60th Anniversary special volume

Advances in planktonic foraminifer research: New perspectives for paleoceanography☆

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ARTICLE INFO

ABSTRACT

Planktonic foraminifer tests are major archives of environmental change and provide a multitude of proxies in paleoceanography and paleoclimatology. The application of such proxies is contingent upon a collaborative effort to better understand how the living organisms record the properties of their environment and how the resulting signals are recorded in marine sediments. In this contribution, we provide a review of the rapidly developing sub-fields of research, where new advances have been made possible by technological developments, and by cross-disciplinary work of the scientific community. Following brief historical overviews of the sub-fields, we discuss the latest advances in planktonic foraminifer research and highlight the resulting new perspectives in ocean and climate research. Natural classification based on consistent species concepts forms the basis for analysis of any foraminifer-derived proxy. New approaches in taxonomy and phylogeny of Cenozoic planktonic foraminifers (Section 2) are presented, highlighting new perspectives on sensitivity and response of planktonic foraminifers to the changing climate and environment (Section 4). Calibration of foraminifer-specific data and environmental parameters is improving along with the technical development of probes and the access to samples from the natural environment (Section 3), enhancing our understanding of the ever-changing climate and ocean system. Comprehension of sedimentation and flux dynamics facilitates maximum gain of information from fossil assemblages (Section 5). Subtle changes in the physical (e.g., temperature), chemical (e.g., *p*H), and biological (e.g., food) conditions of ambient seawater affect the abundance of species and composition of assemblages as well as the chemical composition of the foraminifer shell and provide increasingly-detailed proxy data on paleoenvironments (Section 6).

R É S U M É

Les coquilles des foraminifères planctoniques sont des archives majeures des changements océaniques et climatiques et fournissent une multitude de proxies en paléocéanographie et en paléoclimatologie. L'utilisation de tels proxies nécessite une approche pluridisciplinaire afin de mieux comprendre comment les organismes vivants enregistrent les propriétés de leur environnement et comment le signal résultant est enregistré dans les sédiments marins. Dans cet article, nous présentons une revue des sous-domaines de recherche évoluant rapidement, où de nouveaux progrès sont rendus possibles par les développements technologiques, et par le travail interdisciplinaire de la communauté scientifique. Après de brefs aperçus historiques des sous-domaines, nous discutons des dernières avancées en matière de recherche sur les foraminifères planctoniques et soulignons les nouvelles perspectives qui en résultent dans la recherche sur les océans et le climat. La classification naturelle basée sur des concepts d'espèces constitue la base de toute analyse des proxies dérivés de foraminifères. De nouvelles approches en taxonomie et en phylogénie des foraminifères planctoniques du cénozoïque (Section 2) sont présentées, mettant en évidence de nouvelles perspectives de recherche sur la sensibilité des foraminifères planctoniques aux changements climatiques et à l'environnement (Section 4). La calibration des données spécifiques aux foraminifères et des paramètres environnementaux s'améliore avec le développement technique des sondes et l'accès aux échantillons provenant de l'environnement naturel (Section 3). Mieux comprendre la sédimentation et la dynamique des flux de coquilles permet d'obtenir plus d'informations à partir des assemblages fossiles (Section 5). Cela améliore notre compréhension du système climatique et océanique, en constante évolution. De subtils changements dans la composition physique (e.g., température), chimique (e.g., pH) et biologique (e.g., nourriture) de l'eau de mer ambiante affectent l'abondance des espèces de foraminifères, la composition de leurs assemblages ainsi que la composition chimique de leur coquille et fournit des données de proxies paléoenvironnementaux de plus en plus détaillées (Section 6).

1. Introduction

Planktonic foraminifers were first identified by d'Orbigny in 1826 (Vénec-Peyré, 2005), and later described as heterotrophic planktonic protists in the 19th century. Their single-celled nature (by Dujardin in 1835; see Vénec-Peyré, 2005) and planktonic (i.e., 'drifting' or 'freely-floating') existence in the upper water column was recognized, largely thanks to the observations of J. Murray. By the time the first issue of the Revue de Micropaléontologie was published in 1958, the spatial distribution, species diversity and floatation strategies (e.g., Murray and Renard, 1891) of planktonic foraminifers had been discussed by the international community for over a century (e.g., Andrée, 1920). Indeed, much of our current understanding of these organisms stems from observations and ideas proposed by these pioneer researchers. With developments in mass spectrometry for paleoclimate research since the 1950s, foraminifer shell carbonate ($CaCO_3$) has emerged as an important archive of stable isotopes as proxies of trophic state and temperature of ambient seawater.

Planktonic foraminifer shells constitute a large portion of marine calcareous sediments in all major ocean basins starting from the Late Cretaceous about 100 Million years (Ma) ago. Due to their wide distribution, large numbers of shells, and large individual size (several hundred micrometers), foraminifers are among the most frequently used archives in paleoceanography and paleoclimate reconstruction and have been applied as stratigraphic markers in hydrocarbon exploration since the early 20th century.

Over the course of their evolution since the Mid Jurassic about 170 Ma ago, hundreds of morphotypes can be distinguished by the morphological features of their shell, or 'test'. Average longevity of a species ranges from 10 to 20 Ma. However, at certain times and in some groups, morphospecies turnover was faster and some species had ranges as short as 1–5 Ma years, which, combined with their global distribution, makes them valuable for biostratigraphy (McGowran, 2008). At any given time in the past 100 million years, the combined information from some tens of species can be used to determine the geological age and the ocean climate. Some 300 morphospecies evolved over the course of the Cretaceous, and several hundred new morphospecies evolved over the course of the Cenozoic following the catastrophic taxonomic losses (> 90%) of Cretaceous species at the Cretaceous-Paleogene extinction event about 66 Ma ago (Caron, 1985; Olsson et al., 1999; Arenillas and Arz, 2017).

The present-day ocean hosts around 50 morphotypes, and many more genotypes. Technological advances in molecular genetics and mass spectrometry have yielded a wealth of new information on the ecology and biogeochemistry of planktonic foraminifers. Development and calibration of proxies using live individuals contribute important tools for more detailed paleo-reconstruction. Whereas planktonic foraminifers are major producers of marine particulate inorganic carbon (PIC, i.e. calcite, and metastable carbonate phases; Jacob et al., 2017) flux, their overall contribution to the global marine biomass and biological carbon pump is minor. As such, planktonic foraminifers are rather passive recorders of marine carbon turnover allowing reconstruction of the biological carbon pump and carbonate counter pump, and ambient seawater pH without affecting carbon budgets on short (millennial) time intervals (Zeebe, 2012).

In the following, we highlight state of the art techniques for sample collection, processing and analysis, and some of the latest findings in planktonic foraminiferal research, which represents a concerted effort of the scientific community to push the boundaries of our current understanding in paleoceanography and paleoclimate.

2. Classification and Taxonomy

Given the primary interest in fossil tests, the taxonomy of planktonic foraminifers has traditionally been based on the morphospecies concept (species recognized on the basis of morphological dissimilarity) and the classification based on tests of adult individuals as found in marine sediments. The underlying framework for classifying fossil and living species has shifted from defining and grouping taxa based solely on gross test morphology (for example, chamber shape, the presence of peripheral keels and

coiling geometry) to also considering details of the wall microstructure, including the mineral construction of the test wall, the size and distribution of pores and the presence of acicular (needle like crystal-form) spines, or their remains (Lipps, 1966; Olsson et al., 1999).

The first planktonic foraminifer species correctly identified from beach sands of Cuba and Rimini (Italy) by the French naturalist Alcide d'Orbigny were empty tests of *Globigerina bulloides* (Vénec-Peyré, 2005). The planktonic nature of the species was later confirmed from plankton net tow samples of the English *Challenger* expedition in the 1870s. Ever since, planktonic and benthic foraminifers have been used as stratigraphic markers, ecological indicators, and climate archives. Research on foraminifers still resides mainly in the fields of geology, paleoceanography, and paleoclimate. However, as soon as these organisms were discovered in the planktonic realm (e.g., Brady, 1884), biology and ecology of live foraminifers was recognized as the reason for their presence or absence in marine waters and underlying sediments. Scanning electron microscopy (SEM) images on the ultrastructural details of the foraminifer shell fostered major progress in the systematic understanding of the taxonomy and phylogeny of planktonic foraminifers from the second half of the 20th century (e.g., Bé, 1968; Hemleben, 1969; Wade et al., 2018). Technological advances have facilitated analyses of the molecular genetics of live individuals since the 1990s. In combination with the traditional morphospecies concept, the new biological species concept has refined our understanding of the ecology and paleoceanography of species. Most morphotypes include more than one genotype (e.g., Darling and Wade, 2008). Some morphotypes were only discovered after their genotypes were differentiated (e.g., Huber et al., 1997; Bijma et al., 1998; de Vargas et al., 1999; André et al., 2014). In contrast, the different morphotypes of *Trilobatus sacculifer* (syn. *Globigerinoides sacculifer*) are produced by only one genotype (André et al., 2013). Phylogenetic differences between species behaving more or less conservatively are assumed to result from independent evolutionary developments. In addition, molecular data have led to a more standardized and objective species concept, allowing different individual perspectives and experiences, philosophies, and "taxonomic schools" to be merged and harmonized (de Vargas et al., 2002; André et al., 2014). Ultimately, a consistent species concept will help to better discern presence and absence of species at the regional to ocean basin scale, and over the course of seasons, as well as to reconstruct species migration over longer time scales such as glacial-interglacial climate cycles (e.g., Spero and Lea, 1993; Mary and Knappertsbusch, 2013; Broecker and Pena, 2014; Kretschmer et al., 2016). Tracing ecophenotypes and the biogeographic variability of fossil species through time may even facilitate a better understanding of evolutionary changes within the suborder of planktonic foraminifers, i.e. *Globigerinina*, and relationships with close relatives such as benthic foraminifers and radiolarians (Darling et al., 1997; Darling and Wade, 2008; Darling et al., 2009).

2.1. Phylogeny

Tracing evolutionary history and reconstructing phylogeny is an integral part of planktonic foraminifer studies. Initially this was driven by a desire to develop a 'natural' higher-level taxonomy to organize modern and fossil taxa in time and space and provide a globally correlative biostratigraphic scheme based on contemporaneous evolutionary changes (e.g., Bolli et al., 1957; McGowran, 1968; Blow, 1979; Banner and Lowry, 1985). Subsequently, interest has spread to the patterns of evolution itself (Pearson, 1993) and the most recent Cenozoic phylogenies of planktonic foraminifers are used to explore fundamental questions about the mechanisms of evolution and drivers of biodiversity in the pelagic realm (Aze et al., 2011; Ezard et al., 2011). Creating a phylogeny for fossil

foraminifers that might reflect something biologically meaningful, however, is challenging and early attempts are now regarded as incorrect or incomplete. This is not surprising given that, in order to build a phylogeny in the absence of molecular data, we must infer the relationships between taxa by weighing morphological traits, a step which in itself contains a great deal of subjectivity, including the basis of the taxonomic system, the choices of taxonomic units, the consistency and rigor with which the taxonomy is applied and the quality of fossil preservation.

Attempts at reconstructing evolutionary relationships in planktonic foraminifers started in the 1950s once their utility as biostratigraphic markers, especially in oil and gas exploration, had gained significant traction (e.g., Cushman, 1927; Finlay, 1939; Subbotina, 1947). The early taxonomic work resulted in the recognition of many morphospecies for the Mesozoic and Cenozoic periods. Pearson (1993) provides a review of the earliest efforts towards understanding the relationships between Paleogene morphospecies and the first planktonic foraminifer phylogenies involving identification of lineages, i.e. an ancestor-descendant series of populations. Landmark works referred to in this include Bolli et al. (1957), Banner and Blow (1959), Hofker (1959), Berggren (1968) and Blow (1979). At this stage, the higher taxonomy (i.e., family- and genus-level assignments) was largely based on gross test architecture, which we now understand is not a good basis as homeomorphy is rife among planktonic foraminifers (Lipps, 1966; Coxall et al., 2007). A turning point came in the late 1960s and early 1970s when the widespread use of SEM for imaging individual tests revealed that test-wall ultrastructure could be useful for higher-level taxonomy and thus for tracing ancestor–descendant relationships (Lipps, 1966; Olsson et al., 1999). In parallel, the advent of deep-sea drilling provided access to kilometers of marine sediments rich in planktonic foraminifer tests and, thus, more continuous evolutionary sequences. The first of the major synthetic phylogenic works to appear after these advancements was a 'Phylogenetic Atlas of Neogene Planktonic Foraminifera' (Kennett and Srinivasan, 1983). This employed a stratophenetic approach (Gingerich, 1979), now commonplace in foraminifer micropaleontology, that aims to reconstruct ancestor–descendant relationships using objective assessment of relatedness based on morphological similarity that is underpinned by independent evidence of geological age.

Due to their use in biostratigraphy, it was in the interest of early workers to taxonomically split fossil populations into as many readily identifiable taxonomic units as possible. Since the focus of this work was on the identification of the first and last occurrences of given test morphologies, the taxonomy was largely typological (Scott, 2011). As a result, planktonic foraminifers have been subject to possible "over-splitting" in terms of morphospecies divisions, to the extent that taxonomic workers may be regarded as "lumpers" or "splitters" depending on the degree of morphological disparity required for attempted subdivisions. Careful synthesizing steps have been necessary to standardize taxonomic approaches. Fortunately, the relative completeness of the planktonic foraminifer fossil record combined with ease of access to material through deep-sea drilling archives and internet-based data-sharing vehicles, including the Cushman Collection of foraminifer type material SEM images (https://paleobiology.si.edu/forams/), facilitates this. Central to this work is the recognition that it is possible to trace phyletic gradualism between morphospecies and reconstruct "evolutionary species" (Simpson, 1951). This approach was initially applied to planktonic foraminifers by Malmgren and Kennett (1981) who produced the first "evolutionary lineage phylogeny" and continued by Pearson (1993) and Aze et al. (2011). All attempted to synthesize the morphospecies phylogenies into evolutionary lineage phylogenies that are considered to reflect genuine evolutionary branching events (cladogenesis), thereby removing
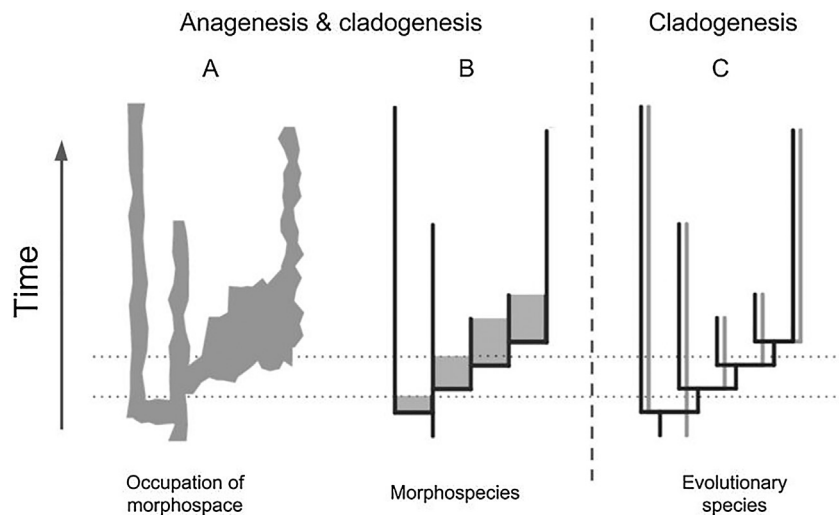
Fig. 1. Steps involved in creating a lineage phylogeny based on part of a hypothetical morphospecies phylogeny (after Pearson, 1993; Aze et al., 2011). (A) Grey shaded area is the "morphospace" occupied by the recognized taxa. (B) Stratigraphic ranges of identified morphospecies and inferred relationships in time. Morphological intergradation of the morphospecies (intermediates) is indicated by the grey blocks. (C) Merging intermediates removes pseudospeciations and pseudoextinctions resulting in an "evolutionary lineage" phylogeny that now illustrates the relationships between lines of descent. Adapted from Ezard et al. (2012).

cases of "pseudospeciation" and "pseudoextinction", which reflect gradual evolution within lineages (anagenesis) (Fig. 1).

