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PLANKTONIC FORAMINIFERA AS TRACERS OF PAST OCEANIC ENVIRONMENTS

Michal Kucera

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1. INTRODUCTION

Paleoceanography has always been closely connected with the study of planktonic foraminifera. The prolific production and excellent preservation of foraminiferal fossils in oceanic sediments (Figure 1) has produced probably the best fossil record on Earth, providing unparalleled archives of morphological change, faunal variations, and habitat characteristics. Planktonic foraminifera are the most common source of paleoceanographic proxies, be it through the properties of their fossil assemblages or as a substrate for extraction of geochemical signals. The steady rain of foraminiferal shells is responsible for the deposition of a large portion of deep-sea biogenic carbonate. Vincent and Berger (1981) estimated that over a period of 500 years planktonic foraminifera deposit a mass of carbon equal to that of the entire biosphere. Fossilized planktonic foraminifera form the backbone of Cenozoic biostratigraphy (Berggren, Kent, Swisher, & Aubry, 1995) and have been instrumental in the study of rates and patterns of evolution (Norris, 2000).

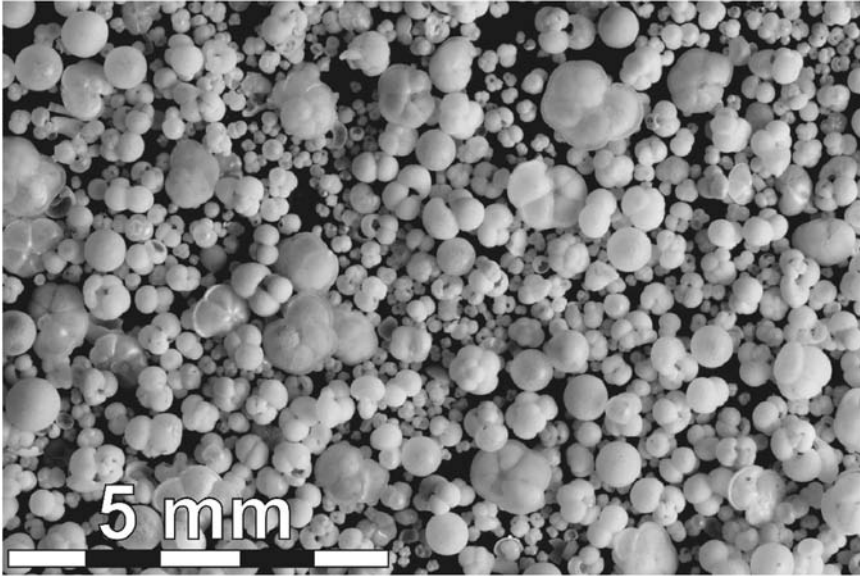


Figure 1 Light-microscope image of the sand-fraction residue from a tropical deep-sea sediment sample. The residue is dominated by planktonic foraminiferal shells representing ~20 species. The foraminifera are well preserved and illustrate the large variation in shell sizes typical for tropical assemblages. (Photo: Wilfried Rönnefeld.)

The potential for planktonic foraminifera to be used as tracers of surface-water properties was first noted by Murray (1897), who recognized that extant species in the plankton and in sea floor sediments are distributed in global belts related to surface-water temperatures. Schott (1935) pioneered the use of quantitative census counts and discovered that fossil assemblages in short deep-sea cores changed between glacial and interglacial times. The prominent role of planktonic foraminifera in reconstructions of Pleistocene climate variation has been established since the birth of paleoceanography. Pflieger (1948) and Arrhenius (1952) used planktonic foraminifera to describe Quaternary climate cycles in the first long piston cores recovered from the deep sea by the Swedish Deep Sea Expedition with the four-mast schooner *Albatross* in 1947–1948. In less than 20 years, enormous progress has been made in the understanding of the biology and ecology of planktonic foraminifera, culminating in the development of the first sophisticated transfer function by Imbrie and Kipp (1971), that laid the foundation for the grandest virtual time-travelling exercise of its time: the reconstruction of the surface of the Earth at the time of the last glacial maximum (CLIMAP, 1976).

