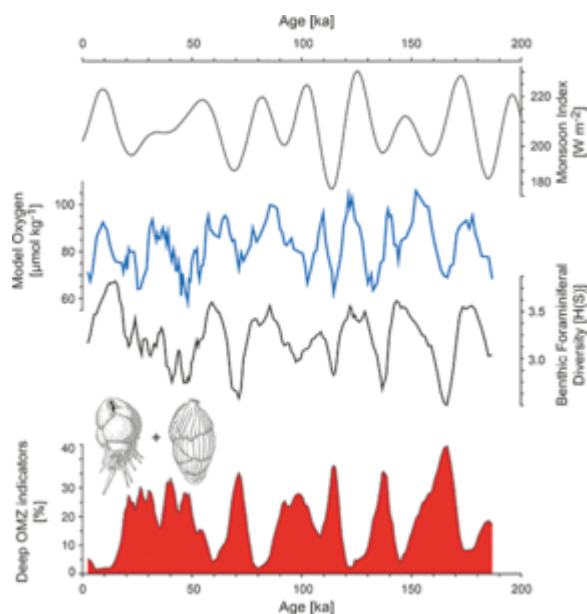


Figure 17. Comparison of proxies for deep-water oxygen concentration in the western Arabian Sea. Intensification of the deep oxygen minimum zone (OMZ) is indicated by increased abundance of the low-oxygen-tolerant taxa *Bulimina aculeata* and *Uvigerina peregrina*, drops in benthic foraminiferal diversity, and the estimated oxygen concentrations based on the stable carbon isotope difference between epifaunal and deep infaunal species applying the function shown in Fig. 15 (Schmiedl & Leuschner, 2005; Schmiedl & Mackensen, 2006). The SW monsoon index of Leuschner & Sirocko (2003) is shown for comparison.

Deep-sea ecosystems reflect orbital-scale climate changes through the immediate processes of benthic-pelagic coupling, including the export of organic matter from the photic zone (Fig. 7). In addition, the deep-sea is ventilated by the advection of intermedi-

Use of Foraminifera in Climate Science

ate, deep, or bottom-water masses, which may result in a lagged response of the deep-sea benthos to climate forcing, depending on the residence time of the water mass. A good example for the interaction between organic matter fluxes and ventilation rate is the deep Arabian Sea. The relative abundances of oxygen-tolerant infaunal benthic foraminifera and faunal diversity reveal periodic changes in the deepening of the oxygen minimum zone (Fig. 17). Reconstructed oxygen values vary between approximately 50 and 105 $\mu\text{mol kg}^{-1}$, applying the $\delta^{13}\text{C}$ -based transfer function of Hoogakker et al. (2015) (Fig. 15). The estimated changes in oxygen concentration lag the coherent changes in SW monsoon strength and related organic matter fluxes by several thousand years (Fig. 17). The data suggest that the deep-sea benthic ecosystems of the Arabian Sea are forced by the combined influence of regional organic matter fluxes and the entrainment of oxygen-enriched deep-water from the Atlantic Ocean (Schmiedl & Leuschner, 2005; Schmiedl & Mackensen, 2006).

Resilience and Recovery Potential of Marine Ecosystems With Respect to Perturbations

The ecological impact of past ocean perturbations can provide valuable information for the assessment of marine ecosystem response to future anthropogenic changes. Relevant examples include the mass extinction at the Cretaceous–Paleogene boundary (KPg boundary), the ecosystem crisis during the carbon cycle disturbance at the Paleocene–Eocene thermal maximum (PETM), and the deep-water anoxia during Neogene sapropel formation in the Mediterranean Sea.

The mass extinction at the KPg boundary, around 66 million years ago, has been associated with the impact of a large asteroid on the Yucatan carbonate platform in the southern Gulf of Mexico (Alvarez, Alvarez, Asaro, & Michel, 1980; Hildebrand et al., 1991). Approximately 76% of all species became extinct globally, of which the marine planktic ecosystems were most severely affected (Schulte et al., 2010). The role of Deccan volcanism in the mass extinction is highly disputed. Enhanced volcanic CO_2 emission before and during the KPg event may have contributed to ocean acidification and stress for marine calcifiers (Punekar et al., 2016), but the resulting climate effects were probably only moderate (Schulte et al., 2010), and the environmental impacts cannot account for the observed extinction patterns of planktic foraminifera (Molina, 2015).

The breakdown of stable carbon isotope gradients between surface ocean and deep-sea of $\sim 500,000$ years duration (Zachos, Arthur, & Dean, 1989) was associated with a global collapse of pelagic marine primary productivity (“Strangelove” Ocean; Hsü & McKenzie, 1985) or export productivity (“Living” Ocean; D’Hondt, Donaghay, Zachos, Luttenberg, & Lindinger, 1998). However, benthic foraminifera were but slightly affected by the mass extinction, suggesting regional and only moderate decrease in export productivity (Thomas, 2007; Culver, 2003; Alegret et al., 2012). The interpretation of sustained export productivity across the KPg event is supported by biomarker data suggesting only a short decline of eukaryotic algal and continuation of cyanobacterial primary productivity (Sepúlveda, Wendler, Summons, & Hinrichs, 2009).

Use of Foraminifera in Climate Science

In the Chixculub crater basin first life returned within years and a productive ecosystem re-established within 30,000 years after the impact, implying a high recovery potential of planktic communities (Lowery et al., 2018). The evolutionary recovery of planktic foraminifera peaked a few million years after the KPg boundary, concurrent to the full recovery of the marine carbon cycle (Coxall et al., 2006) and the evolution of foraminiferal photosymbiosis around 63.5 million years ago (Birch, Coxall, & Pearson, 2012).

The marine ecological crisis of the PETM, around 56 million years ago, was associated with a negative carbon isotope excursion, which was likely caused by rapid emission of a large volume of greenhouse gasses resulting in a transient temperature increase of 5–8°C (Zachos et al., 2003; McInerney & Wing, 2011). The period of carbon release has likely lasted for less than 20,000 years and the duration of the whole PETM is estimated to around 200,000 years (McInerney & Wing, 2011; Zeebe, Dickens, Ridgwell, Sluijs, & Thomas, 2014). The carbon sources remain controversial, and may have included the dissociation of methane hydrates (Dickens, O'Neil, Rea, & Owen, 1995), volcanic carbon from the North Atlantic Igneous Province (Gutjahr et al., 2017), or both.

Deep-sea benthic foraminifera experienced a massive extinction, concerning 30–50% of all species during a few thousand years (Thomas & Shackleton, 1996; Thomas, 2007). By contrast, planktic organisms, including dinoflagellates, calcareous nannofossils, and planktic foraminifera, exhibit rapid evolutionary turnover, distributional range shifts, and species-specific growth response, but lack major extinctions (Speijer, Scheibner, Stassen, & Morsi, 2012; Self-Trail, Powars, Watkins, & Wandless, 2012; Gibbs et al., 2006, 2013). The mass extinction of deep-sea benthic foraminifera and its biogeographic pattern is complex, and has been attributed to the combined effects of ocean warming, deep-water circulation changes, ocean acidification, oxygen depletion, and reduced food supply (Thomas, 1998; Winguth, Thomas, & Winguth, 2012). This combination was confirmed by the dwarfing of some surviving benthic foraminiferal taxa at deeper sites (Schmidt et al., 2018), implying bathymetric gradients in the resilience of deep-sea benthic ecosystems, depending on the magnitude of perturbation.

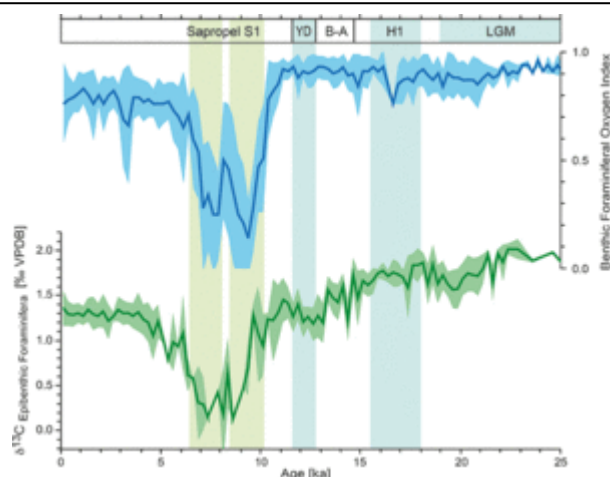


Figure 18. Compiled and averaged records of the Benthic Foraminiferal Oxygen Index (OI; calculated according to Schmiedl et al., 2003) and epibenthic stable carbon isotopes from bathyal eastern Mediterranean sediment cores for the past 25,000 years. The OI record displays the onset, interruption, and termination of dysoxic to anoxic conditions during the formation of early Holocene sapropel S1. The stable carbon isotope record reflects the contemporaneous stagnation and reventilation of intermediate and deep-water masses (compiled from Schmiedl et al., 2010 and Grimm et al., 2015). LGM = Last Glacial Maximum, H1 = Heinrich 1 cold event, B-A = Bølling-Allerød, YD = Younger Dryas.