Key instigators of the above lineage phylogenies have been the Paleogene Planktonic Foraminifera Working Group, who championed the wall-texture approach. They synthesized the existing literature, together with original SEM studies of new material and, importantly, type-specimens from museum collections, to produce three separate taxonomic Atlases for the Paleocene (Olsson et al., 1999), Eocene (Pearson et al., 2006) and Oligocene (Wade et al., 2018), each with an embedded phylogeny that included most taxa. As of writing, June 2018, a "Neogene working group" is being formed to tackle the Miocene-Recent. Starting with the Paleocene was crucial. The Cretaceous/Paleogene (K/Pg) mass extinction removed over 90% of Cretaceous planktonic foraminifer taxa, which provided a unique opportunity to trace a new evolutionary radiation. The K/Pg event is captured in many land- and marine-sediment sequences, yet identifying the evolutionary "seeds" for the Cenozoic planktonic foraminifer radiation turns out to be more difficult than anticipated. There is ongoing controversy regarding how long Cretaceous taxa survived into the Paleocene (Keller et al., 1993), whether the Paleocene radiation was seeded from one or more surviving Cretaceous planktonic taxa (Olsson et al., 1999) or if some or all Paleocene taxa evolved from ecologically flexible benthic ancestors that made the jump to a planktonic niche once pelagic "real estate" became available (Darling et al., 2009; Arenillas and Arz, 2017). Recent marine records from inside the K/Pg Chixculub impact crater have shed light on this question, confirming in unique detail that three planktonic foraminifer taxa, namely *Guembelitrioides cretacea*, *Muricohedbergella monmouthensis* and *M. holmdelensis*, survived the extinction (Lowery et al., 2018). Importantly, the new records argue that these survivor taxa were rather uncommon in the late Cretaceous and limited to shallower marginal environments, but invaded deeper waters to dominate planktonic foraminifer communities in the first 100 kyrs of the Paleocene. This implies evolutionary resilience and ecological plasticity existed within Cretaceous planktonic foraminifer lineages and strengthens the idea that planktonic survivors played a primary role in the early Paleocene reseeding, at least of normal perforate species.

Reconstructing the phylogeny of Jurassic and Cretaceous planktonic foraminifers presents additional challenges due to the increasing scarcity of well-preserved archives back in time. Efforts

are ongoing to update the taxonomy and biostratigraphy of the Jurassic (e.g., Gradstein et al., 2017; Waskowska et al., 2017) and Cretaceous taxa (e.g., Georgescu and Huber, 2009; Huber and Leckie, 2011; Haynes et al., 2015), following similar approaches to the Paleogene working group, but stratophenetic documentation of a number of lineages is still needed.

Most molecular phylogenies produced to date (e.g., Aurahs et al., 2009a) seem to vindicate the current family-level classification of extant planktonic foraminifers and seem largely congruent with stratophenetically-derived phylogeny within individual genera (Aze et al., 2011). Whilst some discrepancies can be solved by joint re-evaluation of molecular data and the fossil record (Aurahs et al., 2011; Spezzaferri et al., 2015), other cases, especially those concerning the deep phylogenetic relationships within families and among the families, are still not definitively solved. The discovery that most modern morphospecies are composed of a complex of several distinct genetic types, or "cryptic species" (e.g., Darling and Wade, 2008), certainly complements the picture, and work has started from both paleontology and genetic sides to address implied taxonomic and phylogenetic inconsistencies (e.g. André et al., 2014; Etienne et al., 2011; Spezzaferri et al., 2015; Morard et al., 2018).

The bigger picture of planktonic foraminifer phylogeny is still clearing. A common view has been that all living and extinct macroperforate planktonic foraminifers can be placed in one phylogenetic clade, the Superfamily Globigerinacea, Family Globigerinidae (Carpenter et al., 1862) (Kennett and Srinivasan, 1983; Pearson et al., 2006; Olsson et al., 1999), which can be traced to a single evolutionary expansion into the planktonic niche in the Early-Middle Jurassic (Tappan and Loeblich, 1988). This, however, has been challenged by molecular data, which imply polyphyletic origins of modern taxa from at least two ancestral benthic lines that bridged the planktonic-benthic divide through an opportunistic "tychopelagic" ecology in both microperforate and macroperforate groups (Darling et al., 1997; Darling et al., 2009; Kučera et al., 2017; Pearson, 2018). This may have happened multiple times in the geologic history of planktonic foraminifers, and indeed, similar benthic-planktonic leaps are imagined for the Jurassic and Cretaceous, as well as for the origin of at least some of the Cenozoic Globigerinidae through an independent colonization by plankton in the aftermath of the Cretaceous/Paleogene extinction event (Arenillas and Arz, 2017). The pelagic realm is highly susceptible to abiotic forcing and extremes in temperature, pH, and even light,

that have been shown to have serious impacts on calcifying planktonic organisms (D'Hondt, 2005; Hönisch et al., 2012), such that reseeding from the benthos is a likely and necessary pathway for recolonization after large scale perturbations. This is an area where molecular studies have overturned traditional ideas and spurred micropaleontology in new directions.

The production of the complete Cenozoic phylogeny for the macroperforate planktonic foraminifer morphospecies and its associated derived evolutionary lineage phylogeny (Aze et al., 2011) has raised the profile of planktonic foraminifers as a model system for testing evolutionary theories. For example, using the phylogeny as a basis, Ezard et al. (2011) identified the key drivers of speciation and extinction rates over the Cenozoic, while Edgar et al. (2017) showed that long-term evolutionary history has shaped the evolution of species-specific $\delta^{13}C$ vital effects, which is important for reconstructing marine carbon cycling. Further agreement between morphological and molecular phylogenies is likely to be achieved via greater efforts on the part of the paleontological community to identify previously-overlooked morphological traits that are taxonomically meaningful, together with a comprehensive analysis of molecular genetic datasets with better taxonomic and genomic coverage. These efforts will provide increasingly accurate insight into long-term pelagic biodiversity and resilience.

2.2. Two decades of single-cell genetic analyses in planktonic foraminifers: overview and implications

The earliest single-cell genetic analyses of the ribosomal Small Sub Units (SSU rDNA) of planktonic foraminifers in the mid 1990s confirmed the existence of the main clades, and revealed that the group is polyphyletic, showing that its extant diversity is the result of multiple invasion events of plankton by benthic ancestors (Darling et al., 1996; Wade et al., 1996; Darling et al., 1997; de Vargas et al., 1997). This discovery was concomitant with the detection of cryptic diversity in the two spinose morphospecies *Globigerinella siphonifera* (Huber et al., 1997) and *Orbulina universa* (de Vargas et al., 1999). Indeed, the sequencing of individual specimens collected across oceanic provinces revealed large divergences in their sequences, compatible with the presence of several biological species within morphological taxa, thus referred to as cryptic species. These findings triggered a series of publications on modern morphospecies that consistently showed the same patterns where the genetic diversity exceeds morphological diversity (for reviews, see for example Darling and Wade (2008) and André et al. (2014)), with the only exception of *T. sacculifer* where no cryptic diversity has been evidenced despite extensive worldwide sequencing (André et al., 2013). This sequencing effort carried out by multiple research teams showed that there is no correlation between the amount of genetic data produced and the cryptic species described (Fig. 2). However, the cryptic diversity is unique in every single morphospecies. For example, in stark contrast to *T. sacculifer*, *G. siphonifera* appears to be "hyper-diversified" including 12 cryptic

species (Weiner et al., 2014). The three cryptic species of *O. universa* seem to have diverged millions of years ago (de Vargas et al., 1999) whilst the cryptic species within *Globigerinoides ruber* diverged only recently (Kuroyanagi et al., 2008; Aurahs et al., 2009b; Aurahs et al., 2011). In addition, although the frequency of cryptic species within a given morphospecies is generally correlated with environmental parameters (e.g., temperature, food availability) through geography and/or water depth, most of them exhibit a large degree of overlap in their distribution (e.g., de Vargas et al., 2002; Ujiié and Lipps, 2009; Ujiié et al., 2012). Only the cryptic species of *Globorotalia inflata* (Morard et al., 2011) and *Hastigerina pelagica* (Weiner et al., 2012) show an exclusive ecological distribution with surface currents and water depth, respectively. Finally, morpho-genetic comparisons show a disconnection between rates of evolution and shell morphology. Detailed morphometric analyses evidence only subtle morphological differences for the cryptic species of *Globorotalia truncatulinoides* (de Vargas et al., 2001; Quillévéré et al., 2013), *O. universa* (Morard et al., 2009), and *Globorotalia inflata* (Morard et al., 2011) while in other cases it may result in taxonomic revision. For example, Darling et al. (2006) showed that the right- and left-coiling morphotypes found in *Neogloboquadrina pachyderma* are genetically highly divergent. These authors consequently reinstated *Neogloboquadrina incompta* initially described by Cifelli (1961) for the right-coiling morphotype. In the same way, Aurahs et al. (2011) recognized *Globigerinoides elongatus* as one of the previously described genotypes of *G. ruber* (Aurahs et al., 2009b), and Weiner et al. (2015) showed that the diagnostic morphological characters of *Globigerinella calida* and *Globigerinella radians* match that of two of the cryptic species of *G. siphonifera* (Weiner et al., 2014).

In the two decades that followed the first single-cell sequencing of the SSU rDNA in planktonic foraminifers, a large body of genetic data has been generated, which unfortunately suffers from a lack of taxonomic homogeneity across studies. While the SSU rDNA was the most commonly used marker, the Internal Transcribed Spacer (ITS) rDNA has been used in three morphospecies (de Vargas et al., 2001; Morard et al., 2011; André et al., 2013; Quillévéré et al., 2013). Different authors have used differents criteria to delineate and name cryptic species, resulting in a profusion of labels to describe cryptic diversity (André et al., 2014). This bewildering situation still constitutes a major obstacle in the communication of results across disciplines of the stakeholder community that is particularly diverse for planktonic foraminifers. Ultimately, by applying standardized methods, cryptic diversity would have the potential to improve the resolving power of paleoenvironmental reconstructions based on these organisms (Darling et al., 1999; Kučera and Darling, 2002; Morard et al., 2013, 2016a, b; Marshall et al., 2015; Sadekov et al., 2016), but this would work only if the current knowledge is standardized and easily accessible. To this end, the SCOR/IGBP Working Group 138 (Modern Planktonic Foraminifera and Ocean Changes) held a workshop in Prague in 2013 launching an initiative to standardize the available
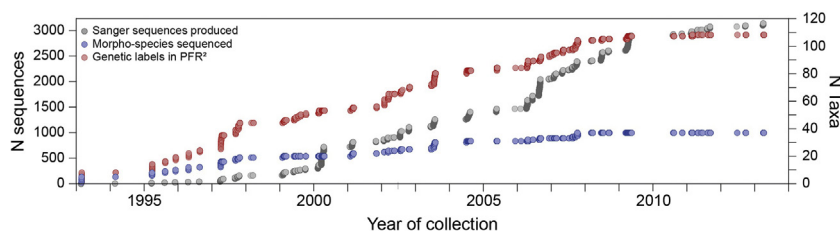
Fig. 2. Results of two decades of single-cell genetic analyses in planktonic foraminifera. The horizontal axis shows the year of collection in the world oceans. The vertical axes show the number of rDNA sequences produced (grey dots) from the collected morphospecies (blue dots), and the number of genetic labels (red dots) attributed to the sequences by various studies. Data extracted from the PFR^2 (Morard et al., 2015). The number of genetic species is reaching a plateau suggesting that the characterization of cryptic diversity in modern planktonic foraminifera might be close to being achieved.

single-cell genetic data on planktonic foraminifers, and define the names given to cryptic species. This gave rise to the *Planktonic Foraminifera Ribosomal Reference Database* (PFR²; Morard et al., 2015), which includes all the SSU rDNA sequences produced so far, and a proposed naming scheme with nomenclatural rules (Morard et al., 2016a). The availability of the PFR² database in association with proper rules for nomenclature is fundamental for the interpretation of metabarcoding datasets. Metabarcoding refers to the sequencing of environmental DNA using High-Throughput Sequencing (HTS) that allows exhaustive estimation of diversity in a given water volume or sediment sample. Interpretation of the data relies on a reference database to produce the essential link between environmental sequences and the existing taxonomy. This approach is a powerful alternative to the time consuming single-cell barcoding (Weiner et al., 2016). The application of metabarcoding to planktonic foraminifers shows that their diversity is limited to the range of what has been estimated with the classical single-cell genetic analyses (Morard et al., 2017; Morard et al., 2018). Despite the availability of these methods, the exact number of cryptic species is still not known, even for the best-documented cases such as *N. pachyderma, G. bulloides*, and *Turborotalita quinqueloba* because cryptic species with restricted distribution are still being discovered (e.g., Bauch et al., 2003; Darling et al., 2017). Therefore, even if the diversity seems to be saturated in many morphospecies (Fig. 2), the discovery of new rare genotypes cannot be precluded. Finally, HTS can also be applied to single-cell foraminifers to identify the organisms with which they associate, in particular the prokaryotes (Bird et al., 2018). This has the potential to provide new insight into the biological interactions of planktonic foraminifers with other organisms, such as symbiosis or parasitism.