The value of foraminiferal calcite as a recorder of chemical and isotopic signals was recognized by Emiliani (1954a, 1954b). Stable isotopic signals extracted from planktonic foraminifera soon became a standard tool for the recognition of glacial cycles and eventually facilitated the recognition of orbital pacing of the ice-ages (Shackleton & Opdyke, 1973; Hays, Imbrie, & Shackleton, 1976). The chemical composition of foraminiferal calcite proved to be a fertile ground for the

development of proxies: almost every trace element and stable or radiogenic isotope imaginable has been, or is being, measured and calibrated in an effort to reconstruct past seawater chemistry and biogeochemical cycles (Henderson, 2002).

Early work on the biology and ecology of planktonic foraminifera has been treated comprehensively in the reviews by Hedley and Adams (1974, 1976), Bé (1977), Vincent and Berger (1981), and Hemleben, Spindler, and Anderson (1989). This chapter will thus focus on the work of the previous 20 years with the objective of highlighting the most common and most promising foraminiferal proxies, and put them in the context of modern biological knowledge. The reader should be aware that stable-isotopic and geochemical proxies, as well as transfer functions, are treated comprehensively in separate chapters of this volume (Chapters 7 and 13, respectively). The use of planktonic foraminifera as tracers of ocean properties is a mature field of science. As a result, we know a great deal about the limitations of foraminiferal proxies and the circumstances in which they can or cannot be applied, and these are well covered in this review. This sign of maturity of the field should not be interpreted by the reader as an argument against the use of planktonic foraminiferal proxies. Planktonic foraminifera continue to play a central role in paleoceanography, providing the science with robust and reliable proxies, and will continue to do so for some time. These inconspicuous organisms and their tiny shells are the true heroes of our quest to reveal the past of our planet.

2. BIOLOGY AND ECOLOGY OF PLANKTONIC FORAMINIFERA

2.1. Cellular Structure, Reproduction, and Shell Formation

Planktonic foraminifera are marine heterotrophic protists that surround their unicellular body with elaborate calcite shells¹. Cytoplasm inside the shells contains typical eukaryotic cellular organelles, supplemented by the so-called fibrillar bodies, which are unique to planktonic foraminifera and may act to control buoyancy (Hemleben et al., 1989). Outside the shell, the cytoplasm is stretched into thin, anastomosing strands (rhizopodia), which may extend several shell-diameter lengths away from the shell. The external rhizopodial network serves to collect food particles and transport them toward the primary opening of the shell (aperture). Inside the shell, food particles are digested and stored as lipids and starches in specialized vacuoles.

Planktonic foraminifera exhibit a range of trophic behaviors from indiscriminate omnivory to selective carnivory (Hemleben et al., 1989). Herbivorous and omnivorous species consume phytoplankton, mainly diatoms and dinoflagellates, while carnivorous species prey on copepods, ciliates, and other similarly sized zooplankton (Hemleben et al., 1989). Species that inhabit the photic zone often harbor intracellular algal symbionts (dinoflagellates or chrysophytes). A symbiotic relationship with photosynthesizing algae is particularly advantageous in warm oligotrophic waters, where nutrients and food are scarce but light is abundant. Typical population

¹ The correct technical term for foraminiferal skeleton is *test*, from Latin *testa* = shell, however, this term has an English homonym with a very different meaning. To avoid confusion, the term *shell* will be used throughout this chapter.

densities of planktonic foraminifera range from $>1,000$ individuals/ m^3 in polar ocean blooms to <100 individuals/ m^3 in oligotrophic gyres (Schiebel & Hemleben, 2005). Given their low population densities and low nutrient/weight ratio (due to the shells), it is not surprising that no selective predators of planktonic foraminifera have been discovered. Instead, planktonic foraminifera appear to be indiscriminately ingested by filter-feeding planktotrophs (Lipps & Valentine, 1970; Hemleben et al., 1989).

Except for the Antarctic species *Neogloboquadrina pachyderma*, which overwinters in brine channels in sea ice (Spindler & Diekmann, 1986), all extant species of planktonic foraminifera are holoplanktonic, spending their entire life freely floating in surface waters. The mixed layer and the upper thermocline are the most densely populated, while virtually no living individuals are found at depths below 1,000 m (Vincent & Berger, 1981). Laboratory observations indicate that some individuals survive when placed on the sediment surface (Hilbrecht & Thierstein, 1996), but there have been no reports of living (or resting) planktonic foraminifera on the sea floor.