The marine ecosystems of marginal basins, such as the Mediterranean Sea and the Red Sea, react very sensitively to global and regional climate changes and have experienced substantial regime shifts in their marine ecosystems during the past (Hemleben et al., 1996; Rohling, Marino, & Grant, 2015). Basin-wide compilations of deep-sea benthic foraminiferal oxygen index values and epibenthic $\delta^{13}\text{C}$ data delivered a detailed history of deep-water stagnation and reventilation across the past 25,000 years of the eastern Mediterranean Sea, including the last glacial termination and the early Holocene sapropel S1 interval (Schmiedl et al., 2010; Grimm et al., 2015) (Fig. 18). The observed rapid deep-sea benthic ecosystem collapse at the onset of sapropel deposition reflects a lagged response to the insolation-driven intensification of the African monsoon system, and associated hydrological changes. Abrupt high-latitude hydrological perturbations and associated cooling events are superimposed on the long-term evolution, which is highlighted by a transient reventilation of benthic ecosystems during the 8.2 ka cold event (Rohling, Jorissen, & de Stigter, 1997; Schmiedl et al., 2010) (Fig. 18). Under the oligotrophic boundary conditions of the late Holocene Mediterranean Sea, the recovery of deep-sea faunas strongly depended on the duration of the anoxic phase. While deep-sea ecosystems exhibited a rapid recolonization by opportunistic taxa (Jorissen, 1999), the full recovery of abyssal benthic ecosystems under the influence of ultra-oligotrophic conditions may have taken up to several millennia (Schmiedl, Hemleben, Keller, & Segl, 1998).

Use of Foraminifera in Climate Science

The contemporary rapid global warming affects the biogeography of marine protists as reflected by latitudinal shifts of distribution belts and colonization of new marine ecosystems by temperature-sensitive taxa (e.g., Weinmann et al., 2013; Schmidt et al., 2015). Enhanced greenhouse gas emissions and the associated temperature rise impose thermal stress and acidification of surface waters, particularly affecting the life of calcifying organisms. Culture experiments suggest that some coccolithophorids respond to ocean acidification by reduced growth and calcification rates, but other species or strains seem to be able to maintain their survival and functionality by rapid adaptive evolution (e.g., Langer, Nehrke, Probert, Ly, & Ziveri, 2009; Lohbeck, Riebesell, & Reusch, 2012; Schlüter et al., 2014). Similarly, shallow-water benthic foraminifera exhibit specific tolerance levels in terms of acidification and thermal stress (Haynert, Schönfeld, Schiebel, Wilson, & Thomsen, 2014; Schmidt et al., 2016). In the geological record, phases of ocean acidification were commonly associated with extinction and evolutionary turnover of marine calcifying organisms (Hönisch et al., 2012). The rapidity of ongoing anthropogenic warming and CO₂ emission rates are probably unprecedented during the past 66 million years (Zeebe, Ridgwell, & Zachos, 2016) but the abrupt climate perturbation, acidification, and ecological and evolutionary responses at the KPg boundary event may probably serve as an analogue for the anticipated future changes.

Conclusion

Marine micropaleontology investigates the diversity, biostratigraphy, ecology, and geochemistry of planktic and benthic microfossil groups. The paleo-environmental applications of marine microfossils are manifold, and deliver a wealth of information on past ocean circulation and climate, and evolution of oceanic biota. Specifically, microfossil-based proxies have been developed for the quantitative reconstruction of past changes in water depth, sea-surface temperature and salinity, surface productivity and organic matter fluxes, oxygen concentration, and current strength. The majority of these proxies use transfer functions, which are based on modern training data sets and a variety of statistical methods.

Contemporary micropaleontological research is challenged by technical innovations, such as the availability of sophisticated analytical techniques, which are used for the establishment of novel geochemical proxies. For many proxies the use of single taxon material is essential, which requires a careful taxonomy of the selected specimens.

Regardless the analytical progress, a well-grounded understanding of plankton and benthos systematics and ecology forms the basis for micropaleontological research involving appropriate biological and ecological field studies, laboratory experiments, and compilation of existing data. Microfossil-based paleoclimate research creates added value in the frame of interdisciplinary research, for example through combining proxy studies with experiments from earth system models. Last but not least, marine micropaleontological research is invoked to address important societal future challenges, such as pollution monitoring or assessment of coastal ecosystem resilience. In this context, the profound under-

standing of past ecosystem dynamics appears invaluable to assess the future impacts of global climate change and biodiversity loss.

Acknowledgments

The author thanks Dania Achermann and Simone Rödder for organizing the workshop Towards a History of Paleoclimatology: Changing Roles and Shifting Scales in Climate Research at Hamburg University, September 2017, which motivated this contribution. The author is grateful to the members of the micropaleontology group at the Institute for Geology for discussion, and to Silke Schmiedl for constructive comments on the manuscript. The author greatly appreciates the thorough comments of an anonymous reviewer, which helped to improve the manuscript.

Further Reading

Haq, B. U., & Boersma, A. (1998). *Introduction to marine micropaleontology* (2nd ed.). Amsterdam, The Netherlands: Elsevier.

Hillaire-Marcel, C., & De Vernal, A. (Eds.). (2007). *Proxies in late Cenozoic paleoceanography*. Developments in Marine Geology 1. Amsterdam, The Netherlands: Elsevier.

Jones, R. W. (1994). *The Challenger foraminifera*. Oxford, U.K.: Oxford University Press.

Jones, R. W. (2014). *Foraminifera and their applications*. Cambridge, U.K.: Cambridge University Press.

Kucera, M., Schneider, R., & Weinelt, M. (Eds.). (2006). *MARGO—Multiproxy approach for the reconstruction of the glacial ocean surface*. Amsterdam, The Netherlands: Elsevier.

Murray, J. W. (2006). *Ecology and applications of benthic foraminifera*. Cambridge, U.K.: Cambridge University Press.

Mutterlose, J. (Ed.). (2005). Marine plankton—a proxy for the understanding of recent and fossil environments [Special issue]. *Paläontologische Zeitschrift*, 79(1).

Schiebel, R., & Hemleben, C. (2017). *Planktic foraminifers in the modern ocean*. Berlin, Germany: Springer.

Sen Gupta, B. K. (Ed.). (1999). *Modern foraminifera*. Dordrecht, The Netherlands: Kluwer Academic.

Thierstein, H. R., & Young, J. R. (Eds.). (2004). *Coccolithophores: From molecular processes to global impact*. Berlin, Germany: Springer.

WoRMS Editorial Board. (2018). *World Register of Marine Species*.

References

- Abelmann, A., Gersonde, R., Knorr, G., Zhang, X., Chaplign, B., Maier, E., . . . Tiedemann, R. (2015). **The seasonal sea-ice zone in the glacial Southern Ocean as a carbon sink.** *Nature Communications*, *6*, 8136.
- Alegret, L., Thomas, E., & Lohmann, K. C. (2012). **End-Cretaceous marine mass extinction not caused by productivity collapse.** *Proceedings of the National Academy of Sciences*, *109*(3), 728–732.
- Alvarez, L. W., Alvarez, W., Asaro, F., & Michel, H. V. (1980). **Extraterrestrial cause for the Cretaceous-Tertiary extinction.** *Science*, *208*(4448), 1095–1108.
- Alve, E., & Goldstein, S. T. (2010). **Dispersal, survival and delayed growth of benthic foraminiferal propagules.** *Journal of Sea Research*, *63*, 36–51.
- Alve, E., Korsun, S., Schönfeld, J., Dijkstra, N., Golikova, E., Hess, S., . . . Panieri, G. (2016). **Foram-AMBI: A sensitivity index based on benthic foraminiferal faunas from North-East Atlantic and Arctic fjords, continental shelves and slopes.** *Marine Micropaleontology*, *122*, 1–12.
- Anand, P., Elderfield, H., & Conte, M. H. (2003). **Calibration of Mg/Ca thermometry in planktonic foraminifera from a sediment trap time series.** *Paleoceanography*, *18*(2), 1050.
- Annan, J. D., & Hargreaves, J. C. (2015). **A perspective on model-data surface temperature comparison at the Last Glacial Maximum.** *Quaternary Science Reviews*, *107*, 1–10.
- Armbrust, E. V. (2009). **The life of diatoms in the world's oceans.** *Nature*, *459*, 185–192.
- Bandy, O. L., & Chierici, M. A. (1966). **Depth-temperature evaluation of selected California and Mediterranean bathyal foraminifera.** *Marine Geology*, *4*(4), 259–271.
- Bard, E., Hamelin, B., Arnold, M., Montaggioni, L., Cabioch, G., Faure, G., & Rougerie, F. (1996). **Deglacial sea-level record from Tahiti corals and the timing of global meltwater discharge.** *Nature*, *382*, 241–244.
- Barker, R. W. (1960). Taxonomic notes on the species figured by H. B. Brady in his report on the foraminifera dredged by H.M.S. Challenger during the years 1873–1876. *Society of Economic Paleontologists and Mineralogists, Special Publication*, *9*, 1–238.
- Barker, S., Cacho, I., Benway, H., & Tachikawa, K. (2005). **Planktonic foraminiferal Mg/Ca as a proxy for past oceanic temperatures: A methodological overview and data compilation for the Last Glacial Maximum.** *Quaternary Science Reviews*, *24*(7–9), 821–834.

Use of Foraminifera in Climate Science

Barker, S., Chen, J., Gong, X., Jonkers, L., Knorr, G., & Thornalley, D. (2015). **Icebergs not the trigger for North Atlantic cold events.** *Nature*, 520, 333–336.

Bé, A. W. H. (1977). An ecological, zoogeographic and taxonomic review of Recent planktonic foraminifera. In A. T. S. Ramsey (Ed.), *Oceanic micropaleontology: Vol. 1* (pp. 1–100). London, U.K.: Academic Press.

Beaufort, L., de Garidel-Thoron, T., Mix, A. C., & Pisias, N. G. (2001). **ENSO-like forcing on oceanic primary production during the late Pleistocene.** *Science*, 293(5539), 2440–2444.

Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F., & Labeyrie, L. (1997). **Insolation cycles as a major control of equatorial Indian Ocean primary production.** *Science*, 278(5342), 1451–1454.

Bemis, B. E., Spero, H. J., Bijma, J., & Lea, D. W. (1998). **Reevaluation of the oxygen isotopic composition of planktonic foraminifera: Experimental results and revised paleotemperature equations.** *Paleoceanography*, 13(2), 150–160.