In the coming years, single-cell genetic analyses will still be used to stabilize molecular nomenclature and resolve phylogenetic questions (Spezzaferri et al., 2015; Ujiié and Ishitani, 2016) whilst HTS will produce rapid knowledge on the global and vertical distribution of cryptic species, help to resolve their ecological preferences and seasonality, and understand their trophic strategies. We expect that a consistent picture of cryptic diversity in planktonic foraminifers will provide paleoceanographers with a new framework for paleoenvironmental reconstructions.

3. Sampling at sea

Live planktonic foraminifers are sampled at sea for different purposes and by different techniques for paleoceanographic proxy calibration. Undamaged individuals for laboratory culture experiments are possibly best sampled with vials by SCUBA divers (Huber et al., 1996). Pumps and towed plankton nets are suited for collecting large numbers of individuals, but may damage the spines, shells, and cytoplasm of fragile individuals. Net-tow samples provide detailed short term (snap-shot) data on population dynamics in surface waters and may be combined for time-series analyses (e.g., Schiebel and Hemleben, 2000). Continuous Plankton Recorders (CPRs) sample low volumes of sea water from each location but can be towed in surface waters over long distances and provide a first glance at the large-scale distribution of species in the main water bodies (Meilland et al., 2016b). Moored and drifting sediment traps provide time-integrated samples over hours to weeks, which may be combined for time-series sampling over several years (e.g., Rigual-Hernández et al., 2012). Finally, sea floor sediment samples from the modern and past ocean integrate over annual (varved sediments) to millennial time intervals and allow for long-term reconstruction of the changing environment and climate.

3.1. Net tow samples

Net tow sampling has been employed onboard research vessels since the beginning of modern scientific expeditions in the second half of the 19th century. One of the most successful expeditions in terms of planktonic foraminifer research was the British *Challenger* expedition (Brady, 1884; Murray and Renard, 1891). By means of horizontally- and vertically-towed plankton nets, the regional-to-global distribution of species was well described by the 1970s (e.g., Bé and Tolderlund, 1971). Sampling resolution was improved by the use of multiple opening-closing nets (multi-nets), increasingly fine net gauze, and concerted international sampling programs such as the Joint Global Ocean Flux Study (JGOFS), particularly for regions such as the North Atlantic and Arabian Sea. While the planktonic foraminifer population dynamics of these regions have been sampled either for their seasonal variability or significance in understanding of the monsoonal circulation, other regions have been poorly covered by sampling campaigns. The latter regions are remote and/or difficult to access because of stormy weather and rough seas (e.g., the Southern Ocean), or harbour low standing stocks of small and large biota such as the oligotrophic subtropical gyres and provide samples too small to yield significant results from some analytical approaches, for example, in biogeochemistry. These regions are particularly difficult to sample with net tows, because of the costliness of ship-time for medium and large seagoing research vessels.

New approaches, more than a hundred years after the 19th century expeditions (e.g., Murray and Renard, 1891) employ rather cost-efficient and low-emission sail-boats such as the *Tara* Ocean expeditions for sampling plankton, including from regions previously regarded as "unfeasible" (e.g., de Vargas et al., 2015; Caron, 2016; Morard et al., 2018). The small "green" 72-foot custom-made research sailboat *RV Eugen Seibold* has been designed to fill this niche, sampling the full range from eutrophic to oligotrophic, starting 2019. Equipped with plankton nets, planktonic foraminifers will be continuously sampled from the surface ocean. At the same time, the physical and chemical properties of the lower atmosphere and surface ocean will be monitored. Time-series sampling will be achieved by using a multinet (Hydrobios midi titanium, 0.25 m² opening) in a "*NetTrap*" drifting approach, for example, in oligotrophic waters over time periods of hours to days (Peterson et al., 2005). The *RV Eugen Seibold* is operated in a collaborative effort by the Max Planck Institute for Chemistry (Mainz, Germany).

3.2. Continuous Plankton Recorder, CPR

Historically developed to horizontally sample the surface ocean distribution of zooplankton in the upper 15 m of the water column, the Continuous Plankton Recorder (CPR) allows sampling over large geographical zones (several degrees of latitudes) at a regional resolution of about 5 nautical miles, i.e. about 10 km. As such, the CPR is used to sample mesoscale plankton variability (Reid et al., 2003; Beaugrand, 2009). CPR programs are coordinated by the Sir Alister Hardy Foundation (SAHFOS, Plymouth, UK) in northern hemisphere waters, and by the Scientific Committee of Antarctic Research (SCAR) and the international program of the Southern Ocean-CPR (SO-CPR), Australian Antarctic Division (AAD, Kingston, Tasmania, Australia), in the southern hemisphere. Quantitative observations of calcareous plankton such as coccolithophores or planktonic foraminifers are made possible by the CPR sampling protocol that includes *p*H-adjustment for carbonate preservation (Beaugrand et al., 2002). In 2014, the large-scale biogeography of planktonic foraminifers in the Southern Indian Ocean was mapped using a CPR (Meilland, 2015; Meilland et al., 2016b). Since 2017, seven planktonic foraminifer species have been systematically enumerated within the Southern Ocean-CPR program

(Takahashi et al., 2017), improving our understanding of planktonic foraminifer biogeography (data are available from the SO-CPR).

3.3. Sediment traps

Sediment traps intercept the particle export flux from the surface ocean (Buesseler et al., 2007; Honjo and Doherty, 1988). They provide information on the shell and mass flux dynamics, shell composition as well as downward alteration of these properties (e.g. Curry et al., 1992; Deuser et al., 1981; Thunell and Honjo, 1981). In general, sediment traps only intercept the export flux of foraminifers that have completed their life cycle or died prematurely. Together with (stratified) plankton tows, sediment traps provide a means to investigate the population dynamics of planktonic foraminifers. Most sediment traps used to investigate planktonic foraminifers are attached to bottom-tethered moorings and are used to make observations at weekly to monthly resolution for periods of months to several years (Jonkers and Kučera, 2015). Drifting sediment traps have been applied in short-term deployments (Siccha et al., 2012).

The first sediment traps were single bottle traps and needed frequent servicing (e.g. Deuser et al., 1981). Modern automated sediment traps have multiple bottles and can be deployed for longer time periods. They have a conical or cylindrical shape with an opening of 0.3 to 1.0 m^2 and are covered with a gridded baffle to prevent entry of large swimmers that could bias and/or damage the intercepted particles (Honjo and Doherty, 1988). Underneath the cone is a carousel holding the sample bottles that can be rotated at pre-programmed intervals. The number of sample bottles varies by trap design and make. Prior to deployment, sample bottles should be filled with poisoned and buffered filtered seawater, ideally from the depth of deployment, or adjusted to just above local water density using NaCl to prevent dilution/flushing of the sampling fluid. Poisoning with formaldehyde, sodium azide or mercury chloride, is needed to prevent biological degradation of the intercepted material. To prevent dissolution of carbonates at *p*H below seawater values, buffering with borax is recommended. Upon recovery, sample *p*H is checked and, if necessary, additional buffer is added. Samples should be stored cool or at ambient seawater temperature. Further processing, including removal of swimmers (typically those larger than 1 mm), freeze-drying, and splitting, can be done in on-shore laboratories.

The intercepted particle flux may be affected by under- or over-trapping, leading to erroneous estimates of the export flux (Buesseler et al., 2007; Yu et al., 2001). The degree of over- or under-sampling can be estimated from radiogenic isotope analysis on the lithogenic fraction (Scholten et al., 2001; Yu et al., 2001), although this may not be an accurate measure of the degree to which the foraminifer flux is affected, since foraminifer shells are relatively heavy and fast sinking (Takahashi and Bé, 1984). Tilt and current meters can be attached to the sediment traps to measure mooring line motion and hydrography during deployment and to assess trapping efficiency (e.g., Jonkers et al., 2010). In cases where traps have been moored close to the seafloor, or in areas with abundant nepheloid layers, the presence of benthic foraminifers, or degraded planktonic foraminifers, can serve as an indication that the intercepted flux contains resuspended material (Kuhnt et al., 2013). Despite their relatively large size, planktonic foraminifers are susceptible to advection, both during their life and during their post-mortem descent through the water column (Siegel and Deuser, 1997; van Sebille et al., 2015). This implies that, especially for deep traps, the settling time and collection area (up to several hundred kilometers around the mooring) represented by the intercepted flux should be taken into account (van Sebille et al., 2015; von Gyldenfeldt et al., 2000).

4. Ecology

Limiting environmental factors such as water depth, temperature, salinity, and food (ordered from independent to dependent variables) define the ecological niche of each species. Consequently, the same factors drive the temporal and spatial distribution of species. Symbiont-bearing species further depend on solar irradiance and turbidity (i.e., light availability) to meet the light demand of their symbionts. Most species living in high-light conditions at low turbidity in more oligotrophic waters (such as *G. ruber*, *T. sacculifer*, and *G. siphonifera*) harbor dinoflagellate, prymnesiophyte, chrysophycophyte, or chrysophyte symbionts (Spero, 1987; Faber et al., 1988; Gast et al., 2000). Recently, new putative algal (Pelagophyceae) and bacterial (*Synechococcus*) symbionts were described from *N. dutertrei* and *G. bulloides* Type IId, foraminifer taxa typical of more turbid (eutrophic) waters (Bird et al., 2018). The distribution and abundance of symbiont-barren planktonic foraminifers depends on the availability of food, i.e. quality and quantity of prey (including bacteria, algae and small zooplankton). Ba/Ca signals of *N. dutertrei* shell calcite have recently provided evidence for an aggregate- (i.e., marine snow) related microhabitat the use of bacteria on marine snow as a food source (Fehrenbacher et al., 2018).

Both stable carbon and oxygen isotopes are acquired from ambient seawater, affected by symbiont activity and the chemical microenvironment surrounding an individual foraminifer. Therefore, changes in the physical and chemical state of the surface ocean directly affect the species-specific foraminifer ecological niche. Consequently, the time and place of foraminifer shell production may change, affecting isotope signals and the interpretation of proxy signals. Phytoplankton blooms may occur earlier or later depending on the onset of spring (or fall), and the interplay of light and nutrients over the seasons (phenology; see Kretschmer et al., 2016). Water-depth distributions of species may change (e.g., Rebotim et al., 2017) and the presence and absence of species may vary with the changing environment and climate (e.g., Field et al., 2006; Schiebel et al., 2017; Chernihovsky et al., 2018). As small as environmental changes may seem, and as little as they might affect the inherently robust ecologies of one or the other species (e.g., accepting wide temperature ranges; e.g., Lombard et al., 2009), these changes can certainly be reflected in the assemblage composition (i.e., all species) and recorded by fossil assemblages. In addition to the original (production) signal, differential preservation and dissolution during sedimentation and burial can dampen or enhance proxy signals of climate change (Dittert et al., 1999). For example, increasing numbers of *T. quinqueloba* over *N. pachyderma* toward higher latitudes during periods of climate warming may not be preserved to their full extent due to a lower preservation potential of thin-shelled tests of *T. quinqueloba* relative to the thicker and often encrusted shells of *N. pachyderma* (Kučera et al., 2005; Kučera, 2007; Guiot and de Vernal, 2007). While climatic and environmental changes are still recorded by high-latitude assemblages with lower diversity (Schiebel et al., 2017), the more diverse assemblages found at lower latitudes may provide more (reliable and robust) information (Kučera et al., 2005).

In addition to their ecological and paleoceanographic significance, planktonic foraminifers affect carbon turnover in high-latitude waters to a measurable degree (Barker and Elderfield, 2002; Salter et al., 2014). Uptake of CO_2 in the cold polar and subpolar waters causes a decrease in modern surface ocean *p*H (ocean acidification) affecting foraminifer shell calcification rates (Takahashi et al., 2002; Khatiwala et al., 2009; Moy et al., 2009). In the southern Indian Ocean, average annual planktonic foraminifer shell $CaCO_3$ flux amounts to about 2.48 g m^{-2} (Meilland et al., 2018). In the same region, planktonic foraminifer shell carbon turnover (the carbonate counter pump) reduces the transfer of CO_2 to the

deep ocean by up to 32% (Salter et al., 2014). Under varying environmental conditions (e.g., temperature and productivity) different planktonic foraminifer species may be affected to different degrees, and the effect on calcification may be lower or even reversed (Beer et al., 2010; Manno et al., 2012; Salter et al., 2014; Rembauville et al., 2016). Finally, the size-normalized weight and thickness of fossilized shells provide additional information on the marine biological carbon pump, complementing other proxies such as $\delta^{13}C$ (e.g., Broecker, 1971).

4.1. Tropical and subtropical assemblages

The species diversity of planktonic foraminifers is highest in tropical and subtropical surface waters between ~40°N and 40°S, with *G. ruber*, *T. sacculifer*, *Pulleniatina obliquiloculata*, *Globorotalia menardii*, *N. dutertrei*, *G. siphonifera*, and *Globigerinita glutinata* being the main components of the assemblages in the size fraction > 100 µm (Bé and Tolderlund, 1971; Bé, 1977; Bé and Hutson, 1977). Common subsurface dwellers in the tropics and subtropics include *G. truncatulinoides*, *Globorotalia tumida*, and *Globorotalia crassaformis* (Bé and Tolderlund, 1971). *Globigerinoides ruber* and *T. sacculifer* are the most abundant and widespread warm-water species in the global ocean (Bé, 1977). Both species host dinoflagellate symbionts, prey on a variety of zooplankton groups, and have a lifespan of two to four weeks, ending with reproduction likely synchronized with the synodic lunar cycle (e.g., Berger and Soutar, 1967; Schiebel and Hemleben, 2017, and references therein). *T. sacculifer* is frequent under warm oligotrophic conditions (e.g., Arabian Sea, Schiebel et al., 2004; western Pacific, An et al., 2018; Caribbean Sea, Jentzen et al., 2018), whereas *G. ruber* is abundant in a range of ecological environments, from oligotrophic to eutrophic, typifying opportunistic behavior (Schmuker and Schiebel, 2002; Schiebel et al., 2004). Two chromotypes of *G. ruber* (white and pink varieties) correspond to distinct genetic lineages. The white variety is present in all modern ocean basins, while the genetically homogenous modern pink variety is limited to the Atlantic Ocean and its marginal seas since its diachronous extinction in the Pacific and Indian Oceans during the penultimate interglacial between about 130,000 and 120,000 years ago (Tolderlund and Bé, 1971; Thompson et al., 1979).