Although benthic foraminifera exhibit a complex life cycle including an array of reproductive strategies, solely sexual reproduction has been observed among planktonic foraminifera (Hemleben et al., 1989). Given the lack of morphological dimorphism, which is often indicative of multiple reproductive strategies in foraminifera, it is most likely that all fossil species reproduced exclusively sexually as well. During reproduction, the cytoplasm is divided into hundreds of thousands of biflagellated isogametes that are released into the environment. In order to maximize the chances of gametes from different individuals finding each other, the reproduction has to be synchronized in space and time. Indeed, most shallow-water species appear to reproduce in pace with the synodic lunar cycle (*Hastigerina pelagica*, *Globigerinoides sacculifer*, *Globigerina bulloides*) or half-synodic lunar cycle (*Globigerinoides ruber*) (Spindler, Hemleben, Bayer, Bé, & Anderson, 1979; Bijma, Erez, & Hemleben, 1990a; Schiebel, Bijma, & Hemleben, 1997), and lunar pacing appears important for carbonate production in the tropical oceans (Kawahata, Nishimura, & Gagan, 2002). Recently, the prevalence of the lunar reproductive cycle became a matter of debate (Lončarić, Brummer, & Kroon, 2005). Deep-dwelling species like *Globorotalia truncatulinoides* may follow longer, perhaps yearly, reproductive cycles (Hemleben et al., 1989) and individuals of *N. pachyderma* isolated from Antarctic sea-ice were kept in culture for 230 days (Spindler, 1996).

During their life, individual species are known to migrate vertically within the water column and release gametes at well-defined, species-specific depths, often close to the pycnocline (Schiebel & Hemleben, 2005). The need for deep oceanic waters to complete their life cycles is perhaps the reason why planktonic foraminifera avoid neritic waters over continental shelves (Schmuker, 2000) and resist every effort made to reproduce them under laboratory conditions (Hemleben et al., 1989).

Following gamete fusion, shell growth is facilitated by the sequential addition of chambers, gradually increasing the dimensions of the shell. The process of shell formation and calcification is described in detail by Hemleben et al. (1989). The external rhizopodial network forms the outline of the new chamber and secretes the primary organic membrane (POM) that acts as the nucleation centre for

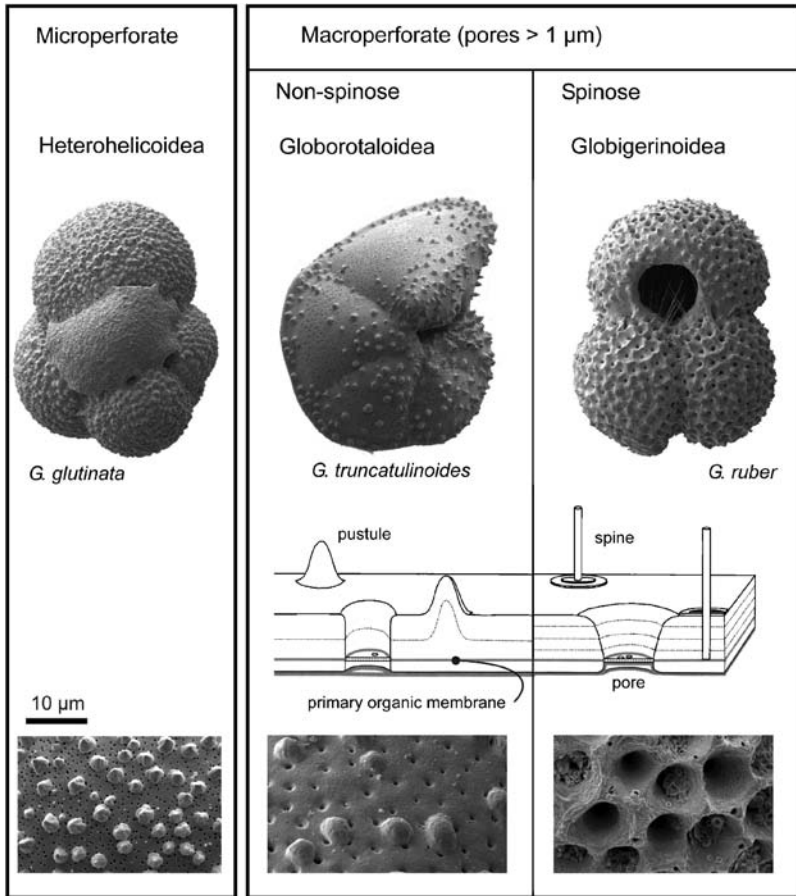


Figure 2 Classification scheme of the three main groups of extant planktonic foraminifera. Representative specimens of the three groups (not to scale) document typical morphology and wall ornament (enlarged sections, all to the same scale). Shell walls are layered, perforated by pores and the outer surface features either pustules or spines (diagram modified from Schiebel & Hemleben, 2005).