Berger, W. H., & Diester-Haass, L. (1988). **Paleoproductivity: The benthic/planktic ratio in foraminifera as a productivity index.** *Marine Geology*, 81(1–4), 15–25.

Berger, W. H., & Herguera, J. C. (1992). Reading the sedimentary record of the ocean's productivity. In P. G. Falkowski & A. D. Woodhead (Eds.), *Primary productivity and biogeochemical cycles in the Sea* (pp. 455–486). New York, NY: Plenum Press.

Berger, W. H., & Wefer, G. (1990). **Export production: Seasonality and intermittency, and paleoceanographic implications.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 89(3), 245–254.

Berkeley, A., Perry, C. T., Smithers, S. G., Horton, B. P., & Taylor, K. G. (2007). **A review of the ecological and taphonomic controls on foraminiferal assemblage development in intertidal environments.** *Earth-Science Reviews*, 83(3–4), 205–230.

Bernhard, J. M., Geslin, E., & Jordan, R. W. (Eds.). (2018). Benthic foraminiferal ultra-structure studies. *Marine Micropaleontology*, 138, 1–104

Betzer, P. R., Showers, W. J., Laws, E. A., Winn, C. D., DiTullio, G. R., & Kroopnick, P. M. (1984). **Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean.** *Deep-Sea Research*, 31(1–11).

Bianchi G. (1739). *De conchis minus notis. Liber cui accessit specimen aestus reciproci maris superi ad littus portumque arimini.* Rome, Italy: In aedibus Palladis, I.P.A.

Birch, H. S., Coxall, H. K., & Pearson, P. N. (2012). **Evolutionary ecology of early Paleocene planktonic foraminifera: Size, depth habitat and symbiosis.** *Paleobiology*, 38(3), 374–390.

Use of Foraminifera in Climate Science

Bollmann, J., Herrle, J. O., Cortés, M. Y., & Fielding, S. R. (2009). **The effect of sea water salinity on the morphology of *Emiliana huxleyi* in plankton and sediment samples.** *Earth and Planetary Science Letters*, 284(3-4), 320-328.

Bork, P., Bowler, C., de Vargas, C., Gorsky, G., Karsenti, E., & Wincker, P. (2015). **Tara Oceans studies plankton at planetary scale.** *Science*, 348(6237), 873.

BouDagher-Fadel, M. K. (2018). *Evolution and geological significance of larger benthic foraminifera*. London, U.K.: University College London Press.

Bown, P. R., Lees, J. A., & Young, J. R. (2004). Calcareous nannoplankton evolution and diversity through time. In H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores* (pp. 481-508). Berlin, Germany: Springer.

Brady, H. B. (1884). Report on the foraminifera dredged by H.M.S. Challenger, during the years 1873-1876. In C. W. Thomson & J. Murray (Eds.), Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-1876 [Special issue]. *Zoology*, 9, 1-814.

Brathauer, U., Abelmann, A., Gersonde, R., Niebler, S., & Fütterer, D. K. (2001). **High resolution calibration of *Cycladophora davisiana* events versus oxygen isotope stratigraphy in the subantarctic Atlantic Ocean—a stratigraphic tool for carbonate-poor Quaternary sediments.** *Marine Geology*, 175(1-4), 167-181.

Caralp, M. H. (1989). **Abundance of *Bulimina exilis* and *Melonis barleeaanum*: Relationship to the quality of marine organic matter.** *Geo-Marine Letters*, 9(1), 37-43.

Caromel, A. G. M., Schmidt, D. N., & Rayfield, E. J. (2017). **Ontogenetic constraints on foraminiferal test construction.** *Evolution & Development*, 19(3), 157-168.

Cermeño, P., & Falkowski, P. G. (2009). **Controls on diatom biogeography in the ocean.** *Science*, 325(5947), 1539-1541.

Charles, C. D., & Fairbanks, R. (1992). **Evidence from Southern Ocean sediments for the effect of North Atlantic deep-water flux on climate.** *Nature*, 355, 416-419.

Clemens, S., Prell, W., Murray, D., Shimmield, G., & Weedon, G. (1991). **Forcing mechanisms of the Indian Ocean monsoon.** *Nature*, 353, 720-725.

CLIMAP project members. (1976). **The surface of the ice-age Earth.** *Science*, 191(4232), 1131-1137.

Corliss, B. H. (1985). **Microhabitats of benthic foraminifera within deep-sea sediments.** *Nature*, 314, 435-438.

Coxall, H. K., D'Hondt, S., & Zachos, J. C. (2006). **Pelagic evolution and environmental recovery after the Cretaceous-Paleogene mass extinction.** *Geology*, 34(4), 297-300.

Use of Foraminifera in Climate Science

Crasquin, S., & Forel, M.-B. (2013). **Ostracods (Crustacea) through Permian-Triassic events.** *Earth-Science Reviews*, 137, 52–64.

Cronin, T. M. (2015). Ostracods and sea level. In I. Shennan, A. J. Long, & B. P. Horton (Eds.), *Handbook of sea-level research* (pp. 149–257). Chichester, U.K.: John Wiley & Sons.

Cronin, T. M., & Raymo, M. E. (1997). **Orbital forcing of deep-sea benthic species diversity.** *Nature*, 385, 624–627.

Crosta, X., & Koç, N. (2007). **Diatoms: From micropaleontology to isotope geochemistry.** In C. Hillaire-Marcel & A. De Vernal (Eds.), *Proxies in late Cenozoic paleoceanography: Vol. 1* (pp. 327–369). Amsterdam, The Netherlands: Elsevier.

Culver, S. J. (2003). **Benthic foraminifera across the Cretaceous/Tertiary (K/T) boundary: A review.** *Marine Micropaleontology*, 47(3–4), 177–226.

Culver, S. J., Woo, H. J., Oertel, G. F., & Buzas, M. A. (1996). **Foraminifera of coastal depositional environments, Virginia, U.S.A.: Distribution and taphonomy.** *Palaios*, 11(5), 459–486.

D'Hondt, S., Donaghay, P., Zachos, J. C., Luttenberg, D., & Lindinger, M. (1998). **Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction.** *Science*, 282(5387), 276–279.

d'Orbigny, A. (1826). Tableau méthodique de la classe des céphalopodes. *Annales des Sciences Naturelles*, 7(2), 245–314.

de Nooijer, L. J., Spero, H. J., Erez, J., Bijma, J., & Reichart, G. J. (2014). **Biom mineralization in perforate foraminifera.** *Earth-Science Reviews*, 135, 48–58.

de Vernal, A., Rosell-Mele, A., Kucera, M., Hillaire-Marcel, C., Eynaud, F., Weinelt, M., . . . Kageyama, M. (2006). **Comparing proxies for the reconstruction of LGM sea-surface conditions in the northern North Atlantic.** *Quaternary Science Reviews*, 25(21–22), 2820–2834.

Dickens, G. R., O'Neil, J. R., Rea, D. K., & Owen, R. M. (1995). **Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene.** *Paleoceanography*, 10(6), 965–971.

Duplessy, J.-C., Shackleton, N. J., Fairbanks, R. G., Labeyrie, L., Oppo, D., & Kallel, N. (1988). **Deepwater source variations during the last climatic cycle and their impact on the global deepwater circulation.** *Paleoceanography*, 3(3), 343–360.

Dutkiewicz, A., Müller, R. D., O'Callaghan, S., & Jónasson, H. (2015). **Census of seafloor sediments in the world's ocean.** *Geology*, 43(9), 795–798.

Use of Foraminifera in Climate Science

Epstein, S., Buchsbaum, R., Lowenstam, H. A., & Urey, H. C. (1953). **Revised carbonate-water isotopic temperature scale.** *GSA Bulletin*, 64(11), 1315–1326.

Ericson, D. B., Ewing, M., Wollin, G., & Heezen, B. C. (1961). **Atlantic deep-sea sediment cores.** *Geological Society of America Bulletin*, 72(2), 193–286.

Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofiel, O., & Taylor, F. J. R. (2004). **The evolution of modern eukaryotic phytoplankton.** *Science*, 305(5682), 354–360.

Falkowski, P. G., & Knoll, A. H. (Eds.). (2007). *Evolution of primary producers in the sea.* Amsterdam, The Netherlands: Elsevier.

Fichtel, L., & Moll, J. P. C. (1803). *Mikroskopische und andere kleine Schalthiere aus den Geschlechtern Argonate und Schiffer, nach der Natur gezeichnet und beschrieben.* Wien, Germany: Camesianische Buchhandlung.

Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). **Primary production of the biosphere: Integrating terrestrial and oceanic components.** *Science*, 281(5374), 237–240.

Fontanier, C., Jorissen, F. J., Licari, L., Alexandre, A., Anschutz, P., & Carbonel, P. (2002). **Live benthic foraminiferal faunas from the Bay of Biscay: Faunal density, composition, and microhabitats.** *Deep-Sea Research I*, 49(4), 751–785.

Friedrich, O., Norris, R. D., & Erbacher, J. (2012). **Evolution of middle to late Cretaceous oceans—A 55 m.y. record of Earth's temperature and carbon cycle.** *Geology*, 40(2), 107–110.

García-Gallardo, Á., Grunert, P., Voelker, A. H. L., Mendes, I., & Piller, W. E. (2017). **Re-evaluation of the “elevated epifauna” as indicator of Mediterranean Outflow Water in the Gulf of Cadiz using stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$).** *Global and Planetary Change*, 155, 78–97.

Gersonde, R., Crosta, X., Abelmann, A., & Armand, L. (2005). **Sea-surface temperature and sea ice distribution of the Southern Ocean at the EPILOG Last Glacial Maximum—a circum-Antarctic view based on siliceous microfossil records.** *Quaternary Science Reviews*, 24(7–9), 869–896.