Seasonality is not as pronounced at low latitudes as at high latitudes. However, seasonal variability in hydrographic conditions affected, for example, by river runoff or upwelling events can drive changes in nutrient concentrations, and hence food availability, modulating the abundance of planktonic foraminifers in the tropics (Deuser et al., 1981; Schmuker and Schiebel, 2002; Jonkers and Kučera, 2015). Local upwelling caused by eddies and nutrient-rich patches in the Caribbean Sea, for instance, enhance the production of *G. glutinata*, associated with high abundances of diatoms, which may serve as a food source (Schiebel et al., 2001; Schmuker and Schiebel, 2002; Jentzen et al., 2018). *Neogloboquadrina dutertrei* tends to thrive during intensive upwelling events in the Arabian Sea (Kroon, 1988) and in seasonal river plumes (e.g., Congo River, Ufkes et al., 1998; Amazon and Orinoco Rivers, Schmuker and Schiebel, 2002). The subsurface dweller *G. truncatulinoides* is assumed to follow an annual reproduction cycle, with high abundances during colder months (Bermuda, Hemleben et al., 1985; Madeira Basin, Schiebel et al., 2002; Gulf of Mexico, Poore et al., 2013; North Atlantic, Rebotim et al., 2017). In addition to seasonal fluctuations, long-term changes in the faunal composition have been recognized in the tropics. Field et al. (2006) indicate an increasing abundance of tropical and subtropical species off the coast of southern California, indicating a warming trend since the 1970s. Similarly, decreasing abundance of *G. ruber* white in the Caribbean Sea could be linked to increasing sea surface temperatures and decreasing chlorophyll concentrations over the past decades, starting in the 20th century

(Jentzen et al., 2018). In the Gulf of Mexico, the abundance of *T. sacculifer* follows the strength of the Loop Current, which is linked to the position of the Inter-Tropical Convergence Zone on a millennial timescale (Poore et al., 2003).

4.2. Polar and subpolar assemblages

The amplified response of polar regions to global warming is often regarded as a harbinger for global climate change (Masson-Delmotte et al., 2006; Fabry et al., 2009). In the climate-sensitive, high-latitude marine environments, planktonic foraminifers also appear to be affected by climate change. Consequently, they may be used to evaluate and monitor current climate-driven environmental changes, and, as a fossilizing calcareous microplankton, to reconstruct past changes in polar climate and sea-ice extent (Polyak et al., 2013; Consolaro et al., 2018). While previous studies reported assemblages largely dominated by the polar species *N. pachyderma* with variable and climate-dependent contributions of the subpolar *T. quinqueloba*, *G. bulloides*, and *N. incompta* (e.g., Bé, 1960; Bé and Tolderlund, 1971; Carstens et al., 1997), more recent studies report higher numbers of *Globigerinita uvula*, as well as the recurrence of rare species such as *Orcadia riedeli* (Bergami et al., 2009; Pados and Spielhagen, 2014; Meilland et al., 2016a; Schiebel et al., 2017). In the absence of morphological divergence (André et al., 2018), the multiple genotypes of *N. pachyderma* are likely to remain morphologically cryptic. This is unfortunate considering their distinct biogeography and ecology. Out of the eight genotypes of *N. pachyderma* described from polar to subpolar regions, only Type IV appears to hibernate in brine channels of Antarctic sea-ice (Spindler and Dieckmann, 1986; Dieckmann et al., 1991). The single Arctic genotype is restricted to colder temperatures than the Antarctic genotypes (Darling et al., 2006) and all of the upwelling genotypes appear endemic (Darling and Wade, 2008). Future studies including culture experiments are needed to investigate the adaptations of these species to extreme polar habitats.

4.3. Transitional assemblages

Transitional planktonic foraminifer assemblages of the mid-latitude ocean and mixed water bodies along current systems and hydrographic fronts are more than a simple mixture of different assemblages from adjacent water bodies. Upwelling and downwelling associated with fronts and eddies cause varying nutrient concentrations and production regimes over the seasonal cycle, which is most pronounced in the temperate ocean at mid latitudes (Obata et al., 1996). While true transitional species possibly do not exist, cosmopolitan species such as *G. glutinata*, and different genotypes of *G. bulloides* and *T. quinqueloba* display strong seasonal cyclicity in the temperate ocean (Schiebel and Hemleben, 2000; Kuroyanagi et al., 2002), and may be regarded as "transitional". Perhaps the "most temperate" species, or least adapted species to polar or tropical waters, may be *N. incompta* (e.g., Cifelli, 1961; Schiebel et al., 2001; Darling et al., 2006).

Given that they are affected by recurring cyclicity of changing environmental conditions and changing seasonality (phenology), the mixed assemblages of the transitional environments (including more cosmopolitan and more specialized planktonic foraminifer species) may best display the transient conditions caused by rapid climatic changes, both in the present-day ocean and during past climate transitions (Field et al., 2006; Kretschmer et al., 2016; Schiebel et al., 2017, Chernihovsky et al., 2018).

4.4. Biodiversity

Planktonic foraminifers, along with the calcareous nanoplankton, constitute one of the best proxies for pelagic diversity over
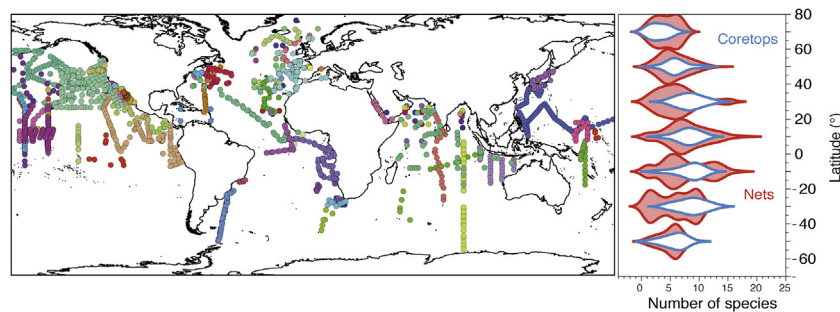
Fig. 3. Map of plankton net locations including a planktonic foraminifera census from the FORCIS working group. The color scheme corresponds to each oceanographic cruise and includes cruises since the 1950s. The right panel shows the latitudinal range of planktonic foraminifera diversity from the FORCIS preliminary database (red violin plots) compared to the diversity assessed in the surface sediment database (blue violin plots; Siccha and Kučera, 2017).

the last ∼150 million years because they form extensive deposits of calcareous ooze across much of the seafloor. Most planktonic eukaryotes have effectively no fossil record, as the many of the adaptations for floating (i.e., reduced biomineralization, increased tissue water content, small size or high surface to volume ratios) also greatly reduce the likelihood of preservation. For the rest of the eukaryotic plankton, a number of factors conspire to reduce their utility in pelagic biodiversity studies: the minerals utilized by biomineralizers, like the silicious diatoms and radiolarians and celestine acantharians, are undersaturated through much of the global ocean and are, thus, relatively rarely preserved. Organic-walled plankton are only well-preserved in a rather limited number of settings, and organic biomarkers can only distinguish among a handful of major clades. As a result, pelagic calcifiers are uniquely well-suited for answering macroevolutionary and macroecological questions. Such questions include understanding latitudinal gradients in marine biodiversity (Rutherford et al., 1999; Fenton et al., 2016) and the factors controlling the diversification and extinction of species (Norris, 1992; Ezard et al., 2011; Peters et al., 2013). With about 50 morphospecies and likely two to three times as many genotypes (Fig. 2), the modern biodiversity of planktonic foraminifers is low but comparable to that of many eukaryotic plankton groups, including krill, pteropods, chaetognaths, appendicularians, nermeteans, rotifers, and ctenophores (McGowan, 1971; de Vargas et al., 2015; Morard et al., 2018; Vereshchaka et al., 2018). By utilizing a number of different trophic regimes, planktonic foraminifers colonize most upper-water column pelagic habitats (from the deep thermocline to surface waters) and all major pelagic biomes (Schiebel and Hemleben, 2017).

Many diversity studies on planktonic foraminifers utilize core-top sediment samples rather than net-tows of living assemblages due to the relative availability of surface sediment material. Our current knowledge of recent spatial biodiversity of foraminifers mainly rests on the CLIMAP studies (CLIMAP, 1976), which extensively documented the surface seafloor sediment distribution of foraminifers, an effort that has been sequentially updated (e.g., Prell et al., 1999; Kučera et al., 2005; Siccha and Kučera, 2017). These databases have been used to develop environmental transfer functions based on assemblage composition (Kučera et al., 2005), to extract patterns and drivers of species diversity (e.g., Rutherford et al., 1999; Brayard et al., 2005; Fenton et al., 2016), and to model the production of planktonic foraminifers (Fraile et al., 2008) and their subsequent dissolution on the seafloor (Anderson and Archer, 2002).

A recent synoptic compilation of more than 4000 net tows of living planktonic foraminifers (FORCIS) has revealed a peak in planktonic foraminifer species richness at mid latitudes (Fig. 3) (Bradshaw, 1957; Belyaeva, 1964; Jones, 1967; Bé, 1977; Schmuker and Schiebel, 2002; Rebotim et al., 2017; Schiebel et al., 2017),

as has been observed in core-top sediments. The lowest species richness is observed at higher latitudes, the highest in the low mid-latitudes, and intermediate values in the equatorial band. Body size and functional diversity also vary systematically with latitude. The largest and most functionally diverse planktonic foraminifer assemblages are found at relatively low latitudes, i.e., subtropical (Schmidt et al., 2004; Fenton et al., 2016). The bimodal richness gradient in planktonic foraminifers matches those of other marine taxa (Bé and Hutson, 1977; Chaudhary et al., 2016) and a number of ecological, evolutionary, and statistical hypotheses have been put forward to explain this latitudinal diversity gradient (Fenton et al., 2016). Although sea surface temperature has been repeatedly found to be best correlated with the observed pattern (Rutherford et al., 1999; Brayard et al., 2005; Tittensor et al., 2010), there is likely a combination of underlying drivers, including variation in vertical niche availability in different thermal regimes and the long-lived stability of the subtropical biome (Fenton et al., 2016). Nonetheless, sea surface temperature is the dominant predictor of evenness, mean evolutionary age, and functional richness in planktonic foraminifers (Fenton et al., 2016).

Differences between living and fossil patterns of biodiversity have been observed with regards to the delineation of the major planktonic foraminifer biomes. Biogeographic studies of Bradshaw (1960) and Bé and Tolderlund (1971) first delineated the five major biomes of planktonic foraminifers. These five biomes (Arctic/Antarctic, Subarctic/Subantarctic, Temperate, Subtropical, Tropical) largely correspond to those later proposed based on assemblage structure across multiple plankton groups (McGowan, 1974), with the addition of an Eastern Tropical Pacific biome, and have been widely accepted and applied to explain patterns of species distribution (e.g., Darling and Wade, 2008). The size and connectivity of pelagic biomes likely account for the low diversity of many pelagic clades (see richness by clade in de Vargas et al., 2015) compared to the terrestrial realm (May and Godfrey, 1994). Bé and Hutson (1977) showed that biome delineation based on net-tow material, as opposed to surface-sediment and down-core assemblages, yields an additional four biomes, including splitting the Southern from the Northern Subtropical assemblage, identifying two Tropical assemblages, and a Tropical/Subtropical boundary current assemblage. Bé and Hutson (1977) attributed the reduction of biomes in fossil material to the mixing of short-term population variation and differential dissolution amongst taxa, with the major patterns comparable between core-top and plankton net-based approaches. Many cosmopolitan morphospecies have been found to consist of cryptic species (i.e., genotypes) contained within a more limited number of biomes or environments (see above). Intriguingly, many of these cryptic species still have anti-tropical to bi-polar distributions, i.e., populations in either hemisphere and typically across multiple ocean basins without connectors in
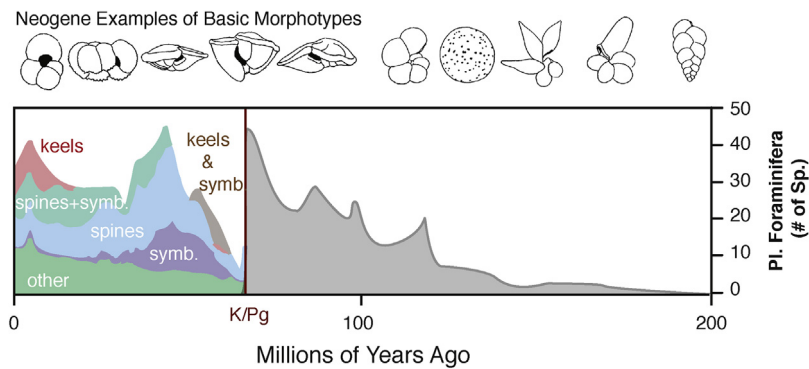
Fig. 4. Schematic of trends in species richness of planktonic foraminifera through time approximated by scaling the long-term compilation of Frass et al. (2015), which lacks taxonomic standardization, to the standardized Cenozoic compilation of Ezard et al. (2011). Cenozoic richness is shown with regards to the associations of morphology and photosymbiosis as in Ezard et al. (2011). The ten major morphotypes of planktonic foraminifera shared across evolutionary faunas are shown at the top, as illustrated by Norris (1991) for the Neogene and are reproduced directly from that paper.

between (see Darling and Wade, 2008), a remarkable pattern first described by Ekman (1953), supporting the importance of environmental conditions over dispersal limitation in shaping pelagic biodiversity.