calcification (Figure 2). With the exception of the monolamellar Hastigerinidae, calcite layers are added on both sides of the POM, with the external layer extending across the entire outer surface of the shell. Pores are formed within the early stages of wall calcification, while surface ornament including pustules and ridges are formed simultaneously. Spines are plugged into pre-formed cavities in the outer shell layer. They are solid and can be repeatedly shed, or resorbed and regrown. The exact mechanism of foraminiferal calcification is not fully understood. However, laboratory observations on benthic foraminifera indicate that the calcification is extra-cellular and mediated through cation enrichment and transport of seawater in specialized vacuoles (Erez, 2003) and that two separate processes producing different mineral phases may be involved (Bentov & Erez, 2005).

During growth, the shape of a planktonic foraminiferal shell may change dramatically (Brummer, Hemleben, & Spindler, 1986; Hemleben et al., 1989). Adult characteristics, important for the identification of species, develop late in the ontogeny, making classification of juvenile stages next to impossible. Transitions between ontogenetic stages may be linked to changes in trophic behavior and the onset of symbiont infestation. Algal symbionts play an important role in the calcification process, providing extra energy to the host and modulating the chemical microenvironment by lowering dissolved CO_2 concentration. Laboratory experiments show that specimens that were grown in darkness or without symbionts produce substantially smaller shells (Bé, Spero, & Anderson, 1982). The metabolic activity of algal symbionts alters the stable isotopic composition of foraminiferal calcite (Spero & Deniro, 1987) and this distinctive signature (Figure 3) can be used to detect the presence of photosymbiosis in fossil species (Norris, 1996). Significant changes to the shell are associated with reproduction. Some species deposit an

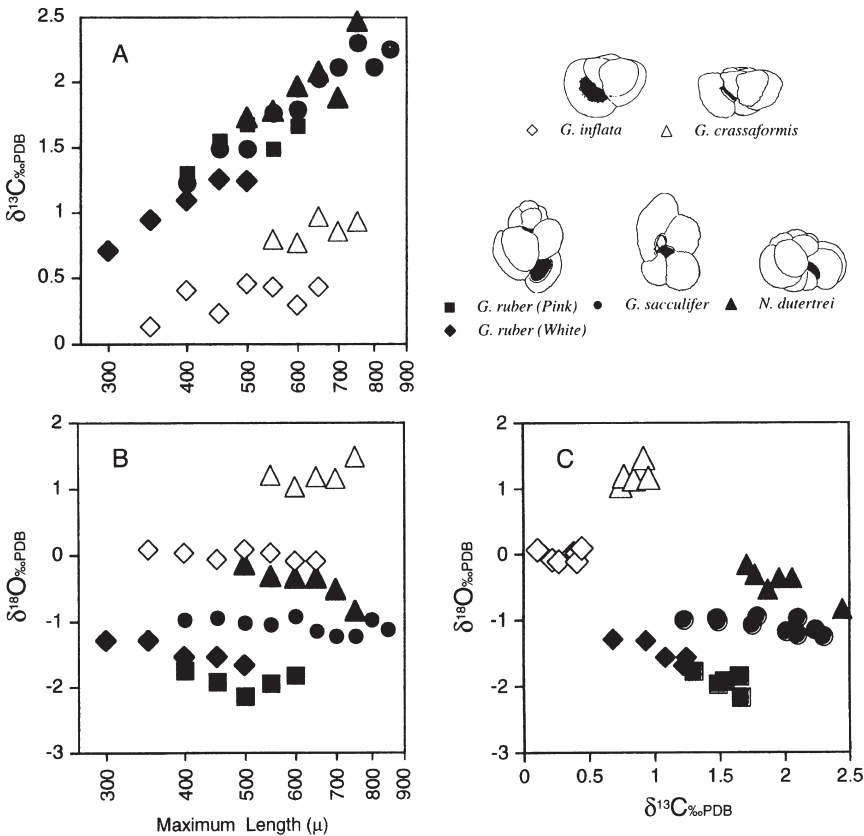


Figure 3 Effects of algal symbionts on stable isotopic composition of planktonic foraminiferal shells. Symbiont-bearing species (filled symbols) show a distinct increase with size toward heavier carbon signature, reflecting an increasing rate of removal of light carbon by the photosymbionts. The distinct isotopic signatures can be used to trace the presence of symbionts in the past (adapted from Norris (1996). Copyright 1996, The Paleontological Society).

additional thick layer of gametogenic calcite prior to reproduction, while others shed spines and *H. pelagica* even resorbs its inner septa (Hemleben et al., 1989). The final chamber of the shell may be disfigured and dislocated. The significance of these kummerform chambers is not fully understood (Berger, 1970b; Hecht & Savin, 1972), but some are likely to represent the products of residual cytoplasm still active after gamete release (Hemleben et al., 1989).