Gibbs, S. J., Bown, P. R., Sessa, J. A., Bralower, T. J., & Wilson, P. A. (2006). **Nannoplankton extinction and origination across the Paleocene-Eocene thermal maximum.** *Science*, 314(5806), 1770–1773.

Gibbs, S. J., Poulton, A. J., Bown, P. R., Daniels, C. J., Hopkins, J., Young, J. R., . . . Newsam, C. (2013). **Species-specific growth response of coccolithophores to Palaeocene-Eocene environmental change.** *Nature Geoscience*, 6, 218–222.

Gibson, T. G. (1989). **Planktonic benthonic foraminiferal ratios: Modern patterns and Tertiary applicability.** *Marine Micropaleontology*, 15(1-2), 29-52.

Glock, N., Eisenhauer, A., Liebetrau, V., Wiedenbeck, M., Hensen, C., & Nehrke, G. (2012). **EMP and SIMS studies on Mn/Ca and Fe/Ca systematics in benthic foraminifera from the Peruvian OMZ: A contribution to the identification of potential redox proxies and the impact of cleaning protocols.** *Biogeosciences*, 9, 341-359.

Glock, N., Eisenhauer, A., Milker, Y., Liebetrau, V., Schönfeld, J., Mallon, J., . . . Hensen, C. (2011). **The sensitivity of pore density in tests of *Bolivina spissa* to ambient oxygen and nitrate concentrations.** *Journal of Foraminiferal Research*, 41(1), 22-32.

Glock, N., Erdem, Z., Wallmann, K., Somes, C. J., Liebetrau, V., Schönfeld, J., . . . Eisenhauer, A. (2018). **Coupling of oceanic carbon and nitrogen facilitates spatially resolved quantitative reconstruction of nitrate inventories.** *Nature Communications*, 9, 1217.

Glock, N., Liebetrau, V., Eisenhauer, A., & Rocholl, A. (2016). **High resolution I/Ca ratios of benthic foraminifera from the Peruvian oxygen-minimum-zone: A SIMS derived assessment of a potential redox proxy.** *Chemical Geology*, 447, 40-53.

Gooday, A. J. (1988). **A response by benthic foraminifera to the deposition of phytodetritus in the deep sea.** *Nature*, 332, 70-73.

Gooday, A. J., & Jorissen, F. J. (2012). **Benthic foraminiferal biogeography: Controls on global distribution patterns in deep-water settings.** *Annual Review of Marine Science*, 4, 237-262.

Gooday, A. J., Jorissen, F., Levin, L. A., Middelburg, J. J., Naqvi, S. W. A., Rabalais, N. N., . . . Zhang, J. (2009). **Historical records of coastal eutrophication-induced hypoxia.** *Biogeosciences*, 6, 1707-1745.

Gooday, A. J., & Rathburn, A. E. (1999). **Temporal variability in living deep-sea benthic foraminifera: A review.** *Earth-Science Reviews*, 46(1-4), 187-212.

Gradstein, F. M. (2012). Biochronology. In F. M. Gradstein, J. G. Ogg, M. Schmitz, & G. Ogg (Eds.), *The geologic time scale* (pp. 43-61). Amsterdam, The Netherlands: Elsevier.

Graf, G. (1989). **Benthic-pelagic coupling in a deep-sea benthic community.** *Nature*, 341, 437-439.

Grant, K. M., Rohling, E. J., Ramsey, C. B., Cheng, H., Edwards, R. L., Florindo, F., . . . Williams, F. (2014). **Sea-level variability over five glacial cycles.** *Nature Communications*, 5, 5076.

Use of Foraminifera in Climate Science

Grimm, R., Maier-Reimer, E., Mikolajewicz, U., Schmiedl, G., Müller-Navarra, K., Adloff, F., . . . Emeis, K. C. (2015). **Late glacial initiation of Holocene eastern Mediterranean sapropel formation.** *Nature Communications*, 6, 7099.

Grossman, E. L. (1987). **Stable isotopes in modern benthic foraminifera: A study of vital effect.** *Journal of Foraminiferal Research*, 17(1), 48–61.

Grossman, E. L. (2012). Oxygen isotope stratigraphy. In F. M. Gradstein, J. G. Ogg, M. Schmitz, & G. Ogg (Eds.), *The geologic time scale* (pp. 181–206). Amsterdam, The Netherlands: Elsevier.

Gutjahr, M., Ridgwell, A., Sexton, P. F., Anagnostou, E., Pearson, P. N., Pälike, H., . . . Foster, G. L. (2017). **Very large release of mostly volcanic carbon during the Palaeocene-Eocene thermal maximum.** *Nature*, 548, 573–577.

Haeckel, E. (1887). Report on the radiolaria collected by H.M.S. Challenger during the years 1873–1876. In C. W. Thomson & J. Murray (Eds.), Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876 [Special issue]. *Zoology*, 18, 1–1803.

Haq, B. U., & Al-Qahtani, A. M. (2005). Phanerozoic cycles of sea-level change on the Arabian Platform. *GeoArabia*, 10(2), 127–160.

Haynert, K., Schönfeld, J., Schiebel, R., Wilson, B., & Thomsen, J. (2014). **Response of benthic foraminifera to ocean acidification in their natural sediment environment: A long-term culturing experiment.** *Biogeosciences*, 11, 1581–1597.

Heinz, P., Kitazato, H., Schmiedl, G., & Hemleben, C. (2001). **Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions.** *Journal of Foraminiferal Research*, 31(3), 210–227.

Helly, J. J., & Levin, L. A. (2004). **Global distribution of naturally occurring marine hypoxia on continental margins.** *Deep-Sea Research I*, 51(9), 1159–1168.

Hemleben, C., & Kitazato, H. (1995). **Deep-sea foraminifera under long time observation in the laboratory.** *Deep-Sea Research*, 42(6), 827–832.

Hemleben, C., Meischner, D., Zahn, R., Almogi-Labin, A., Erlenkeuser, H., & Hiller, B. (1996). **Three hundred eighty thousand year long stable isotope and faunal records from the Red Sea: Influence of global sea level change on hydrography.** *Paleoceanography*, 11(2), 147–156.

Henson, S. A., Sanders, R., & Madsen, E. (2012). **Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean.** *Global Biogeochemical Cycles*, 26, GB1028.

Use of Foraminifera in Climate Science

Herguera, J. C., & Berger, W. H. (1991). **Paleoproductivity from benthic foraminifera abundance: Glacial to postglacial change in the west-equatorial Pacific.** *Geology*, 19(12), 1173–1176.

Herrle, J. O., Bollmann, J., Gebühr, C., Schulz, H., Sheward, R. M., & Giesenberg, A. (2018). **Black Sea outflow response to Holocene meltwater events.** *Scientific Reports*, 8, 4081.

Hildebrand, A. R., Penfield, G. T., Kring, D. A., Pilkington, M., Camargo, A., Jacobsen, S. B., & Boynton, W. V. (1991). **Chicxulub Crater: A possible Cretaceous/Tertiary boundary impact crater on the Yucatán Peninsula, Mexico.** *Geology*, 19(9), 867–871.

Hinnov, L. A., & Hilgen, F. J. (2012). Cyclostratigraphy and astrochronology. In F. M. Gradstein, J. G. Ogg, M. Schmitz, & G. Ogg (Eds.), *The geologic time scale* (pp. 63–83). Amsterdam, The Netherlands: Elsevier.

Holbourn, A. E., Kuhnt, W., Clemens, S. C., Kochhann, K. G. D., Jöhnck, J., Lübbers, J., & Andersen, N. (2018). **Late Miocene climate cooling and intensification of southeast Asian winter monsoon.** *Nature Communications*, 9, 1584.

Hönisch, B., Ridgwell, A., Schmidt, D. N., Thomas, E., Gibbs, S. J., Sluijs, A., . . . Williams, B. (2012). **The geological record of ocean acidification.** *Science*, 335(6072), 1058–1063.

Hoogakker, B. A. A., Elderfield, H., Schmiedl, G., McCave, I. N., & Rickaby, R. E. M. (2015). **Glacial-interglacial changes in bottom-water oxygen content on the Portuguese margin.** *Nature Geoscience*, 8, 40–43.

Hoogakker, B. A. A., Lu, Z., Umling, N., Jones, L., Zhou, X., Rickaby, R. E. M., . . . Galbraith, E. D. (2018). **Glacial expansion of oxygen-depleted seawater in the eastern tropical Pacific.** *Nature*, 562, 410–413.

Horton, B. P., & Edwards, R. J. (2006). Quantifying Holocene sea-level change using intertidal foraminifera: Lessons from the British Isles. *Cushman Foundation for Foraminiferal Research, Special Publication*, 40, 1–97.

Hsü, K. J., & McKenzie, J. (1985). **A “Strangelove” ocean in the earliest Tertiary.** In W. S. Broecker & E. T. Sundquist (Eds.), *The carbon cycle and atmospheric CO₂: Natural variations, archaic to present* (pp. 487–492). AGU Geophysical Monographs 32 Washington, DC, USA: American Geophysical Union.

Imbrie, J., Hays, J. D., Martinson, D. G., McIntyre, A., Mix, A. C., Morley, J. J., . . . Shackleton, N. (1984). The orbital theory of Pleistocene climate: Support from a revised chronology of the marine $\delta^{18}\text{O}$ record. In A. Berger, J. Imbrie, J. Hays, G. Kukla, & B. Saltzman (Eds.), *Milankovitch and climate: Part 1* (pp. 269–304). Dordrecht, The Netherlands: D. Reidel.