Planktonic foraminifers have a fairly limited range of body shapes compared to benthic foraminifers (Fig. 4) and range from relatively globular and round (the most spherical taxa being the golf-ball shaped *Orbulina universa*) to biconvex and compressed (i.e., *Globorotalia menardii*), with test ornamentation including pustules, spines, keels, and variations in wall texture from smooth to cancellate to muricate. The clade is notable for repeatedly re-evolving similar morphologies in independent lineages over their evolutionary history, i.e., iterative evolution (Cifelli, 1969; Norris, 1991a). By one count, eight of the ten basic gross morphologies have convergently evolved in each of the three major evolutionary faunas, i.e., Cretaceous, early Paleogene, and Neogene (Norris, 1991b). Wall structures like keels also show iterative evolution and arise multiple times in each of the major evolutionary faunas (Norris, 1991a). Even the relatively derived digitate (or finger-like) morphologies occur in 13 genera with multiple independent origins since the Early Cretaceous (Coxall et al., 2007). In some cases, gross morphology appears related to a specific function: the digitate forms are primarily deep-dwelling taxa and the morphology is thought to aide either in oxygen uptake or predation in the relatively food- and oxygen-scarce midwaters (Coxall et al., 2007). In other cases, there is no clear single adaptive significance of a given morphology. For instance, spinose planktonic foraminifers in the Neogene were primarily dinoflagellate-hosting, but in the earliest Paleogene they were primary symbiotic-barren (on the basis of stable isotopic evidence) (Fig. 4). Similarly, keeled (i.e., reinforced rimmed) taxa are relatively deep dwelling in the Neogene, but shallow-dwelling and strongly symbiotic in the Paleogene. This raises the question as to why morphologies convergently evolve in the first place: is it primarily due to the limited available morphospace (Tyszka, 2006), or due to as yet unknown functions of the various morphologies? Recent ecological work with extant planktonic foraminifers has expanded our understanding of their life histories, revealing, for instance, a possible association between *N. dutertrei* and marine snow (Fehrenbacher et al., 2018), and cyanobacterial associations in one genotype of *G. bulloides* (Bird et al., 2018). Similarly, new hypotheses for morphological features, like the relative resistance of certain morphologies to crushing predation (Burke and Hull, 2017), point to other features of the pelagic-selective environment that could vary through time but be poorly quantified in the fossil record. Indeed, rates of speciation point to the role of biotic and abiotic variables in regulating

species richness through time (Ezard et al., 2011), and the three main radiations of planktonic foraminifers have reached roughly comparable levels of global species diversity despite secular trends in the marine environmental change including global cooling and the rise of diatoms (Fig. 4). Details aside, the apparent disconnect between gross morphology and stable isotopic inferences of ecology remains a major puzzle. Both are strongly conserved within lineages (Edgar et al., 2017), but the relative association between stable isotope ecology and gross morphology differs amongst the evolutionary faunas (Ezard et al., 2011).

4.5. Ecological models of assemblage composition

The strong equator-to-pole gradient in species composition and species diversity inspired paleoceanographers to utilize the abundance of individual species, species groups and assemblage composition to interpret past climate change from the composition of Quaternary planktonic foraminifer assemblages preserved in marine sediments. Whereas the first attempts were largely qualitative (Ericson, 1959), Imbrie and Kipp (1971) devised a method to invert the observed relationship between species composition and sea surface temperature into the form of a "transfer function", expressing temperature as a function of species composition. This approach was the backbone of the CLIMAP Project (CLIMAP, 1976). It benefits from the existence of large calibration datasets based on assemblage counts in surface sediments (Siccha and Kučera, 2017) and from the recurrent emergence of temperature as the sole most important factor explaining assemblage composition (Morey et al., 2005). The last decades have seen a proliferation of different mathematical models used to develop such transfer functions (Kučera et al., 2005), but recent work highlighted the importance of parameter selection, including the effect of variables other than temperature (Siccha et al., 2009), and the choice of the depth level at which temperature is affecting the assemblages (Telford et al., 2013). These results call for care when interpreting transfer function results: It is not sufficient to show that temperature affects modern assemblage composition, it is equally essential to demonstrate that temperature was the dominant factor affecting the variability among fossil assemblages (Telford et al., 2013). Progress in this area can be expected to arise from explicit modelling of assemblage composition (Fraile et al., 2008; Lombard et al., 2011; Kretschmer et al., 2018), or any other method that will allow treating fossil assemblages as an integrated signal of multivariable climate change.
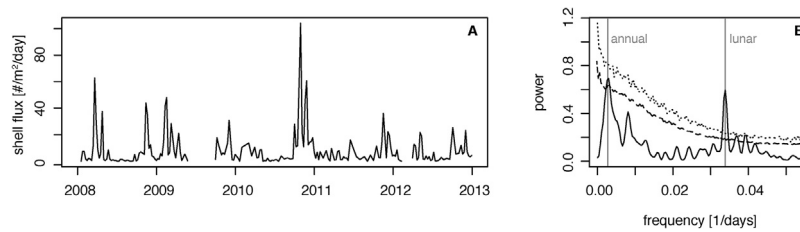
Fig. 5. Annual to sub-seasonal shell flux variability. Flux time series (A) of *G. menardii* in the Gulf of Mexico showing clear evidence of annual and lunar periodicity (B). Dashed and dotted lines in B denote 95% and 99% confidence intervals, respectively. After Jonkers et al. (2015).

5. Test flux dynamics

The abundance and export flux of planktonic foraminifers from the surface ocean to the deep sea is variable on time scales from days to far beyond. A large part of what we know about the past state of the ocean is based on changes in the abundance of planktonic foraminifers over long (decadal-centennial-millennial) time scales. However, the environmental signal preserved in sedimentary planktonic foraminifer tests also carries an imprint of abundance dynamics on shorter time scales. These arise predominantly from seasonal variability that potentially lead to biases in the reconstruction of past climates.

Most of what we know about medium-term (sub-decadal) dynamics stems from studies using moored sediment traps that measure the export flux of empty foraminifer shells from the surface ocean. Given the generally short life span of planktonic foraminifers, the export flux can be translated into abundance variations and is used to assess the influence of short term population dynamics on the record of climate change preserved in foraminifer shells, including the parametrization of numerical models simulating planktonic foraminifer biomass as a function of the physical and chemical ocean environment (Fraile et al., 2008; Lombard et al., 2011).

5.1. Sub-seasonal flux dynamics

Shell flux time series of planktonic foraminifers are virtually all characterized by significant sub-seasonal variability, which may range over at least an order of magnitude (Lončarić et al., 2005; Fallet et al., 2011; Jonkers et al., 2015). Given the average sampling resolution of most sediment trap time series, most of what we know about sub-seasonal variability relates to time scales on the order of multiple weeks to months; shorter-term variability remains poorly characterized by sediment trap samples and is studied using net tow samples (e.g., Schiebel, 2002). Some authors have attributed flux variability to the passage of (meso-scale) eddies (Storz et al., 2009; Fallet et al., 2011) and attempts have been made to utilize this to build a proxy for eddy activity (Steinhardt et al., 2014). Several studies have reported shell flux variability with lunar periodicity (Kawahata et al., 2002; Lončarić et al., 2005; Jonkers et al., 2015), which is generally taken as evidence for lunar-synchronized reproduction in planktonic foraminifers (Fig. 5). Whether or not the flux of some species for which a semi-lunar reproductive cycle has been reported (Bijma et al., 1990) shows such periodicity remains unknown as no time series of sufficiently high resolution are available. Moreover, the phasing of the flux with respect to the lunar cycle appears to vary among species and sites, and periodicity may vary between species at the same location (Lončarić et al., 2005). Thus, whereas synchronized reproduction has obvious benefits for planktonic foraminifers that occur at very low densities in the ocean, the absence of a globally-uniform phasing renders the nature (endogenous or exogenous) of the cyclicity difficult to constrain. Irrespective of its origin, lunar periodicity in shell fluxes reinforces the idea that many shallow-dwelling planktonic foraminifers have a life span of about a month. This has important implications for paleoceanography as it implies that each foraminifer shell integrates environmental information over its entire ontogeny, i.e., between a fortnight and one year, but most often one month in case of surface dwelling species. Given that a sediment sample generally integrates at least a century of time, temporal under-sampling is thus an important source of noise in planktonic foraminifer proxy records (Laepple and Huybers, 2013; Fraass and Lowery, 2017).

5.2. Seasonal flux dynamics

Early studies of modern planktonic foraminifers documented seasonality in the abundance and shell flux (e.g., Tolderlund and Bé, 1971; Deuser et al., 1981; Thunell and Honjo, 1981). The seasonality at a single site differs among (groups of) species, often with a clear seasonal succession of species during the seasonal cycle (e.g., Reynolds and Thunell, 1985; Schiebel and Hemleben, 2000; King and Howard, 2003; Mohiuddin et al., 2005). The amplitude of seasonal flux variability can range over several orders of magnitude (e.g., Abrantes et al., 2002; Schiebel, 2002; Barcena et al., 2004; Jonkers et al., 2010) and some species can show long periods (months) of zero fluxes (Curry et al., 1992; Mohiuddin et al., 2002), raising the question as to how planktonic foraminifer blooms are seeded. Importantly, seasonality patterns also vary spatially within species (e.g., Tolderlund and Bé, 1971; Zaric et al., 2005; Jonkers and Kučera, 2015). Globally, the seasonality of planktonic foraminifer test flux contains a predictable component for three groups of species that show similar seasonality modes (Jonkers and Kučera, 2015). Tropical-to-subtropical, predominantly symbiont-bearing species (e.g., *G. ruber*, *T. sacculifer*, *N. dutertrei*, and *P. obliquiloculata*) show low-amplitude flux variability with random peak flux timing in warm waters. Toward the lower limit of their temperature range, these species show a pronounced flux pulse focused in a narrow seasonal window of relatively high temperatures in late summer to autumn (Fig. 6a). The pattern suggests that the seasonality of these species is largely driven by temperature. Mid-to high-latitude species (e.g., *G. glutinata*, *N. incompta*, *G. bulloides*, and *T. quinqueloba*) generally show two flux pulses per year that both shift to earlier in the year when annual mean conditions are warmer (Fig. 6b). This shift in the timing of the flux pulse is not necessarily associated with a clear change in the amplitude of the flux. Despite the clear temperature relationship, peak timing in this group appears to follow food availability. Finally, the subsurface-dwelling species, *G. truncatulinoides* and *G. inflata*, show synchronous flux pulses in winter and spring. It has been suggested that these subsurface-dwelling species also respond to food availability (Itou et al., 2001; Salmon et al., 2015), but such a relationship is not observed on a global scale (Jonkers and Kučera, 2015).

Irrespective of the mode of seasonality, it appears that any change in seasonality acts to reduce the magnitude of environmental change that foraminifers experience (Jonkers and Kučera, 2015). This leads not only to a seasonal bias in proxy records based
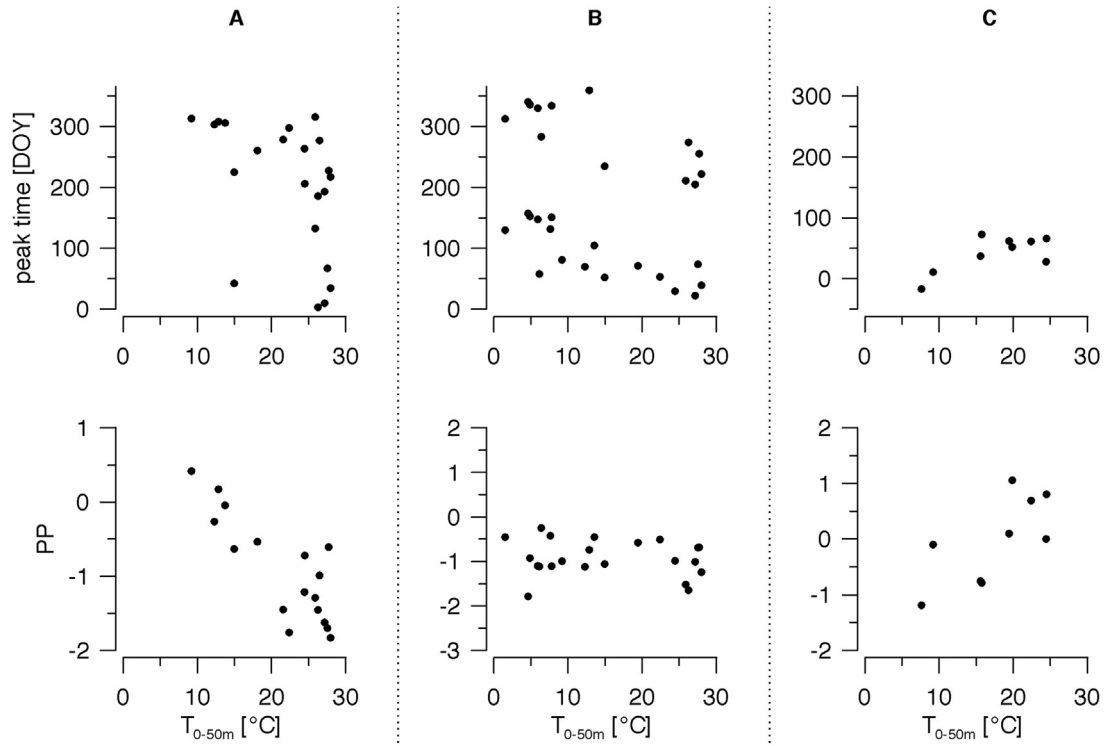
Fig. 6. Seasonality patterns in three groups of planktonic foraminifera flux, (A, left panels) tropical-to-subtropical species (e.g., *G. ruber* white), (B, middle panels) mid-latitude species (e.g., *N. incompta*), and (C, right panels) subsurface-dwellers (e.g., *G. truncatulinoides*). Upper panels show timing of the main flux pulse as a function of mean annual temperature in the upper water column; DOY is day of year. Lower panels show the peak prominence (PP), which is defined as the amplitude of the flux divided by the average flux, plotted on a logarithmic scale. Higher PP values indicate higher relative amplitude, i.e. more flux focusing. After Jonkers and Kučera (2015).

on chemical composition (Mg/Ca, $\delta^{18}O$) of single species, but also indicates that, because flux seasonality is directly related to climate, the magnitude of past environmental change is unlikely to be completely captured by the foraminifer record (Mix, 1987; Mulitza et al., 1997; Jonkers and Kučera, 2017).

Seasonality in the flux also affects assemblage-based paleoenvironmental reconstructions. Calibration of transfer functions to infer information from planktonic foraminifer assemblages is affected by the fact that such transfer function models attempt to link assemblages that may never have co-existed (in time) to a single environmental variable. Thus, the performance of such transfer functions is sensitive to the season used for calibration (Telford et al., 2013). Given the dependence of planktonic foraminifer test flux seasonality on climate, disentangling ecological from climate effects is crucial to improve the accuracy of climate reconstructions based on fossil shells. One way to achieve this is to combine observations from proxies and climate simulations using ecological/foraminifer sensor models (Fraile et al., 2008; Lombard et al., 2011; Kretschmer et al., 2018).