2.2. Classification and Species Concept

Classification of planktonic foraminifera is based entirely on the properties of their shells. At the highest taxonomic level, late Cenozoic planktonic foraminifera are subdivided into three superfamilies: Globigerinoidea, Globorotaloidea, and Heterohelicoidea (Figure 2). The taxonomic position of the family Hastigerinidae, which produces monolamellar shells, remains unclear (Schiebel & Hemleben, 2005). There are ~50 living species of planktonic foraminifera in the modern oceans, but only ~20 of these are sufficiently abundant in the larger sediment fractions to be used for paleoenvironmental reconstructions (Table 1). Planktonic foraminiferal faunas have remained relatively uniform throughout the entire late Cenozoic. As a result, paleoceanographers working with Quaternary climate change can normally get away with the knowledge of only a few dozen taxa. Species-level classification of Quaternary planktonic foraminifera follows the concept developed by Parker (1962). For a detailed overview of foraminifera taxonomy, the reader is referred to the compilations of Bé (1967), Saito, Thompson, and Breger (1981), Vincent and Berger (1981), and Hemleben et al. (1989).

Following the pioneering work by Darling, Kroon, Wade, and Leigh Brown (1996), the taxonomy of extant planktonic foraminifera could be tested using molecular genetic data. Thus, Darling, Wade, Kroon, and Leigh Brown (1997) and de Vargas, Zaninetti, Hilbrecht, and Pawlovski (1997) were able to confirm that the three major clades of planktonic foraminifera, defined by shell ultrastructure, are monophyletic, although it appears that they may have originated from different benthic lineages. It was further shown that every consistently recognized species and morphotype proved to be genetically distinct. This holds true even for forms whose taxonomic status was long unclear, such as the biologically distinct but morphologically identical types of *Globigerinella siphonifera* (Huber, Bijma, & Darling, 1997), the pink and white varieties of *G. ruber* (Darling, Wade, Kroon, Leigh Brown, & Bijma, 1999), and the two coiling forms of *N. pachyderma* (Darling et al., 2000; Darling, Kucera, Kroon, & Wade, 2006; Bauch et al., 2003). However, the genetic data also showed that morphology has not always been effective in describing the diversity of planktonic foraminifera. Apart from confirming the status of existing taxonomic groups, molecular data also revealed the presence of distinct genetic types within planktonic foraminiferal morphospecies, where no intraspecific clusters were suspected (Kucera & Darling, 2002; de Vargas, Sáez, Medlin, & Thierstein, 2004).

Many of the cryptic genetic types recognized within species of planktonic foraminifera show a considerable degree of genetic separation, comparable to that seen among morphologically defined species. In addition, molecular clock estimates suggest that these cryptic species diverged hundreds of thousands to millions of

Table 1 Ecologically Important Species of Extant Planktonic Foraminifera.