Use of Foraminifera in Climate Science

- Jennions, S. M., Thomas, E., Schmidt, D. N., Lunt, D., & Ridgwell, A. (2015). **Changes in benthic ecosystems and ocean circulation in the Southeast Atlantic across Eocene thermal maximum 2.** *Paleoceanography*, *30*, 1059–1077.
- John, E. H., Pearson, P. N., Coxall, H. K., Birch, H., Wade, B. S., & Foster, G. L. (2013). **Warm ocean processes and carbon cycling in the Eocene.** *Philosophical Transactions of the Royal Society A*, *371*, 20130099.
- Jones, R. W. (1994). *The Challenger foraminifera*. Oxford, U.K.: Oxford University Press.
- Jorissen, F. J. (1999). **Benthic foraminiferal successions across late Quaternary Mediterranean sapropels.** *Marine Geology*, *153*(1-4), 91–101.
- Jorissen, F. J., de Stigter, H. C., & Widmark, J. G. V. (1995). **A conceptual model explaining benthic foraminiferal microhabitats.** *Marine Micropaleontology*, *26*(1-4), 3–15.
- Jorissen, F. J., Fontanier, C., & Thomas, E. (2007). **Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics.** In C. Hillaire-Marcel & A. De Vernal (Eds.), *Proxies in late Cenozoic paleoceanography: Vol. 1* (pp. 277–328). Amsterdam, The Netherlands: Elsevier.
- Kaiho, K. (1994). **Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean.** *Geology*, *22*(8), 719–722.
- Kandiano, E. S., Bauch, H. A., & Müller, A. (2004). **Sea surface temperature variability in the North Atlantic during the last two glacial-interglacial cycles: Comparison of faunal, oxygen isotopic, and Mg/Ca-derived records.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, *204*(1-2), 145–164.
- Keeling, R. F., Körtzinger, A., & Gruber, N. (2010). **Ocean deoxygenation in a warming world.** *Annual Review of Marine Science*, *2*, 199–229.
- Kemp, A. C., Horton, B. P., Donnelly, J. P., Mann, M. E., Vermeer, M., & Rahmstorf, S. (2011). **Climate related sea-level variations over the past two millennia.** *Proceedings of the National Academy of Sciences of the United States of America*, *108*(27), 11017–11022.
- Kemp, A. C., Kegel, J. J., Culver, S. J., Barber, D. C., Mallinson, D. J., Leorri, E., . . . Horton, B. P. (2017). **Extended late Holocene relative sea-level histories for North Carolina, USA.** *Quaternary Science Reviews*, *160*, 13–30.
- Kemp, A. C., & Telford, R. J. (2015). Transfer functions. In I. Shennan, A. J. Long, & B. P. Horton (Eds.), *Handbook of sea-level research* (pp. 470–499). Chichester, U.K.: John Wiley & Sons.
- Kennett, J. P. (1982). *Marine geology*. Englewood Cliffs, NJ: Prentice-Hall.

Use of Foraminifera in Climate Science

Kitazato, H., & Bernhard, J. M. (Eds.). (2014). *Approaches to study living foraminifera: Collection, maintenance and cultivation*. Tokyo, Japan: Springer.

Knoll A. H., & Follows M. J. (2016). **A bottom-up perspective on ecosystem change in Mesozoic oceans**. *Philosophical Transactions of the Royal Society B*, 283, 20161755.

Koho, K. A., García, R., de Stigter, H. C., Epping, E., Koning, E., Kouwenhoven, T. J., & Van der Zwaan, G. J. (2008). **Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon-Setúbal Canyon (southern Portugal)**. *Progress in Oceanography*, 79(1), 55–82.

Kucera, M. (2007). **Planktonic foraminifera as tracers of past oceanic environments**. In C. Hillaire-Marcel & A. De Vernal (Eds.), *Proxies in late Cenozoic paleoceanography: Vol. 1* (pp. 213–262). Amsterdam, The Netherlands: Elsevier.

Kucera, M., Schneider, R., & Weinelt, M. (Eds.). (2006). *MARGO—Multiproxy approach for the reconstruction of the glacial ocean surface*. Amsterdam, The Netherlands: Elsevier.

Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayes, A., Weinelt, M., . . . Waelbroeck, C. (2005). **Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: Multi-technique approach based on geographically constrained calibration datasets and its application to glacial Atlantic and Pacific Oceans**. *Quaternary Science Reviews*, 24(7–9), 951–998.

Kuhnt, T., Friedrich, O., Schmiedl, G., Milker, Y., Mackensen, A., & Lückge, A. (2013). **Relationship between pore density in benthic foraminifera and bottom-water oxygen content**. *Deep-Sea Research I*, 76, 85–95.

Kuhnt, W., Hess, S., & Jian, Z. (1999). **Quantitative composition of benthic foraminiferal assemblages as a proxy indicator for organic carbon flux rates in the South China Sea**. *Marine Geology*, 156(1–4), 123–158.

Lambeck, K., & Bard, E. (2000). **Sea-level change along the French Mediterranean coast for the past 30,000 years**. *Earth and Planetary Science Letters*, 175(3–4), 203–222.

Langer, G., Nehrke, G., Probert, I., Ly, J., & Ziveri, P. (2009). **Strain-specific responses of *Emiliania huxleyi* to changing seawater carbonate chemistry**. *Biogeosciences*, 6, 2637–2646.

Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A. C. M., & Levrard, B. (2004). **A long term numerical solution for the insolation quantities of the Earth**. *Astronomy & Astrophysics*, 428(1), 261–285.

Laws, E. A., Falkowski, P. G., Smith, W. O., Ducklow, H., & McCarthy, J. J. (2000). **Temperature effect on export production in the open ocean**. *Global Biogeochemical Cycles*, 14, 1231–1246.

Use of Foraminifera in Climate Science

Lazarus, D. (2005). **A brief review of radiolarian research.** *Paläontologische Zeitschrift*, 79(1), 183–200.

Lea, D. W. (2014). **Elemental and isotopic proxies of past ocean temperatures.** In Heinrich D. Holland & Karl K. Turekian (Eds.), *Treatise on geochemistry: Vol. 8* (2nd ed.) (pp. 373–397). Amsterdam, The Netherlands: Elsevier.

Lear, C. H., Coxall, H. K., Foster, G. L., Lunt, D. J., Mawbey, E. M., Rosenthal, Y., . . . Wilson, P. A. (2015). **Neogene ice volume and ocean temperatures: Insights from in-faunal foraminiferal Mg/Ca paleothermometry.** *Paleoceanography*, 30, 1437–1454.

Leuschner, D. C., & Sirocko, F. (2003). **Orbital insolation forcing of the Indian Monsoon—a motor for global climate changes?** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 197(1–2), 83–95.

Leutenegger, S., & Hansen, H. J. (1979). **Ultrastructural and radiotracer studies of pore function in foraminifera.** *Marine Biology*, 54(1), 11–16.

Linke, P., & Lutze, G. F. (1993). **Microhabitat preferences of benthic foraminifera—a static concept or a dynamic adaptation to optimize food acquisition?** *Marine Micropaleontology*, 20(3–4), 215–234.

Lisiecki, L. E., & Raymo, M. E. (2005). **A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records.** *Paleoceanography*, 20, PA1003.

Lohbeck, K. T., Riebesell, U., & Reusch, T. B. H. (2012). **Adaptive evolution of a key phytoplankton species to ocean acidification.** *Nature Geoscience*, 5, 346–351.

Longhurst, A. R. (1991). **Role of the marine biosphere in the global carbon cycle.** *Limnology and Oceanography*, 36(8), 1507–1526.

Lowery, C. M., Bralower, T. J., Owens, J. D., Rodríguez-Tovar, F. J., Jones, H., Smit, J., . . . Zylberman, W. (2018). **Rapid recovery of life at ground zero of the end-Cretaceous mass extinction.** *Nature*, 558, 288–291.

Lu, Z., Hoogakker, B. A. A., Hillenbrand, C.-D., Zhou, X., Thomas, E., Gutchess, K. M., . . . Rickaby, R. E. M. (2016). **Oxygen depletion recorded in upper waters of the glacial Southern Ocean.** *Nature Communications*, 7, 11146.

Mackensen, A. (2008). On the use of benthic foraminiferal ^{13}C in palaeoceanography: Constraints from primary proxy relationships. In W. E. N. Austin & R. H. James (Eds.), *Bio-geochemical controls on palaeoceanographic environmental proxies* (pp. 121–133), Geological Society, London, Special Publications 303. London, U.K.: Geological Society.

Mackensen, A., & Douglas, R. G. (1989). **Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland.** *Deep-Sea Research Part A*, 36(6), 879–900.

Use of Foraminifera in Climate Science

Mackensen, A., Schmiedl, G., Harloff, J., & Giese, M. (1995). **Deep-sea foraminifera in the South Atlantic Ocean: Ecology and assemblage generation.** *Micropaleontology*, 41(4), 342–358.

MARGO project members. (2009). **Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum.** *Nature Geoscience*, 18, 127–132.

McCorkle, D. C., & Emerson, S. R. (1988). **The relationship between pore water carbon isotopic composition and bottom water oxygen concentration.** *Geochimica et Cosmochimica Acta*, 52(5), 1169–1178.

McCorkle, D. C., Keigwin, L. D., Corliss, B. H., & Emerson, S. R. (1990). **The influence of microhabitats on the carbon isotopic composition of deep-sea benthic foraminifera.** *Paleoceanography*, 5(2), 161–185.

McGowran, B., 2012. **Cenozoic environmental shifts and foraminiferal evolution.** In J. A. Talent (Ed.), *Earth and life: Global biodiversity, extinction intervals and biogeographic perturbations through time* (pp. 937–965). International Year of Planet Earth. Dordrecht, The Netherlands: Springer.

McInerney, F. A., & Wing, S. L. (2011). **The Paleocene-Eocene thermal maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future.** *Annual Review of Earth and Planetary Sciences*, 39, 489–516.