5.3. Inter-annual flux dynamics

Superimposed on seasonal variability, shell fluxes of planktonic foraminifers also display inter-annual variability (Fig. 7). Because few time series longer than three years exist, patterns and drivers of such longer-term variability are poorly known. Comparison of time series of over five years in duration suggests that interannual variability is more expressed in the magnitude of the flux than in timing of the main flux pulse (Asahi and Takahashi, 2007; Rigual-Hernández et al., 2012; Jonkers et al., 2015), but this requires more time-series data spanning longer time-intervals. Some studies suggest that shell fluxes may be influenced by (sub-) decadal climate variability associated with climate patterns such as the North
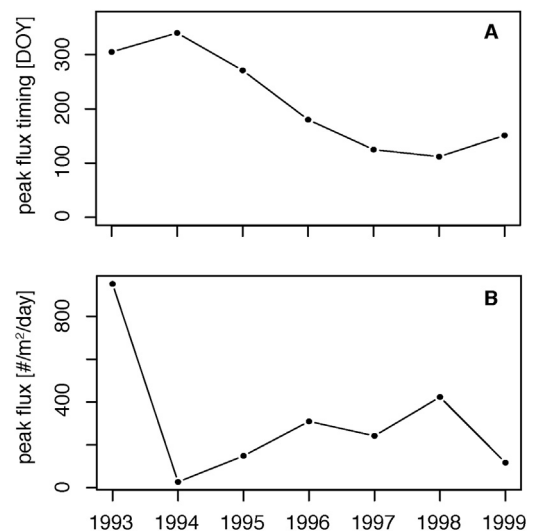

Fig. 7. Inter-annual shell flux variability. Example of extreme inter-annual variability in both timing (A; DOY: day of year) and amplitude (B) of the seasonal flux peak based on flux time series of *T. quinqueloba* from the North Pacific (Asahi and Takahashi, 2007). Both timing and peak amplitude influence the recording bias of planktonic foraminifera, rendering it crucial to determine what drives such interannual variability in shell fluxes.

Atlantic Oscillation or the El-Niño Southern Oscillation (Thunell et al., 1999). However, these links remain questionable due to the generally short duration of flux time series that preclude replication. Given the importance of interannual environmental change and flux variability, not only to better understand the fossil record of planktonic foraminifers, but also to quantify their role in the biological pump, long-term monitoring programs are indispensable.

6. Isotopes and element ratios

Foraminifers oxygen isotopes have been used for more than 60 years as a paleoclimate proxy (Emiliani, 1955). For twenty years, as progress in technology allows for the analysis of more elements and smaller samples, a number of new tracers have been developed, based on the incorporation of different isotopes and trace elements into foraminifer shell calcite. We present here just a few examples of these proxies and how they find application in paleoceanography.

Dissolution and diagenetic processes can alter the composition of foraminifer tests in the water column and sediments, modifying the isotopic composition and/or elemental ratios used as proxies. Thus, paleoceanographic studies should only use well-preserved planktonic foraminifer tests. The isotopic or trace element proxies are based on physical laws and usually depend on several environmental parameters. Their incorporation into planktonic foraminifer calcite is also a function of biomineralization processes. Therefore, using planktonic foraminifers as tracers in paleoceanography must rely on sound classification. Moreover, the presence of genotypes of one morphospecies with different ecological preferences may limit applicability of some of these proxies.

A number of recent studies investigate the possibilities of developing new tracers and tend to improve the calibration and comprehension of existing ones. Trace element analyses provide new clues about biomineralization processes and can be used as a tool in ecologic studies of planktonic foraminifers. Geochemical studies coupled with ecological studies are enhancing our understanding of biomineralization processes, ecological niches of the different planktonic species, and improving the paleoceanographic tool set.

6.1. Oxygen and carbon isotopes

Stable oxygen isotopes in foraminifers have been used as temperature indicators ever since Urey (1947) indicated that "isotopic compounds differ in their thermodynamic properties" and highlighted that it had "important implications as a means of determining the temperature at which geological formations were laid down". After Epstein et al. (1951, 1953) realized that isotopic compositions of organic and inorganic precipitation showed similar temperature relationships, Emiliani (1954, 1955) analyzed the oxygen isotopic composition ($\delta^{18}O$) of a range of planktonic foraminifer species and deduced that different species occupy different depth habitats. This work led to the first foraminifer-based temperature record showing the glacial-interglacial variations that we now know to have characterized the Pleistocene.

The $\delta^{18}O$ of a calcareous foraminifer depends on both the oxygen isotopic composition and the temperature of the water in which it calcifies (Equation (1)). The fractionation between light ^{16}O and heavy ^{18}O isotopes in carbonates relative to seawater is a logarithmic function of the ambient water temperature that has been determined by the precipitation of inorganic calcite (McCrea, 1950; O'Neil et al., 1969; Kim and O'Neil, 1997). It has been approximated by a first or second order polynomial expression for foraminifers (Bemis et al., 1998),

$$T = a + b(\delta^{18}O_{CALCITE} - \delta^{18}O_{WATER}) + c(\delta^{18}O_{CALCITE} - \delta^{18}O_{WATER})^2$$
(1)

where T is the temperature (°C), $\delta^{18}O_{CALCITE}$ and $\delta^{18}O_{WATER}$ are the isotopic compositions of the foraminifer calcite and water, respectively. $\delta^{18}O_{CALCITE}$ is reported relative to VPDB and $\delta^{18}O_{WATER}$ relative to VSMOW. According to paleoceanographic tradition, a constant value of −0.20 to −0.27‰ is subtracted from $\delta^{18}O_{WATER}$ to account for the isotopic difference between CO_2 equilibrated with SMOW at 25 °C and CO_2 generated by reaction of PDB with 100% H_3PO_4 at 25 °C (Hut, 1987; Friedman and O'Neil, 1977). The accepted value of this constant has changed through time so one must use the value that was accepted by the scientific community when a specific relationship was generated (see Bemis et al., 1998, for further details).

Culture experiments and plankton tow studies have allowed for the development of species-specific temperature relationships for the $\delta^{18}O$ of species such as *O. universa, G. bulloides, G. ruber, T. sacculifer,* and *N. pachyderma* (i.e., different values for a, b, and c in Equation (1); Spero et al., 1997; Bemis et al., 1998; Mulitza et al., 2003). The slopes of these equations agree (with some differences) with the slopes of equations from inorganic precipitates (Mulitza et al., 2003). These experiments did not yet take into account the different cryptic species (Darling et al., 1999; de Vargas et al., 1999).

Over glacial–interglacial cycles, the mean ocean $\delta^{18}O$ change, linked to the volume of ice sheets, accounts for more than half of the amplitude in planktonic foraminifer $\delta^{18}O_{CALCITE}$ changes (Shackleton, 1967). Following Hays et al. (1976), the correlation between astronomical forcing (Milankovitch, 1941) and foraminifer $\delta^{18}O$ records became a powerful stratigraphic and chronologic tool that can be used for at least the last 50 Ma (Laskar et al., 2004; Bintanja and van de Wal, 2008). For the past 5.3 Ma, the planktonic record is correlated with the LR04 benthic stack (Lisiecki and Raymo, 2005). For older time-periods, a floating stratigraphy may be obtained by tuning the planktonic foraminifer $\delta^{18}O$ cyclic variations to orbital frequencies (Laskar et al., 2011; Pälike et al., 2006; Westerhold et al., 2008).

Other independent temperature proxies combined with the foraminifer $\delta^{18}O$ record allow for the reconstruction of past seawater $\delta^{18}O$ changes. Seawater $\delta^{18}O$ provides information on the continental ice volume, local evaporation-to-precipitation balance, fresh water fluxes, hydrographic fronts, and surface ocean advection. Such reconstructions of the seawater $\delta^{18}O$ variations were first made using temperature reconstructions from foraminifer assemblages (Duplessy et al., 1991; Duplessy et al., 1993) and alkenone $U^{k'}_{37}$ records (Rostek et al., 1993). However, such approaches combine annual or seasonal sea-surface temperatures with the $\delta^{18}O$ of a foraminifer species that might have developed deeper in the water column and/or during different seasons (Kretschmer et al., 2016). More recently, the development of Mg/Ca content of foraminifer calcite as a temperature tracer, combined with $\delta^{18}O$ measurements on the same foraminifer species, has allowed for the simultaneous reconstruction of temperature and seawater $\delta^{18}O$ for different seasons and water depths at which foraminifer species lived and calcified their tests.

Effects other than temperature and ambient water $\delta^{18}O$ have a secondary influence on planktonic foraminifer shell $\delta^{18}O$, with kinetic fractionation and/or incorporation of metabolic CO_2 varying with foraminifer size (Berger et al., 1978, Curry and Matthews, 1981; Bouvier-Soumagnac and Duplessy, 1985; Spero and Lea, 1996; Peeters et al., 2002; Jonkers et al., 2013) and seawater carbonate ion (CO_3^{2-}) concentration (McCrea, 1950; McConnaughey, 1989; Spero et al., 1997; Russell and Spero, 2000). In symbiont-bearing species, respiration and photosynthesis also affect the isotopic composition (Bouvier-Soumagnac et al., 1986; Spero and Williams, 1990; Spero and Lea, 1993; Bemis et al., 1998). To minimize ontogenetic effects, isotope analyses should be made on adult foraminifers within a narrow size range (Shackleton et al., 1983).

Species-specific fractionation of oxygen isotopes in planktonic foraminifers and other secondary effects have been investigated through culture experiments, indicating an effect of $[CO_3^{2-}]$ and again highlighting the need for species-specific paleotemperature equations (Bemis et al., 1998; Spero et al., 1997). While more culture work is needed to clarify these effects, the $\delta^{18}O$ of

planktonic foraminifers, coupled with other temperature proxies (e.g., Mg/Ca) from the same foraminifer test, is a powerful tool for reconstructing the upper water column (density) structure by combining data from species living at different depths. As some foraminifer species might change their calcification depth during ontogeny (e.g., Emiliani, 1954; Lohmann and Schweitzer, 1990; Simstich et al., 2003; Cléroux et al., 2009; Rebotim et al., 2017), better knowledge of the ecology of the different species is also needed.

For over two decades, attempts have been made to analyze single planktonic foraminifer specimens to provide information on not only mean environmental changes, but also seasonal amplitude changes (Killingley et al., 1981; Billups and Spero, 1995, Ganssen et al., 2011) and thermocline/subsurface water evolution using deep-dwelling foraminifers (Leduc et al., 2009). Such isotope analyses can be carried out for the larger (> 20 μg CaCO$_3$) specimens with the standard analytical techniques available in most isotope laboratories, keeping a standard reproducibility ≤ 0.1 ‰. For the smaller planktonic foraminifers, several laboratories have tuned equipment to analyze samples smaller than 10 μg of CaCO$_3$ at an acceptable precision of 0.12–0.15 ‰ (e.g., Fiebig et al., 2005; Feldmeijer et al., 2015; Metcalfe et al., 2015). Currently, even the 5 μg CaCO$_3$ sample-size boundary is in range (Vonhof, unpublished data) by applying a cryo-focusing technique within conventional continuous flow stable isotope analysis (Fiebig et al., 2005). In addition, foraminifer δ^{18}O data may be combined with the recently developed carbonate clumped isotope thermometry (e.g., Eiler, 2007), based on the measurement of isotopologues (e.g., ^{13}C^{18}O^{16}O) Δ$_{47}$ (Tripati et al., 2010; Grauel et al., 2013; Peral et al., accepted for publication). Clumped isotope Δ$_{47}$ data are purely temperature dependent and, thus, independent of species-specific or ontogenetic (i.e., size) effects. Alternatively, SIMS δ^{18}O analyses on 3–10 μm micro domains in foraminifer test walls have shown promise (Kozdon et al., 2009; Vetter et al., 2013a; Wycech et al., 2018).

Future studies of past oceanic changes might take advantage of coupling biogeochemical data of different surface- and deep-dwelling foraminifers with general circulation models (GCMs; Kageyama et al., 2013) and foraminifer-growth models taking into account species-specific temperature and nutrient demands (e.g., Lombard et al., 2009, 2011). Together, these approaches will facilitate reconstruction of the seasonal surface-to-thermocline temperature and density structure of the paleo-ocean.

6.2. Stable carbon and radiocarbon isotope compositions

The stable carbon isotope composition (δ^{13}C) of planktonic foraminifer shells is measured together with the oxygen isotopic composition, but much fewer δ^{13}C than δ^{18}O data have been published so far. δ^{13}C records usually show more scatter than δ^{18}O, and low-latitude records do not indicate a consistent relationship with glacial-interglacial cycles (Van Donk, 1970; Broecker, 1982a). Various processes modify the surface water distribution of C isotopes in total dissolved inorganic carbon (DIC). During photosynthesis, ^{12}C is preferentially utilized over ^{13}C, and thus the mean ocean carbon isotopic composition changes will record changes in the storage of carbon as organic matter (in the terrestrial biosphere, marine organic matter, fossil fuels, etc.) (Kroopnick et al., 1976; Shackleton, 1977). The marine carbon isotope distribution of DIC (δ^{13}C$_{DIC}$) is affected by ocean circulation and phytoplankton production (Kroopnick, 1974; Kroopnick, 1985). Production of organic matter in the surface ocean leads to ^{13}C$_{DIC}$-enriched waters, and subsequent oxidization of this low-δ^{13}C organic matter below the photic zone decreases ambient δ^{13}C$_{DIC}$. The Holocene ocean displays a difference of ~3 ‰ between ^{13}C$_{DIC}$-enriched surface waters and the ^{13}C$_{DIC}$-depleted mid-depth North Pacific, the latter being the termination of the modern large-scale deep-water circulation (Kroopnick, 1985). This 3 ‰ difference will decrease with increased mixing between the surface and deep ocean or reduced organic matter export from surface waters. In the surface ocean, this feature is complicated by thermodynamic fractionation during ocean-atmosphere carbon exchange (Mook et al., 1974; Charles and Fairbanks, 1990; Broecker and Maier-Reimer, 1992) and by the evasion or invasion of CO$_2$ from or to the ocean (Lynch-Stieglitz et al., 1995). Although thermodynamic isotopic equilibrium between the ocean surface and atmosphere is never reached, these processes still produce variations of more than 1 ‰ in the surface ocean. Modern surface water δ^{13}C$_{DIC}$ also needs to be corrected for the low-^{13}C imprint of fossil fuel-carbon that has invaded the atmosphere (Suess Effect) and ocean (Quay et al., 2007).