Species	Symbionts	Reproduction	Habitat depth	Genetic types	Dissolution resistance
<i>Orbulina universa</i>	Obligatory	Monthly	Surface	3	Moderate
<i>Globigerinoides ruber</i> (pink)	Obligatory	?Bi-weekly	Surface		Susceptible
<i>Globigerinoides ruber</i> (white)	Obligatory	Bi-weekly	Surface	3	Susceptible
<i>Globigerinoides sacculifer</i>	Obligatory	Monthly	Surface		Susceptible
<i>Globigerinella siphonifera</i>	Obligatory	Monthly	Surface to subsurface	3	Susceptible
<i>Globigerina bulloides</i>	None	Monthly	Surface	6	Moderate
<i>Turborotalia quinqueloba</i>	Facultative	Monthly	Surface	5	Moderate
<i>Neogloboquadrina pachyderma</i>	None	?Monthly	Surface to subsurface	5	Resistant
<i>Neogloboquadrina incompta</i>	None	Monthly	Surface to subsurface	2	Moderate
<i>Neogloboquadrina dutertrei</i>	Facultative	Monthly	Surface to subsurface		Resistant
<i>Pulleniatina obliquiloculata</i>	Facultative	Monthly	Surface to subsurface	3	Resistant
<i>Globorotalia inflata</i>	Facultative	Monthly	Subsurface		Resistant
<i>Globorotalia truncatulinoides</i>	None	?Annual	Subsurface		Resistant
<i>Globorotalia hirsuta</i>	None	?Annual	Deep	4	Moderate
<i>Globorotalia scitula</i>	None	Monthly	Deep		Moderate
<i>Globorotalia menardii</i>	Facultative	Monthly	Subsurface		Moderate
<i>Globorotalia tumida</i>	None	?Annual	Subsurface		Resistant
<i>Globigerinita glutinata</i>	Facultative	Monthly	Deep	n.n.	Resistant
<i>Globigerinita wuella</i>	None	Monthly	Surface to subsurface		Moderate
		Monthly	Surface to subsurface		Moderate

Source: Modified from Hemleben et al. (1989), Schiebel and Hemleben (2005) and Kucera and Darling (2002).

years ago (Darling et al., 1999; Darling, Kucera, Wade, von Langen, & Pak, 2003; Darling, Kucera, Pudsey, & Wade, 2004; de Vargas, Bonzon, Rees, Pawlowski, & Zaninetti, 2002; de Vargas, Norris, Zaninetti, Gibb, & Pawlowski, 1999; de Vargas, Renaud, Hilbrecht, & Pawlowski, 2001). Although biological species concepts are difficult to apply to planktonic foraminifera, due to their reluctance to complete their reproductive cycle in laboratory conditions, it appears reasonable to assume that at least some of the genetically identified types represent distinct species. This conclusion is further supported by the distinct biogeographic distribution of these cryptic genetic types, which appears to follow trophic regimes (de Vargas et al., 1999) and surface-water properties (Figure 4; Darling et al., 2004; de Vargas et al., 2001, 2002). Many morphologically defined species are thus in fact lumping ecologically distinct taxa, increasing the amount of noise in foraminifera-based paleoceanographic proxies (Kucera & Darling, 2002).

2.3. Ecology and Distribution

Extant species of planktonic foraminifera can be grouped into five main assemblages that define the tropical, subtropical, temperate, subpolar, and polar provinces (Bradshaw, 1959; Bé & Tolderlund, 1971). Almost two-thirds of the world oceans are covered by the warm-water provinces (Figure 5). The boundary between the warm subtropical and colder transitional province is marked by the annual isotherm of 18°C (Figure 5), which corresponds approximately to the latitude of balanced radiative heat budget (Vincent & Berger, 1981). Most extant species are cosmopolitan within their preferred bioprovince, although three Indopacific (*Globigerinella adamsi*, *Globoquadrina conglomeraata*, *Globorotaloides hexagonus*) and one Atlantic tropical species (*G. ruber* pink) are endemic. The ubiquitous distribution of foraminiferal morpho-species is not mirrored by the cryptic genetic types. Although some of these do occur globally (Darling et al., 1999, 2000), many show a considerable degree of endemism (Kucera & Darling, 2002; Kucera et al., 2005).

The distribution and abundance of planktonic foraminifera species is strongly linked to surface-water properties. Sea-surface temperature (SST) appears to be the single most important factor controlling assemblage composition (Figure 5; Morey, Mix, & Pisias, 2005), diversity (Rutherford, D'Hondt, & Prell, 1999), and shell size (Schmidt, Renaud, Bollmann, Schiebel, & Thierstein, 2004a). Both laboratory experiments (Bijma, Faber, & Hemleben, 1990b) and sediment-trap observations (Zaric, Donner, Fischer, Mulitza, & Wefer, 2005) indicate that planktonic foraminifera species survive under a considerable range of SST, but that their optimum ranges, defined by highest relative and absolute abundances, are typically narrow and distinct (Figure 5). At present, the polar waters of both hemispheres are dominated by a single small species (*N. pachyderma*), while the highest diversity and largest sizes are found in the oligotrophic subtropical gyres. The increase in SST toward the equator is accompanied by a proportional increase in surface-water stratification. The strength of vertical gradients in the ocean determines the number of physical niches available for passively floating plankton, and may thus control their diversity and morphological disparity (as reflected by size range) (Rutherford et al., 1999; Schmidt et al., 2004a).