McIntyre, A., & Bé, A. W. H. (1967). **Modern coccolithophoridae of the Atlantic Ocean—I. Placoliths and cyrtoliths.** *Deep-Sea Research*, 14(5), 561–597.

Mertens, K. N., Bradley, L. R., Takano, Y., Mudie, P. J., Marret, F., Aksu, A. E., . . . Matsuo-ka, K. (2012). **Quantitative estimation of Holocene surface salinity variation in the Black Sea using dinoflagellate cyst process length.** *Quaternary Science Reviews*, 39, 45–59.

Milker, Y., Nelson, A. R., Horton, B. P., Engelhart, S. E., Bradley, L.-A., & Witter, R. C. (2016). **Differences in coastal subsidence in southern Oregon (USA) during at least six prehistoric megathrust earthquakes.** *Quaternary Science Reviews*, 142, 143–163.

Milker, Y., Schmiedl, G., & Betzler, C. (2011). **Paleobathymetric history of the Western Mediterranean Sea shelf during the latest glacial period and the Holocene: Quantitative reconstructions based on foraminiferal transfer functions.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 307, 324–338.

Milker, Y., Schmiedl, G., Betzler, C., Römer, M., Jaramillo-Vogel, D., & Siccha, M. (2009). **Distribution of recent benthic foraminifera in neritic carbonate environments of the Western Mediterranean Sea.** *Marine Micropaleontology*, 73(3–4), 207–225.

Use of Foraminifera in Climate Science

- Milker, Y., Weinkauf, M. F. G., Titschack, J., Freiwald, A., Krüger, S., & Jorissen, F. J. (2017). **Testing the applicability of a benthic foraminiferal-based transfer function for the reconstruction of paleowater depth changes in Rhodes (Greece) during the early Pleistocene.** *PLoS ONE*, 12(11), e0188447.
- Mix, A. C., Bard, E., & Schneider, R. (2001). **Environmental processes of the Ice Age: Land, oceans, glaciers (EPILOG).** *Quaternary Science Reviews*, 20(4), 627–657.
- Molina, E. (2015). **Evidence and causes of the main extinction events in the Paleogene based on extinction and survival patterns of foraminifera.** *Earth-Science Reviews*, 140, 166–181.
- Moodley, L., & Hess, C. (1992). **Tolerance of infaunal benthic foraminifera for low and high oxygen concentrations.** *Biological Bulletin*, 183(1), 94–98.
- Moore, T. C., Jr. (1978). **The distribution of radiolarian assemblages in the modern and ice-age Pacific.** *Marine Micropaleontology*, 3(3), 229–266.
- Morard, R., Escarguel, G., Weiner, A. K. M., André, A., Douady, C. J., Wade, C. M., . . . Kucera, M. (2016). **Nomenclature for the nameless: A proposal for an integrative molecular taxonomy of cryptic diversity exemplified by planktonic foraminifera.** *Systematic Biology*, 65(5), 925–940.
- Mulitza, S., Arz, H., Kemle-von Mücke, S., Moos, C., Niebler, H.-S., Pätzold, J., & Segl, M. (1999). The South Atlantic carbon isotope record of planktic foraminifera. In G. Fischer & G. Wefer (Eds.), *Use of proxies in paleoceanography: Examples from the South Atlantic* (pp. 427–445). Berlin, Germany: Springer-Verlag.
- Murray, J. W. (2006). *Ecology and applications of benthic foraminifera*. Cambridge, U.K.: Cambridge University Press.
- Murray, J. W., & Alve, E. (1999). **Natural dissolution of modern shallow water benthic foraminifera: Taphonomic effects on the palaeoecological record.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 146(1–4), 195–209.
- Mutterlose, J., Bornemann, A., & Herrle, J. O. (2005). **Mesozoic calcareous nannofossils—state of the art.** *Paläontologische Zeitschrift*, 79(1), 113–133.
- Naidu, P. D., & Malmgren, B. A. (1995). **Do benthic foraminifer records represent a productivity index in oxygen minimum zone areas? An evaluation from the Oman Margin, Arabian Sea.** *Marine Micropaleontology*, 26(1–4), 49–55.
- Nydick, K. R., Bidwell, A. B., Thomas, E., & Varekamp, J. C. (1995). **A sea-level rise curve from Guilford, Connecticut, USA.** *Marine Geology*, 124(1–4), 137–159.
- Ohga, T., & Kitazato, H. (1997). **Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan).** *Terra Nova*, 9(1), 33–37.

Use of Foraminifera in Climate Science

Pahnke, K., & Zahn, R. (2005). **Southern hemisphere water mass conversion linked with North Atlantic climate variability.** *Science*, 307(5716), 1741–1746.

Paillard, D., Labeyrie, L., & Yiou, P. (1996). **Macintosh program performs time-series analysis.** *Eos Transactions American Geophysical Union*, 77, 379.

Passow, U., & Carlson, C. A. (2012). **The biological pump in a high CO₂ world.** *Marine Ecology Progress Series*, 470, 249–271.

Pearson, P. N. (2012). **Oxygen isotopes in foraminifera: Overview and historical review.** *The Paleontological Society Papers*, 18, 1–38.

Peeters, F. J. C., Acheson, R., Brummer, G.-J. A., de Ruijter, W. P. M., Schneider, R. R., Ganssen, G. M., . . . Kroon, D. (2004). **Vigorous exchange between the Indian and Atlantic oceans at the end of the past five glacial periods.** *Nature*, 430, 661–665.

Perez-Cruz, L. L., & Machain-Castillo, M. L. (1990). **Benthic foraminifera of the oxygen minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico.** *Journal of Foraminiferal Research*, 20(4), 312–325.

Piña-Ochoa, E., Høglund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., . . . Risgaard-Petersen, N. (2010). **Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida.** *Proceedings of the National Academy of Sciences*, 107, 1148–1153.

Punekar, J., Keller, G., Khozyem, H. M., Adatte, T., Font, E., & Spangenberg, J. (2016). **A multi-proxy approach to decode the end-Cretaceous mass extinction.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441(1), 116–136.

Racki, G., & Cordey, F. (2000). **Radiolarian palaeoecology and radiolarites: Is the present the key to the past?** *Earth Science Reviews*, 52(1–3), 83–120.

Raffi, I., Backman, J., Fornaciari, E., Pälike, H., Rio, D., Lourens, L., & Hilgen, F. (2006). **A review of calcareous nannofossil astrobiochronology encompassing the past 25 million years.** *Quaternary Science Reviews*, 25(23–24), 3113–3137.

Rathburn, A. E., Willingham, J., Ziebis, W., Burkett, A. M., & Corliss, B. H. (2018). **A new biological proxy for deep-sea paleo-oxygen: Pores of epifaunal benthic foraminifera.** *Scientific Reports*, 8, 9456.

Ravelo, A. C., & Hillaire-Marcel, C. (2007). **The use of oxygen and carbon isotopes of foraminifera in paleoceanography.** In C. Hillaire-Marcel & A. De Vernal (Eds.), *Proxies in late Cenozoic paleoceanography: Vol. 1* (pp. 735–764). Amsterdam, The Netherlands: Elsevier.

Riegel, W. (2008). **The late Palaeozoic phytoplankton blackout—Artefact or evidence of global change?** *Review of Palaeobotany and Palynology*, 148(2–4), 73–90.

Use of Foraminifera in Climate Science

Risgaard-Petersen, N., Langezaal, A. M., Ingvarlsen, S., Schmid, M. C., Jetten, M. S. M., Op Den Camp, H. J. M., . . . Van Der Zwaan, G. J. (2006). **Evidence for complete denitrification in a benthic foraminifer.** *Nature*, *443*, 93–96.

Rohling, E. J. (2000). **Paleosalinity: Confidence limits and future applications.** *Marine Geology*, *163*(1–4), 1–11.

Rohling, E. J., & Cooke, S. (1999). Stable oxygen and carbon isotopes in foraminiferal carbonate shells. In B. K. Sen Gupta (Ed.), *Modern foraminifera* (pp. 239–258). Dordrecht, The Netherlands: Kluwer Academic.

Rohling, E. J., Foster, G. L., Grant, K. M., Marino, G., Roberts, A. P., Tamisiea, M. E., & Williams, F. (2014). **Sea-level and deep-sea-temperature variability over the past 5.3 million years.** *Nature*, *508*, 477–482.

Rohling, E. J., Jorissen, F. J., & De Stigter, H. C. (1997). **200 year interruption of Holocene sapropel formation in the Adriatic Sea.** *Journal of Micropalaeontology*, *16*, 97–108.

Rohling, E. J., Marino, G., & Grant, K. M. (2015). **Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels).** *Earth-Science Reviews*, *143*, 62–97.

Rohling, E. J., Sprovieri, M., Cane, T., Casford, J. S. L., Cooke, S., Bouloubassi, I., . . . Kroon, D. (2004). **Reconstructing past planktic foraminiferal habitats using stable isotope data: A case history for Mediterranean sapropel S5.** *Marine Micropaleontology*, *50*(1–2), 89–123.

Romano, M. (2015). **From petrified snakes, through giant “foraminifers,” to extinct cephalopods: The early history of ammonite studies in the Italian peninsula.** *Historical Biology*, *27*, 214–235.

Rosell-Melé, A., Bard, E., Emeis, K. C., Grieger, B., Hewitt, C., Müller, P. J., & Schneider, R. (2004). **Sea surface temperature anomalies in the oceans at the LGM estimated from the alkenone-UK’37 index: Comparison with GCMs.** *Geophysical Research Letters*, *31*, L03208.

Rosenthal, Y., & Lohmann, G. P. (2002). **Accurate estimation of sea surface temperatures using dissolution corrected calibrations for Mg/Ca paleothermometry.** *Paleoceanography*, *17*, 1044.