In addition to the environmentally-caused δ^{13}C$_{DIC}$ variations in seawater, foraminifer δ^{13}C is complicated by a larger difference from calcite isotopic equilibrium than in the δ^{18}O signal (Spero, 1992). Test δ^{13}C displays a large range of δ^{13}C values due to symbiont photosynthesis (Spero and Williams, 1988) and respiration of the foraminifer host (Spero and Lea, 1993; Bemis et al., 2000). Seawater [CO$_3$$^{2-}$] variability has a large effect on

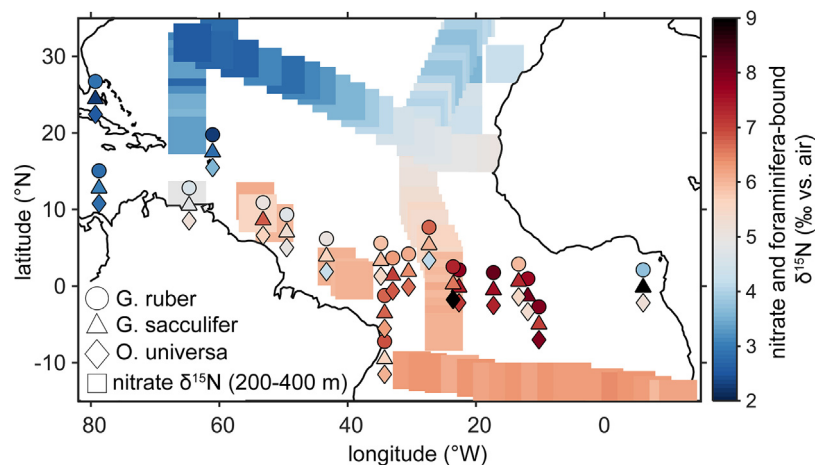**Fig. 8.** For the low- to mid-latitude Atlantic basin, a compilation of surface-sediment foraminifer-bound δ^{15}N (*G. ruber*, circles), *T. sacculifer* (triangles) and *O. universa* (diamonds) (Ren et al., 2009; Ren et al., 2012b; Ren et al., 2015; and unpublished results) overlaid upon thermocline nitrate δ^{15}N (averaged over 200–400 m water depth; shaded squares; Marconi et al., 2017). The eastern-most surface-sediment site may be influenced by incomplete nitrate consumption associated with the equatorial Atlantic upwelling.

shell $\delta^{13}C$, with increasing $[CO_3{}^{2-}]$ decreasing shell $\delta^{13}C$ and vice versa (Spero et al., 1997). The carbonate ion effect can profoundly affect paleoceanographic interpretations. For example, increased surface water $[CO_3{}^{2-}]$ during the last glacial maximum (LGM), linked to lower atmospheric CO_2, could result in a 0.3 ‰ to 0.9 ‰ decrease in test $\delta^{13}C$ (Spero et al., 1997; Lea et al., 1999a). This $\delta^{13}C$ shift is larger than the estimated change in average ocean LGM-Holocene $\delta^{13}C_{DIC}$ that resulted from lower LGM terrestrial biosphere carbon stock. These different effects on planktonic foraminifer $\delta^{13}C$ impede direct reconstruction of the $\delta^{13}C_{DIC}$ from $\delta^{13}C$ changes and require a more complete incorporation of the different controls on test $\delta^{13}C$ to make accurate reconstructions.

The distribution of the radioactive isotope, ^{14}C, in ocean surface waters is the result of ocean-atmosphere exchange, and horizontal and vertical mixing within the ocean. The surface ocean has a radiocarbon isotopic ratio ($\Delta^{14}C$) that is lower than the atmosphere, where ^{14}C atoms are produced, inducing a seawater ^{14}C "reservoir age". In the open ocean, the reservoir age of surface water varies from ~250 years in the rather stratified subtropical gyres to ~1200 years in the Southern Ocean where there is strong mixing with deep, old waters. As with the stable carbon isotopes, thermodynamic fractionation occurs during ocean-atmosphere exchange of ^{14}C, and during photosynthesis. However, all of the fractionation-induced changes are small compared to variation in sea-surface $\Delta^{14}C$ due to seawater mixing and ocean-atmosphere exchange. ^{14}C analyses of planktonic foraminifers from sediment cores are mainly done to establish the chronology. Changes in the reservoir age may be determined by correlation with tephra layers of known volcanic eruptions to facilitate precise chronology, and to allow for the use of $\Delta^{14}C$ as a tracer of past ocean circulation and ocean-atmosphere exchange. Analyzing both $\Delta^{14}C$ and $\delta^{13}C$ of planktonic foraminifers helps to deconvolve ocean circulation changes from productivity, temperature, and vital effects (Siani et al., 2013).

Recent advances have been made in single-specimen ^{14}C analysis, using a minimum of 80–100 μg of foraminifer test calcite and employing a permanent magnet equipped Mini Carbon Dating System (MICADAS) AMS system (for example, at ETH Zurich and CEREGE in Aix-en-Provence; e.g., Lougheed et al., 2018; personal communication with Edouard Bard at MPIC, May 2018). Combining single-specimen ^{14}C, $\delta^{18}O$, and cation/Ca data (e.g., Mg/Ca, using LA-ICP-MS) will yield unprecedented data on late-Pleistocene climate, including time-intervals of rapid climate change such as the onset of Dansgaard-Oeschger cycles.

6.3. Nitrogen isotopes

Variation in ocean nutrient conditions has been identified as a potential driver of the atmospheric CO_2 feedback that amplifies the global temperature changes associated with ice-age cycles (reviewed by Sigman and Boyle, 2000, and Sigman et al., 2010). An increase in the quantities of nutrients in the ocean (Broecker, 1982b) or more complete consumption of the existing nutrients (e.g., Sarmiento and Toggweiler, 1984) would lead to more biologically driven sequestration of CO_2 in the ocean interior, lowering the concentration of atmospheric CO_2. The stable isotopes of nitrogen (N) provide a potential tool for reconstructing past changes in the cycling of this major nutrient, but their use requires the development of sedimentary archives of past N isotopic composition that are robust to diagenetic alteration and contamination by exogenous N.

Recent analytical advances have made it possible to measure the N isotope ratio (or $\delta^{15}N$) where

$$\delta^{15}N = \{[(^{15}N/^{14}N)_{SAMPLE}/(^{15}N/^{14}N)_{N2\,IN\,AIR}]-1\} \times 1000 \qquad (2)$$

in units of per mil (‰) of the organic matter bound within calcareous fossils such as planktonic foraminifer tests (Ren et al., 2009). The N content of the organic matter bound within planktonic foraminifer shells ranges from 2 to 6 nmols per mg of calcite across different species and geographic settings (Ren et al., 2009; Ren et al., 2012a). These N concentrations are too low for accurate isotopic analysis using current "off-the-shelf" on-line combustion technology. Accordingly, a set of methods have been developed for foraminifers and other fossils with low N content (Ren et al., 2009; Ren et al., 2012a; Ren et al., 2017; Straub et al., 2013; Martinez-Garcia et al., 2014). In these methods, planktonic foraminifer tests are first cleaned in a series of steps using reductive and oxidative reagents in order to remove any potential exogenous organic N from the shell surface. After dissolution of the cleaned shells, foraminifer-bound organic N is oxidized to nitrate ($NO_3{}^-$) using potassium peroxydisulfate. The isotopic composition of this nitrate is then measured using the "denitrifier method", in which nitrate is converted to nitrous oxide (N_2O) gas by a strain of denitrifying bacteria that lacks an active N_2O reductase, followed by analysis of the product N_2O with a stable isotope ratio mass spectrometer (Sigman et al., 2001; Weigand et al., 2016). The refinement of this approach over recent years now allows us to routinely measure foraminifer-bound $\delta^{15}N$ in our laboratories (at Princeton University, the Max Planck Institute for Chemistry, and National Taiwan University) with high reproducibility (~0.2 ‰) using relatively low sample amounts (2–5 mg of calcite).

As heterotrophs in the open ocean, planktonic foraminifers are expected to track the $\delta^{15}N$ of the organic matter produced in the surface ocean. The $\delta^{15}N$ of bulk tissue and shell-bound N of foraminifers are similar in absolute value and vary together, supporting the use of shell-bound N as a recorder of upper ocean $\delta^{15}N$ changes (Smart et al., 2018). In the oligotrophic ocean, where surface nitrate (the primary form of fixed N supply) is essentially fully consumed by phytoplankton, the $\delta^{15}N$ of the organic matter produced in and exported from the surface ocean is expected to record the $\delta^{15}N$ of the nitrate supply (Altabet, 1988; Altabet and François, 1994), which in turn, reflects the balance of sources (dominantly N_2 fixation) and sinks (dominantly denitrification) in the ocean's input/output budget for fixed N. Thus, N isotope records from the subtropics have the potential to record changes in the processes that control the nitrate reservoir of the global ocean. In the polar ocean, where much of the nitrate supplied to the mixed layer goes unused, the preferential uptake of ^{14}N-bearing nitrate by phytoplankton initially produces low-$\delta^{15}N$ organic matter and causes the remaining nitrate and the organic matter produced from it to rise in $\delta^{15}N$ as consumption proceeds (Wada and Hattori, 1978; Waser et al., 1998; Sigman et al., 1999). Thus, N isotope records from high-latitude and some upwelling environments, in addition to responding to whole-ocean nitrate $\delta^{15}N$ change, should also reflect changes in the degree of nitrate consumption in the surface ocean (Altabet and François, 1994). Below, we consider these two environments with their contrasting nutrient regimes, demonstrating the value of planktonic foraminifer-bound $\delta^{15}N$ as an archive of the past ocean N cycle and highlighting several of the lessons learned from ground-truthing the proxy in the modern ocean.

At oligotrophic subtropical sites, foraminifer-bound $\delta^{15}N$ in recent surface sediments is strongly correlated with the $\delta^{15}N$ of thermocline (i.e., shallow subsurface water) nitrate (Fig. 8) (Ren et al., 2012b). This nitrate is the main source of new N to the overlying euphotic zone; N_2 fixation is typically too slow to represent a significant fraction of the annual N supply to the surface ocean, but it does lower the $\delta^{15}N$ of thermocline nitrate (Knapp et al., 2005). Thus, changes in N_2 fixation and denitrification are recorded in foraminifer-bound $\delta^{15}N$ dominantly through the effects of these processes on the $\delta^{15}N$ of thermocline nitrate. From studies of living, sinking and sedimentary shells, a clear isotopic distinction has
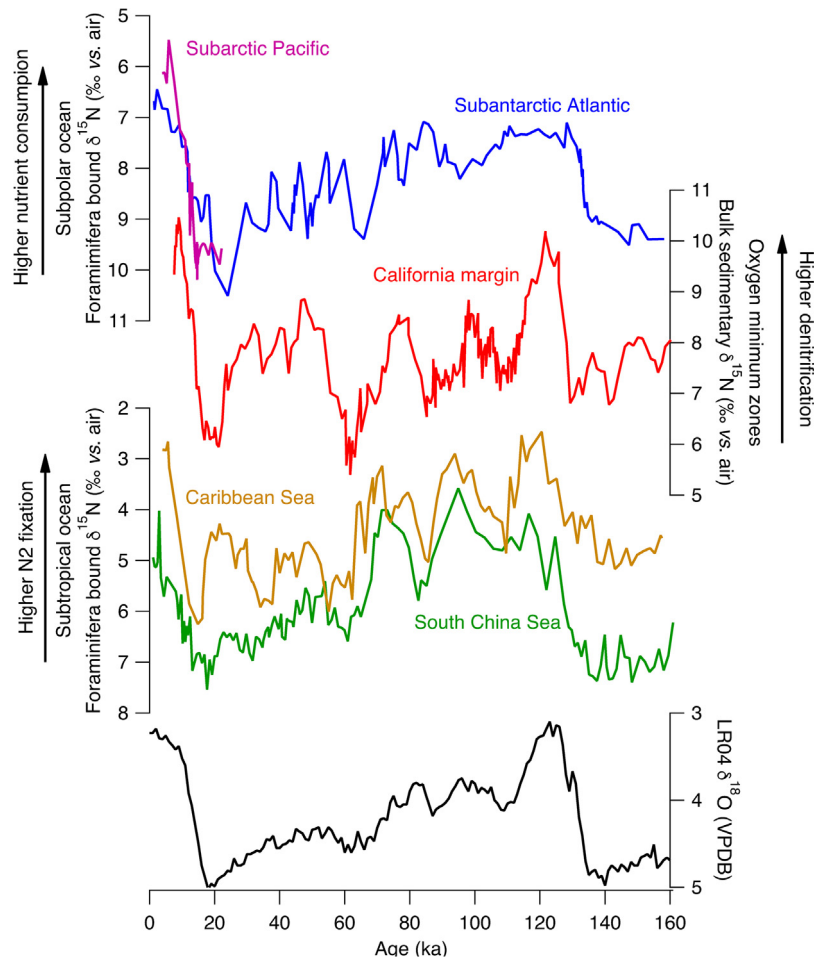
Fig. 9. Selection of down-core foraminifer-bound δ^{15}N records from regions with both nutrient-rich and nutrient-poor surface waters. For the former, *N. pachyderma* from the Subarctic Pacific (magenta) (Ren et al., 2015) and *G. bulloides* from the Subantarctic Atlantic (blue) (Martínez-García et al., 2014), which record changes in the degree of nitrate consumption in surface waters for each region. For the latter, *G. ruber* from the Caribbean Sea (gold) (Straub et al., 2013) and *O. universa* from the South China Sea (green) (Ren et al., 2017), which largely record regional changes in N_2 fixation. A bulk sedimentary δ^{15}N record from the California margin near the North Pacific water column denitrification zone (red) (Liu et al., 2008) is shown for comparison with the Caribbean and South China Sea records. The offsets in timing among the two N_2 fixation-related records and the denitrification-related record are mechanistically significant but relate to regional processes that are beyond the scope of this review (Straub et al., 2013; Ren et al., 2017). The LR04 benthic δ^{18}O stack in black (Lisiecki and Raymo, 2005) is shown to indicate the major global climate events of the last 160 thousand years (i.e., the last major glacial cycle).

emerged between euphotic zone-dwelling, dinoflagellate-bearing species and deeper-dwelling, symbiont-barren species (Ren et al., 2012b; Smart et al., 2018). While the former group approximates the annually averaged nitrate supply, the δ^{15}N of species in the latter group is typically higher by 1–3 ‰. The lower δ^{15}N of shallow-dwelling, dinoflagellate-bearers appears to indicate retention of low-δ^{15}N ammonium within the host-symbiont system, reducing the "trophic elevation" in δ^{15}N that heterotrophs typically exhibit relative to their diet (Uhle et al., 1997; Ren et al., 2012b). On a seasonal timescale, foraminifer δ^{15}N is sensitive to changes in the δ^{15}N of phytoplankton and zooplankton biomass not strictly associated with mean annual nitrate supply. These changes can arise from seasonality in the supply and drawdown of nitrate and in the relative vigor of upper ocean N cycling. Nevertheless, the existing data from regions of complete nitrate consumption argue that this seasonality averages out over the annual cycle to yield a strong δ^{15}N correlation between nitrate supply and planktonic foraminifer δ^{15}N (Ren et al., 2012b; Smart et al., 2018). It remains critical to address whether seasonality in nitrate consumption and upper ocean N cycling is more important in high-latitude and upwelling systems, frequented by symbiont-barren species such as *N. pachyderma* and *G. bulloides* (Ren et al., 2015).