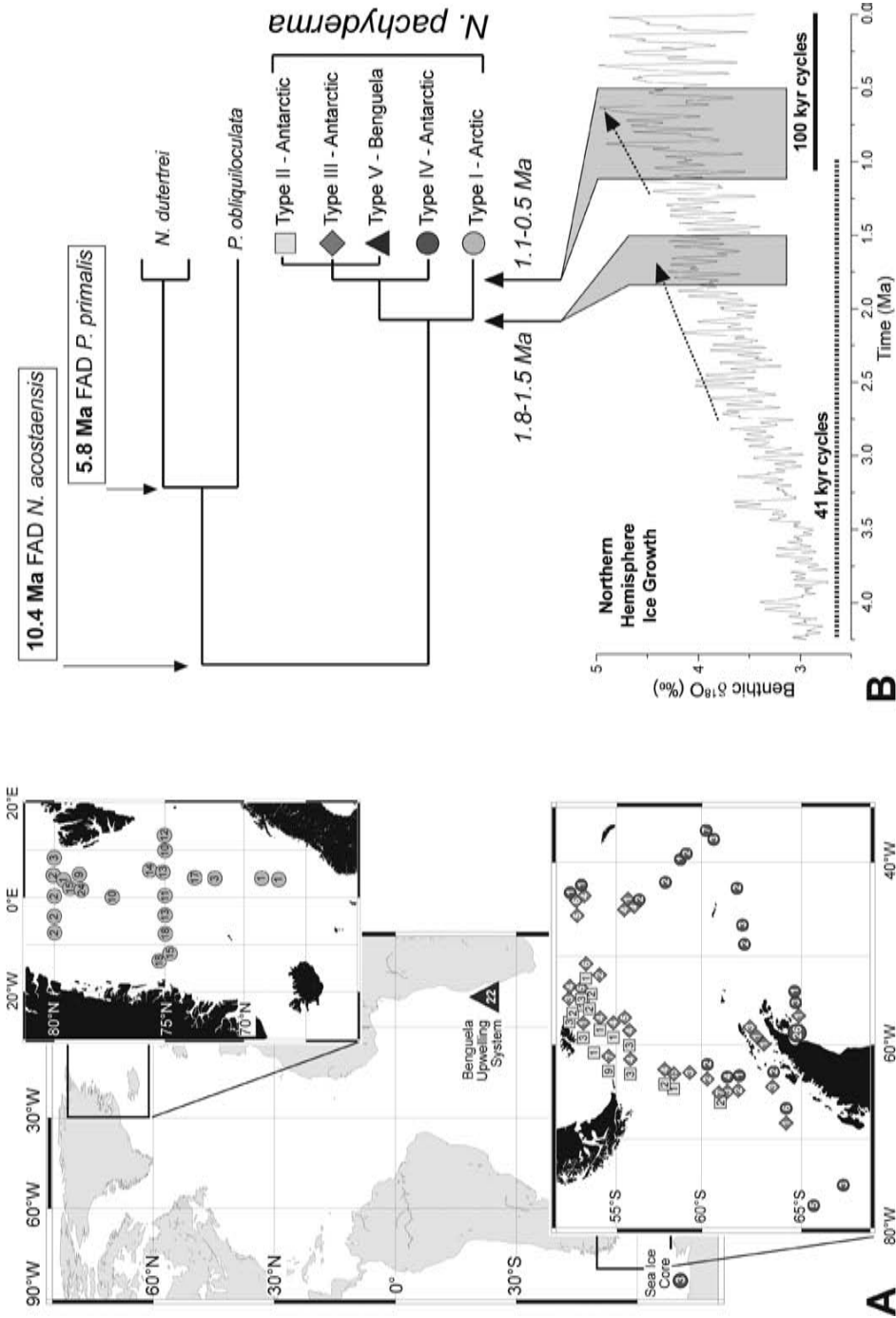


Figure 4 Distribution (A) and phylogeny (B) of molecular genetic types of *N. pachyderma* in the Atlantic Ocean. The data show that genetic diversification within the species began in early Quaternary and that the genetic types show a high degree of endemism (adapted from Darling et al. (2004). Copyright 2004, National Academy of Sciences).