Rossi, V., Horton, B. P., 2009. **The application of subtidal foraminifera-based transfer function to reconstruct Holocene paleobathymetry of the Po Delta, northern Adriatic Sea.** *Journal of Foraminiferal Research*, *39*(3), 180–190.

Ruiz, F., Abad, M., Bodergat, A. M., Carbonel, P., Rodríguez-Lázaro, J., & Yasuhara, M. (2005). **Marine and brackish-water ostracods as sentinels of anthropogenic impacts.** *Earth-Science Reviews*, *72*(1–2), 89–111.

Use of Foraminifera in Climate Science

Saltzman, M. R., & Thomas, E. (2012). Carbon isotope stratigraphy. In F. M. Gradstein, J. G. Ogg, M. Schmitz, & G. Ogg (Eds.), *The geologic time scale* (pp. 207–232). Amsterdam, The Netherlands: Elsevier.

Sarnthein, M., Gebhardt, H., Kiefer, T., Kucera, M., Cook, M., & Erlenkeuser, H. (2004). **Mid Holocene origin of the sea-surface salinity low in the subarctic North Pacific.** *Quaternary Science Reviews*, 23(20–22), 2089–2099.

Sarnthein, M., Gersonde, R., Niebler, S., Pflaumann, U., Spielhagen, R., Thiede, J., . . . Weinelt, M. (2003). **Overview of Glacial Atlantic Ocean Mapping (GLAMAP 2000).** *Paleoceanography*, 18(2), 1030.

Schiebel, R., & Hemleben, C. (2017). *Planktic foraminifers in the modern ocean*. Berlin, Germany: Springer.

Schiebel, R., Zeltner, A., Treppke, U. F., Waniek, J. J., Bollmann, J., Rixen, T., & Hemleben, C. (2004). **Distribution of diatoms, coccolithophores and planktic foraminifers along a trophic gradient during SW monsoon in the Arabian Sea.** *Marine Micropaleontology*, 51(3–4), 345–371.

Schilman, B., Almogi-Labin, A., Bar-Matthews, M., & Luz, B. (2003). **Late Holocene productivity and hydrographic variability in the eastern Mediterranean inferred from benthic foraminiferal stable isotopes.** *Paleoceanography*, 18(3).

Schlüter, L., Lohbeck, K. T., Gutowska, M. A., Gröger, J. P., Riebesell, U., & Reusch, T. B. H. (2014). **Adaptation of a globally important coccolithophore to ocean warming and acidification.** *Nature Climate Change*, 4, 1024–1030.

Schmidt, C., Morard, R., Almogi-Labin, A., Weinmann, A. E., Titelboim, D., Abramovich, S., & Kucera, M. (2015). **Recent invasion of the symbiont-bearing foraminifera *Pararotalia* into the eastern Mediterranean facilitated by the ongoing warming trend.** *PLoS ONE*, 10(8), e0132917.

Schmidt, C., Titelboim, D., Brandt, J., Herut, B., Abramovich, S., Almogi-Labin, A., & Kucera, M. (2016). **Extremely heat tolerant photo-symbiosis in a shallow marine benthic foraminifera.** *Scientific Reports*, 6, 30930.

Schmidt, D. N., Lazarus, D., Young, J. R., & Kucera, M. (2006). **Biogeography and evolution of body size in marine plankton.** *Earth-Science Reviews*, 78(3–4), 239–266.

Schmidt, D. N., Thomas, E., Authier, E., Saunders, D., & Ridgwell, A. (2018). **Strategies in times of crisis—insights into the benthic foraminiferal record of the Palaeocene-Eocene thermal maximum.** *Philosophical Transactions of the Royal Society A*, 376, 20170328.

Schmidtko, S., Stramma, L., & Visbeck, M. (2017). **Decline in global oceanic oxygen content during the past five decades.** *Nature*, 542, 335–339.

Use of Foraminifera in Climate Science

Schmiedl, G., Hemleben, C., Keller, J., & Segl, M. (1998). **Impact of climatic changes on the benthic foraminiferal fauna in the Ionian Sea during the last 330,000 years.** *Paleoceanography*, 13(5), 447-458.

Schmiedl, G., Kuhnt, T., Ehrmann, W., Emeis, K.-C., Hamann, Y., Kotthoff, U., . . . Pross, J. (2010). **Climatic forcing of eastern Mediterranean deep-water formation and benthic ecosystems during the past 22000 years.** *Quaternary Science Reviews*, 29(23-24), 3006-3020.

Schmiedl, G., & Leuschner, D. C. (2005). **Oxygenation changes in the deep western Arabian Sea during the last 190,000 years: Productivity versus deep-water circulation.** *Paleoceanography*, 20, PA2008.

Schmiedl, G., & Mackensen, A. (1997). **Late Quaternary paleoproductivity and deep water circulation in the eastern South Atlantic Ocean: Evidence from benthic foraminifera.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 130(1-4), 43-80.

Schmiedl, G., & Mackensen, A. (2006). **Multispecies stable isotopes of benthic foraminifers reveal past changes of organic matter decomposition and deepwater oxygenation in the Arabian Sea.** *Palaeoceanography*, 21, PA4213.

Schmiedl, G., Mitschele, A., Beck, S., Emeis, K.-C., Hemleben, C., Schulz, H., . . . Weldeab, S. (2003). **Benthic foraminiferal record of ecosystem variability in the eastern Mediterranean Sea during times of sapropel S5 and S6 formation.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 190, 139-164.

Schnitker, D. (1974). **West Atlantic abyssal circulation during the past 120,000 years.** *Nature*, 248, 385-387.

Schönfeld, J. (2002). **A new benthic foraminiferal proxy for near-bottom current velocities in the Gulf of Cadiz, northeastern Atlantic Ocean.** *Deep-Sea Research I*, 49(10), 1853-1875.

Schönfeld, J., & Altenbach, A. V. (2005). **Late Glacial to Recent distribution pattern of deep-water *Uvigerina* species in the north-eastern Atlantic.** *Marine Micropaleontology*, 57(1-2), 1-24.

Schulte, P., Alegret, L., Arenillas, I., Arz, J. A., Barton, P. J., Bown, P. R., . . . Willumsen, P. S. (2010). **The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary.** *Science*, 327(5970), 1214-1218.

Scott, D. S., & Medioli, F. S. (1978). **Vertical zonations of marsh foraminifera as accurate indicators of former sea-levels.** *Nature*, 272, 528-531.

Scott, D. S., Medioli, F. S., & Schafer, C. T. (2001). *Monitoring in coastal environments using foraminifera and thecamoebian indicators.* Cambridge, U.K.: Cambridge University Press.

Use of Foraminifera in Climate Science

Self-Trail, J. M., Powars, D. S., Watkins, D. K., & Wandless, G. A. (2012). **Calcareous nanofossil assemblage changes across the Paleocene-Eocene thermal maximum: Evidence from a shelf setting.** *Marine Micropaleontology*, 92–93, 61–80.

Sen Gupta, B. K. (1999). Foraminifera in marginal marine environments. In B. K. Sen Gupta (Ed.), *Modern foraminifera* (pp. 141–159). Dordrecht, The Netherlands: Kluwer Academic.

Sepúlveda, J., Wendler, J. E., Summons, R. E., & Hinrichs, K.-U. (2009). **Rapid resurgence of marine productivity after the Cretaceous-Paleogene mass extinction.** *Science*, 326(5949), 129–132.

Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R., Munnecke, A., . . . Rasmussen, C. M. Ø. (2016). **The onset of the “Ordovician Plankton Revolution” in the late Cambrian.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, 458, 12–28.

Shackleton, N. J. (1987). **Oxygen isotopes, ice volume and sea level.** *Quaternary Science Reviews*, 6(3–4), 183–190.

Siddall, M., Rohling, E. J., Almogi-Labin, A., Hemleben, C., Meischner, D., Schmelzer, I., & Smeed, D. A. (2003). **Sea-level fluctuations during the last glacial cycle.** *Nature*, 423, 853–858.

Sluijs, A., Pross, J., & Brinkhuis, H. (2005). **From greenhouse to icehouse: Organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene.** *Earth-Science Reviews*, 68(3–4), 281–315.

Soldani A. (1780). *Saggio orittografico ovvero osservazioni sopra le terre nautilitiche ed ammonitiche della Toscana.* Sienna, Italy: Nella Stamperia di Vincenzo Pazzini Carli e Figli.

Soldani, A. (1791). *Testaceographiae ac zoophytographiae parvae et microscopicae. Tomi primi pars altera.* Senis, Italy: In Typographia Francisci Rossi.

Speijer, R. P., Scheibner, C., Stassen, P., & Morsi, A.-M. M. (2012). Response of marine ecosystems to deep-time global warming: A synthesis of biotic patterns across the Paleocene–Eocene thermal maximum (PETM). *Austrian Journal of Earth Sciences*, 105(1), 6–16.

Spencer-Cervato, C. (1999). The Cenozoic deep sea microfossil record: Explorations of the DSDP/ODP sample set using the Neptune database. *Palaeontologica Electronica*, 2(2), article 4.

Spero, H. J., Bijma, J., Lea, D. W., & Bemis, B. E. (1997). **Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes.** *Nature*, 390, 497–500.

Use of Foraminifera in Climate Science

Spero, H. J., Lerche, I., & Williams, D. F. (1991). **Opening the carbon isotope “vital effect” black box, 2, Quantitative model for interpreting foraminiferal carbon isotope data.** *Paleoceanography*, 6(6), 639–655.

Stover, L. E., Brinkhuis, H., Damassa, S. P., de Verteuil, L., Helby, R. J., Monteil, E., . . . Williams, G. L. (1996). Mesozoic–Tertiary dinoflagellates, acritarchs and prasinophytes. In J. Jansonius & D. C. McGregor (Eds.), *Palynology: Principles and applications: Vol. 2* (pp. 641–750). Dallas, TX: American Association of Stratigraphic Palynologists Foundation.