Late Quaternary records of foraminifer-bound δ^{15}N from the Caribbean and South China Sea (gold and green records, respectively; Fig. 9) yield important insights into regional and global changes in the ocean N cycle. In both records, shell-bound δ^{15}N is higher during the last glacial period than the current interglacial. As N_2 fixation adds low-δ^{15}N nitrate to the thermocline in the oligotrophic subtropics today (Knapp et al., 2005; Marconi et al., 2015), these downcore changes are best explained by reduced N_2 fixation during the last ice age (Ren et al., 2009; Ren et al., 2012a; Straub et al., 2013; Ren et al., 2017). When coupled with the evidence for deglacial increases in denitrification (Altabet et al., 1995; de Pol-Holz et al., 2006; Liu et al., 2008) (e.g., red record; Fig. 9), these foraminifer-bound δ^{15}N records argue that N_2 fixation compensates for changes in ocean N loss so as to stabilize the N-to-phosphorus ratio of the ocean over glacial/interglacial cycles (e.g., Broecker, 1982a). Thus, for nutrient reservoir changes to have contributed significantly to glacial/interglacial changes in atmospheric CO_2, the phosphorus reservoir would need to be the driver.

In the subpolar ocean, the sensitivity of foraminifer-bound δ^{15}N to the degree of nitrate consumption is proving valuable for testing hypotheses for the ice-age state of high-latitude regions. The higher δ^{15}N of glacial-aged foraminifers in the Subarctic Pacific (magenta

record; Fig. 9) indicates more complete consumption of the nitrate supply during the last ice age, suggesting that the lower productivity reconstructed for that time and prior ice ages was due to reduced nitrate supply (Ren et al., 2015, and references therein). These findings are analogous with the evidence for reduced surface-to-deep water exchange in the ice age Antarctic from the coupling of diatom-bound $\delta^{15}N$ with export production proxies (Studer et al., 2015 and references therein). Especially in the case of the Antarctic, this oceanographic change would have worked to lower atmospheric CO_2 concentrations during the ice ages. In the Subantarctic Atlantic (blue record; Fig. 9), elevated foraminifer-bound $\delta^{15}N$ during glacial periods coincides with higher productivity and higher dust fluxes, implying more complete nitrate consumption in surface waters when dust fluxes are high (Martínez-García et al., 2014). These results support the iron fertilization hypothesis for enhanced ice-age CO_2 drawdown (Martin, 1990). Thus, it appears that both polar and subpolar Southern Ocean changes contributed to the lowering of atmospheric CO_2 concentrations during the ice ages, through two distinct mechanisms.

Coupled measurements of different foraminifer species as well as of foraminifer- and diatom-bound $\delta^{15}N$ have been recognized as promising strategies to extract information about changes in the seasonality of the surface ocean (Ren et al., 2009; Ren et al., 2015). However, fulfilling this potential necessitates a better understanding of foraminifer $\delta^{15}N$, which requires studies in the modern ocean. While the ecological diversity among planktonic foraminifer species challenges paleoceanographers to develop a comprehensive understanding of both the shared and species-specific signals recorded in their shell-bound organic matter, the reward would be the ability to reconstruct the ocean's past N cycle in rich detail.

6.4. Trace element composition of the shell

6.4.1. Mg/Ca paleothermometry

Mg/Ca in biogenic carbonates is an independent proxy to reconstruct ambient seawater temperature. Mg/Ca of the foraminifer shell as a temperature tracer, combined with $\delta^{18}O$ measurements on the same foraminifer species, allows simultaneous reconstruction of temperature and $\delta^{18}O_{SEAWATER}$ (a proxy for salinity) for the seasons and water depths in which the foraminifer specimens calcified their tests. Incorporation of magnesium into carbonates is related to temperature as indicated by inorganic precipitation studies (Clarke and Wheeler, 1922; Katz, 1973; Burton and Walter, 1987; Mucci, 1987; Oomori et al., 1987). An early study of Savin and Douglas (1973) showed the correlation between magnesium and isotopic temperature in planktonic foraminifers in general. The first species-specific calibrations on the Mg/Ca uptake versus temperature were undertaken in the mid-1990s (Nürnberg, 1995; Nürnberg et al., 1996). Since then, different calibrations from culture experiments, plankton-tow samples, sediment traps, and core-top studies on different planktonic foraminifer species have shown an exponential relationship between temperature and foraminifer Mg/Ca (Lea et al., 1999b; Elderfield and Ganssen, 2000; Anand et al., 2003; Russell et al., 2004; von Langen et al., 2005; Regenberg et al., 2009; Friedrich et al., 2012). Seawater temperature appears to primarily control the Mg^{2+} uptake, while other factors such as salinity and pH affect the Mg/Ca composition of the foraminifer test. Mg/Ca tends to increase at high salinity (e.g., Nürnberg et al., 1996; Kisakürek et al., 2008; Mathien-Blard and Bassinot, 2009; Hönisch et al., 2013; Gray et al., 2018a), and low pH (Lea et al., 1999b; Russell et al., 2004; Kisakürek et al., 2008; Gray et al., 2018a). In addition to environmental effects, Mg/Ca changes during the ontogenetic development of different species to varying degrees (Elderfield et al., 2002; Friedrich et al., 2012).

At the end of their life-cycle some species secrete gametogenetic (GAM) calcite (e.g., Bé and Anderson, 1976; Bé, 1980). GAM calcite contains more Mg than ontogenetic calcite when secreted at the same temperature (Nürnberg et al., 1996). The relative amount of GAM calcite varies between species and specimens. GAM calcite on average adds about 28% (by weight) to pre-gametogenic shells of *T. sacculifer* (Bé, 1980). For *O. universa*, it was shown to be a constant amount of ca. 4 µg of $CaCO_3$, independent of the size of the sphere (Hamilton et al., 2008). Overall, Mg/Ca depends on temperature during GAM calcite secretion. The final (post mortem) Mg/Ca value in tests buried in the seafloor sediment can be lower due to differential dissolution potentials of GAM calcite and ontogenetic calcite (e.g., Caron et al., 1990; Brown and Elderfield, 1996; Rosenthal and Lohmann, 2002), and a decrease in Mg/Ca can be observed below a critical calcite saturation state ΔCO_3^{2-} of 21.3 µmol kg^{-1} in the ocean (Regenberg et al., 2006; Regenberg et al., 2014). It should also be noted that intensive sample cleaning prior to wet chemical analysis can equally lead to lower temperature estimates from Mg/Ca (Sadekov et al., 2010; Vetter et al., 2013b).

High-resolution chemical analyses of foraminifer tests (i.e., profiles from single chambers, and cross-section maps of individual shells, made possible by laser ablation (LA−) ICP–MS and NanoSIMS technology) have revealed alternating high and low Mg/Ca bands within the chamber walls of single specimens that were presumed to reflect daily changes in chamber Mg content (e.g., Eggins et al., 2004; Sadekov et al., 2005). Intra-test and intra-chamber Mg-heterogeneity indicates that incorporation of Mg^{2+} is probably caused by physiological processes (Bentov and Erez, 2006). Culture experiments confirmed the initial observations of Eggins et al. (2004) demonstrating that high-Mg bands calcified at night and low-Mg bands formed during the day (*O. universa*, Spero et al., 2015; *N. dutertrei*, Fehrenbacher et al., 2017). Some planktonic foraminifer species such as *N. dutertrei*, *G. truncatulinoides*, and *G. inflata* develop calcite crusts by thickening their chamber walls during the life cycle (for a review see Schiebel and Hemleben, 2017). Mg/Ca of such crusts varies between specimens and chambers of variable thickness, as well as between chambers with or without such a crust (Hathorne et al., 2009; Steinhardt et al., 2015; Fehrenbacher et al., 2017). Although Mg-heterogeneity in foraminifer tests is high, Mg/Ca values show a significant temperature dependency at the species level (e.g., Spero et al., 2015, *O. universa*), and are in good agreement with calibrations of bulk samples (Lea et al., 1999b; Russell et al., 2004).

6.4.2. B/Ca and $\delta^{11}B$ as proxies of the ocean carbonate system

The boron isotope composition ($\delta^{11}B$) and its concentration (B/Ca) in planktonic and benthic foraminifers have been used to reconstruct seawater pH and pCO$_2$. In seawater, the boric acid and borate ion equilibrium depends on seawater pH through the acid-base equilibrium

$$B(OH)_3 + H_2O \Leftrightarrow B(OH)_4^- + H^+ \qquad (3)$$

with a 27.2 ‰ fractionation between boric acid and borate ion $\delta^{11}B$ (Klochko et al., 2006). The isotopic composition of boron dissolved in seawater is constant (and conservative) throughout the modern ocean (at 39.6 ‰ in the modern ocean; Foster et al., 2010), because the residence time of boron in the ocean is about 10 Ma (Lemarchand et al., 2000), much longer than time scales of ocean overturning. Since the partitioning of boric acid and borate is a function of pH, so too are their isotopic compositions, with a combined $\delta^{11}B$ equal to 39.6 ‰. Assuming that foraminifers only incorporate borate as a substitute for carbonate in the crystal lattice (Vengosh et al., 1991; Hemming and Hanson, 1992; Balan et al., 2016), the $\delta^{11}B$ of the shell should be a function pH. These considerations are supported by inorganic precipitation experiments (Sanyal et al.,

2000), and by a theoretical study of the kinetics of the boric acid-to-borate equilibrium in seawater (Zeebe et al., 2001).

Much of the initial research was devoted to producing empirical calibrations (Sanyal et al., 1996, 2001; Henehan et al., 2013, 2016; Howes et al., 2017), and focused on understanding and quantifying the impact of effects such as photosynthesis, respiration, and calcification (Rink et al., 1998; Wolf-Gladrow et al., 1999; Hönisch et al., 2003; Zeebe et al., 2003; Rae et al., 2011). Zeebe et al. (2008) convincingly demonstrated that vital effects do not compromise $\delta^{11}B$-based paleo-pH reconstructions. On the other hand, the controls on boron concentration are still under debate. Core-top studies indicate a relationship of B/Ca with pH or $B(OH)_4^-/HCO_3^-$ for the symbiont-barren species $G.$ $bulloides$ and $G.$ $inflata$ (Yu et al., 2007). In contrast, analyses from core-top, sediment-trap, and plankton-tow samples suggest that symbiont-bearing species are affected by environmental changes such as symbiont activity, calcification rate, and seawater phosphate concentration (e.g., Henehan et al., 2015, 2016; Haynes et al., 2017; see Rae, 2018, for a review). By deconvolving the carbonate chemistry, Howes et al. (2017) demonstrated that boron concentration is independent of pH and seems to be controlled by DIC or HCO_3^-. The exact mechanism of boron uptake is still unclear but leads to "banding" similar to that observed for magnesium (Branson et al., 2015). It should further be noted that B/Ca of planktonic foraminifers decreases with increasing dissolution (Coadic et al., 2013; Seki et al., 2010). Thus, B/Ca in planktonic foraminifers holds promise, but needs further investigation before it can be applied as a proxy for the past ocean carbonate system.

The relationship between seawater pH and the $\delta^{11}B$ composition of foraminifer carbonate seems to be robust (e.g., Zeebe et al., 2008; Foster and Rae, 2016; Rae, 2018 for a review), and has been widely used to reconstruct past seawater pCO$_2$ (e.g. Hönisch and Hemming, 2005; Foster, 2008; Hönisch et al., 2009; Foster et al., 2012; Martínez-Botí et al., 2015; Gray et al., 2018b; see Rae, 2018, for a review). To convert past borate ion $\delta^{11}B$ to pH and pCO$_2$, another parameter of the past carbonate system is required in addition to ambient seawater temperature and salinity. Temperature can be reconstructed from Mg/Ca, and salinity changes are estimated from combined Mg/Ca and $\delta^{18}O$ with large errors. In the absence of a good estimator for another independent carbonate chemistry parameter, alkalinity estimates can be used (e.g., Martínez-Botí et al., 2015) as $\delta^{11}B$-derived pCO$_2$ changes are relatively insensitive to uncertainties in the estimated alkalinity (Foster and Rae, 2016). Raitzsch et al. (2018) have taken this a step further to reconstruct seasonal CO$_2$ fluxes based on core-top calibrations between the $\delta^{11}B$ of the borate ion and the $\delta^{11}B$ of $O.$ $universa$, $G.$ $bulloides$, $T.$ $sacculifer$, and $G.$ $ruber$, taking the species' depth habitat and seasonality of mass fluxes into account.

7. Concluding remarks

The diversity of sub-fields showcased here demonstrates the broad perspective needed for the application and interpretation of planktonic foraminifer proxies in paleoceanography and paleoclimate reconstruction. Given the long history and breadth of applications, planktonic foraminifers can be considered a role model for other paleoclimate archives. Integration of the various data in a synoptic approach will provide a more comprehensive understanding of the past, present, and future behavior of our dynamic ocean and climate systems. New platforms and technologies provide the tools and basis for concerted programs and corporate advances, which should foster communication with the broader community, layman, and policy makers to facilitate more sustainable use of the resources of our planet Earth.

Author contributions

R.S. accepted the editor's (Fréderique Eynaud) invitation to provide a paper on planktonic foraminifers for the 60th anniversary of the Revue de Micropaléontologie, motivated by the respective colleagues for contributions on their expertise. The different sections were contributed by the coauthors as follows: R.S. on classification; H.K.C. and T.A. on phylogeny; R.M. and F.Q. on molecular genetics; A.J., J.M., and R.S. on population dynamics; P.M.H. and T.d.G.-T. on biodiversity; M.K. on transfer functions; E.M., A.J., H.B.V., J.B., and H.J.S. on isotopes and element ratios; S.S., H.R., A.M.G., D.S., and G.H.H. on N isotopes; L.J. on flux dynamics and sediment traps; J.M. on CPR sampling; R.S. and G.H.H. on plankton nets. All co-authors contributed to the final discussion of the manuscript.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

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