Stramma, L., Schmidtko, S., Levin, L. A., & Johnson, G. C. (2010). **Ocean oxygen minima expansions and their biological impacts.** *Deep-Sea Research I*, 57(4), 587–595.

Streeter, S. S., & Shackleton, N. J. (1979). **Paleocirculation on the deep North Atlantic: 150,000-year record of benthic foraminifera and oxygen-18.** *Science*, 203(4376), 168–170.

Studer, A. S., Sigman, D. M., Martínez-García, A., Benz, V., Winckler, G., Kuhn, G., . . . Haug, G. H. (2015). **Antarctic Zone nutrient conditions during the last two glacial cycles.** *Paleoceanography*, 30(7), 845–862.

Tanimura, Y., & Aita, Y. (Eds.). (2009). *Joint Haeckel and Ehrenberg project: Reexamination of the Haeckel and Ehrenberg microfossil collections as a historical and scientific legacy*. National Museum of Nature and Science Monographs 40. Tokyo, Japan: National Museum of Nature and Science.

Theodor, M., Schmiedl, G., Jorissen, F., & Mackensen, A. (2016). **Stable carbon isotope gradients in benthic foraminifera as proxy for organic carbon fluxes in the Mediterranean Sea.** *Biogeosciences*, 13, 6385–6404.

Thomas, E. (1989). **Development of Cenozoic deep-sea benthic foraminiferal faunas in Antarctic waters.** In J. A. Crame (Ed.), *Origins and evolution of the Antarctic biota* (pp. 283–296). Geological Society, London, Special Publications 47. London, U.K.: Geological Society

Thomas, E. (1998). Biogeography of the late Paleocene benthic foraminifera extinction. In M.-P. Aubry, S. Lucas, & W. A. Berggren (Eds.), *Late Paleocene–early Eocene biotic and climatic events in the marine and terrestrial records* (pp. 214–243). New York, NY: Columbia University Press.

Thomas, E. (2007). **Cenozoic mass extinctions in the deep sea: What perturbs the largest habitat on Earth?** In S. Monechi, R. Coccioni, & M. R. Rampino (Eds.), *Large ecosystem perturbations: Causes and consequences* (pp. 1–23). The Geological Society of America Special Paper 424. Boulder, CO: Geological Society of America.

Thomas, E., Gapotchenko, T., Varekamp, J. C., Mccray, E. L., & Buchholtz ten Brink, M. R. (2000). Benthic foraminifera and environmental changes in Long Island Sound. *Journal of Coastal Research*, 16(3), 641–655.

Use of Foraminifera in Climate Science

Thomas, E., & Gooday, A. J. (1996). **Deep-sea benthic foraminifera: Tracers for Cenozoic changes in oceanic productivity?** *Geology*, *24*, 355–358.

Thomas, E., & Shackleton, N. J. (1996). **Paleocene-Eocene benthic foraminiferal extinction and stable isotope anomalies.** In R. W. O. B. Knox & R. E. Dunay (Eds.), *Correlation of the early Paleogene in northwest Europe* (pp. 401–441). Geological Society, London, Special Publication 101. London, U.K.: Geological Society.

Van der Zwaan, G. J., Duijnste, I. A. P., den Dulk, M., Ernst, S. R., Jannink, N. T., & Kouwenhoven, T. J. (1999). **Benthic foraminifers: Proxies or problems? A review of paleoecological concepts.** *Earth Science Reviews*, *46*, 213–236.

Van der Zwaan, G. J., Jorissen, F. J., & de Stigter, H. C. (1990). **The depth dependency of planktonic/benthic foraminiferal ratios: Constraints and applications.** *Marine Geology*, *95*(1), 1–16.

Van Hinsbergen, D. J. J., Kouwenhoven, T. J., & van der Zwaan, G. J. (2005). **Paleobathymetry in the backstripping procedure: Correction for oxygenation effects on depth estimates.** *Palaeogeography, Palaeoclimatology, Palaeoecology*, *221*(3–4), 245–265.

Verleye, T. J., Mertens, K. N., Young, M. D., Dale, B., McMinn, A., Scott, L., . . . Louwye, S. (2012). **Average process length variation of the marine dinoflagellate cyst *Operculodinium centrocarpum* in the tropical and Southern Hemisphere Oceans: Assessing its potential as a palaeosalinity proxy.** *Marine Micropaleontology*, *86–87*, 45–58.

Wade, B. S., Houben, A. J. P., Quaijtaal, W., Schouten, S., Rosenthal, Y., Miller, K. G., . . . Brinkhuis, H. (2012). **Multiproxy record of abrupt sea-surface cooling across the Eocene-Oligocene transition in the Gulf of Mexico.** *Geology*, *40*(2), 159–162.

Wade, B. S., Pearson, P. N., Berggren, W. A., & Pälike, H. (2011). Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Science Reviews*, *104*, 111–142.

Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J. C., McManus, J. F., Lambeck, K., . . . Labracherie, M. (2002). **Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records.** *Quaternary Science Reviews*, *21*(1–3), 295–305.

Wara, M. W., Ravelo, A. C., & Delaney, M. L. (2005). **Permanent El Niño-like conditions during the Pliocene Warm Period.** *Science*, *309*(5735), 758–761.

Weinmann, A. E., Rödder, D., Lötters, S., & Langer, M. R. (2013). **Traveling through time: The past, present and future biogeographic range of the invasive foraminifera *Amphistegina* spp. in the Mediterranean Sea.** *Marine Micropaleontology*, *105*, 30–39.

Use of Foraminifera in Climate Science

Wiggan, N. J., Riding, J. B., Fensome, R. A., & Mattioli, E. (2018). **The Bajocian (Middle Jurassic): A key interval in the early Mesozoic phytoplankton radiation.** *Earth-Science Reviews*, 180, 126–146.

Winguth, A. M. E., Thomas, E., & Winguth, C. (2012). **Global decline in ocean ventilation, oxygenation, and productivity during the Paleocene-Eocene thermal maximum: Implications for the benthic extinction.** *Geology*, 40(3), 263–266.

Wollenburg, J. E., Kuhnt, W., & Mackensen, A. (2001). **Changes in Arctic Ocean paleo-productivity and hydrography during the last 145 kyr: The benthic foraminiferal record.** *Paleoceanography*, 16, 65–77.

Woods, M. A., Vandenbroucke, T. R. A., Williams, M., Riding, J. B., De Schepper, S., & Sabbe, K. (2014). **Complex response of dinoflagellate cyst distribution patterns to cooler early Oligocene oceans.** *Earth-Science Reviews*, 138, 215–230.

Zachos, J. C., Arthur, M. A., & Dean, W. E. (1989). **Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous/Tertiary boundary.** *Nature*, 337, 61–64.

Zachos, J. C., Dickens, G. R., & Zeebe, R. E. (2008). **An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics.** *Nature*, 451, 279–283.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). **Trends, rhythms, and aberrations in global climate 65 Ma to present.** *Science*, 292(5517), 686–693.

Zachos, J. C., Wara, M. W., Bohaty, S., Delaney, M. L., Petrizzo, M. R., Brill, A., . . . Premoli-Silva, I. (2003). **A transient rise in tropical sea surface temperature during the Paleocene-Eocene thermal maximum.** *Science*, 302(5650), 1551–1554.

Zahn, R., Winn, K., & Sarnthein, M. (1986). **Benthic foraminiferal $d^{13}C$ and accumulation rates of organic carbon: *Uvigerina peregrina* group and *Cibicidoides wuellerstorfi*.** *Paleoceanography*, 1(1), 27–42.

Zeebe, R. E., Dickens, G. R., Ridgwell, A., Sluijs, A., & Thomas, E. (2014). **Onset of carbon isotope excursion at the Paleocene-Eocene thermal maximum took millennia, not 13 years.** *Proceedings of the National Academy of Sciences*, 111(12), E1062–E1063.

Zeebe, R. E., Ridgwell, A., & Zachos, J. C. (2016). **Anthropogenic carbon release rate unprecedented during the past 66 million years.** *Nature Geoscience*, 9, 325–329.

Zeebe, R. E., & Westbroek, P. (2003). **A simple model for the $CaCO_3$ saturation state of the ocean: The “Strangelove,” the “Neritan,” and the “Cretan” Ocean.** *Geochemistry, Geophysics, Geosystems*, 4(12), 1104.

Use of Foraminifera in Climate Science

Zhou, X., Thomas, E., Rickaby, R. E. M., Winguth, A. M. E., & Lu, Z. (2014). **I/Ca evidence for upper ocean deoxygenation during the PETM.** *Paleoceanography*, 29, 964–975.

Ziveri, P., Baumann, K.-H., Böckel, B., Bollmann, J., & Young, J. (2004). Biogeography of selected Holocene coccoliths in the Atlantic Ocean. In H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores: From molecular processes to global impact* (pp. 403–428). Berlin, Germany: Springer.

Zong, Y., & Sawai, Y. (2015). Diatoms. In I. Shennan, A. J. Long, & B. P. Horton (Eds.), *Handbook of sea-level research* (pp. 233–248). Chichester, U.K.: John Wiley & Sons.

Zonneveld, K. A. F., Chen, L., Elshanawany, R., Fischer, H. W., Hoins, M., Ibrahim, M. I., . . . Versteegh, G. J. M. (2012). **The use of dinoflagellate cysts to separate human-induced from natural variability in the trophic state of the Po River discharge plume over the last two centuries.** *Marine Pollution Bulletin*, 64(1), 114–132.

Gerhard Schmiedl

Department of Earth Sciences, University of Hamburg