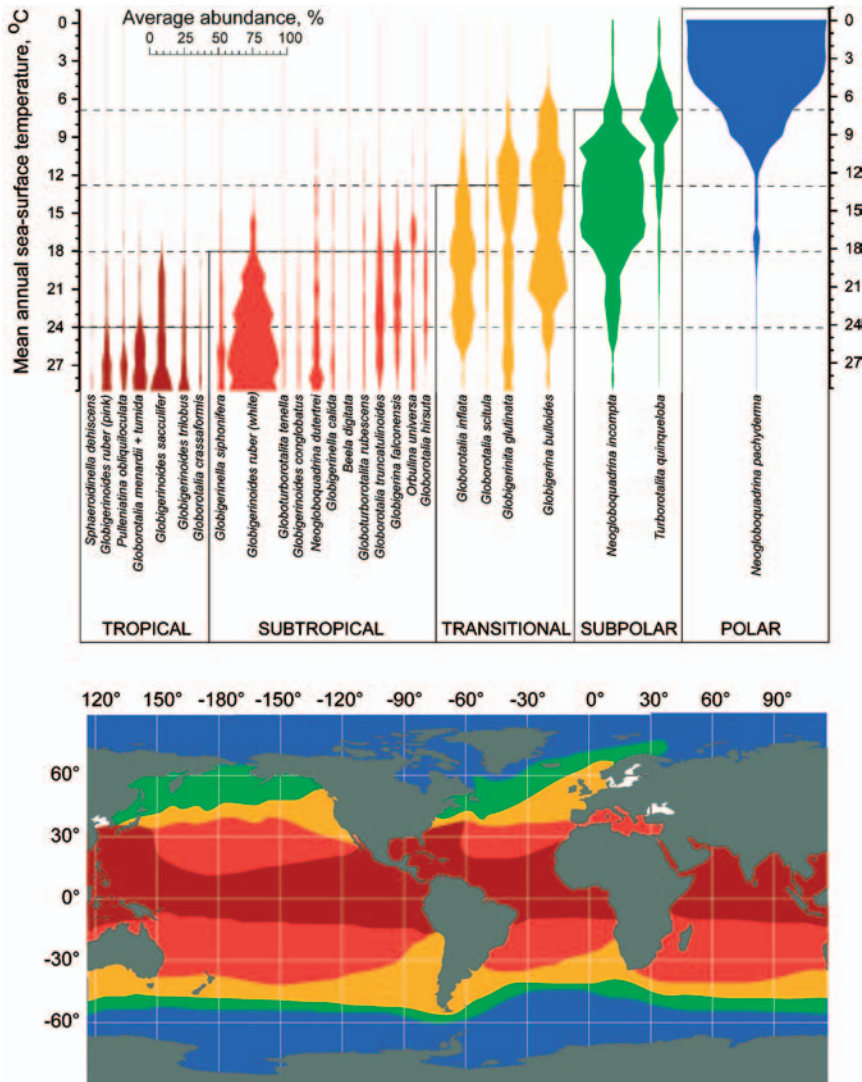


Figure 5 Planktonic foraminiferal provinces in the modern ocean. The distribution of the provinces (Bé, 1977; Vincent & Berger, 1981) follows sea-surface temperature gradients, reflecting the strong relationship between SST and species abundance. The abundance plots are based on surface-sediment data from the Atlantic Ocean (Kucera et al., 2005), averaged at one degree centigrade intervals.

The general trend toward higher diversity and larger sizes with increasing SST is reversed in equatorial and coastal upwelling zones, which are characterized by higher population densities of smaller species (Rutherford et al., 1999; Schmidt et al., 2004a). Large, symbiont-bearing carnivorous specialists are adapted to oligotrophic conditions, and in high-productivity regimes they are easily outnumbered by omnivorous and herbivorous species such as *G. bulloides* and *Globigerinita glutinata*.

These opportunists can rapidly react to organic particle redistribution and phytoplankton blooms following nutrient entrainment (Schiebel, Hiller, & Hemleben, 1995; Schiebel, Wanik, Bork, & Humleben, 2001; Schiebel & Hemleben, 2005).

Episodic pulses of primary productivity, coupled with the seasonal SST cycle result in predictable successions of planktonic foraminifera species, which react to the changing environmental conditions according to their ecological preferences. Such successions have been documented in numerous sediment-trap studies (Figure 6) and their understanding is of great importance for geochemical proxies. Schiebel and Hemleben (2005) give an excellent summary of the main seasonal production patterns. In general, the flux rate of planktonic foraminiferal shells follows primary productivity cycles with a lag of several weeks. In polar oceans, the

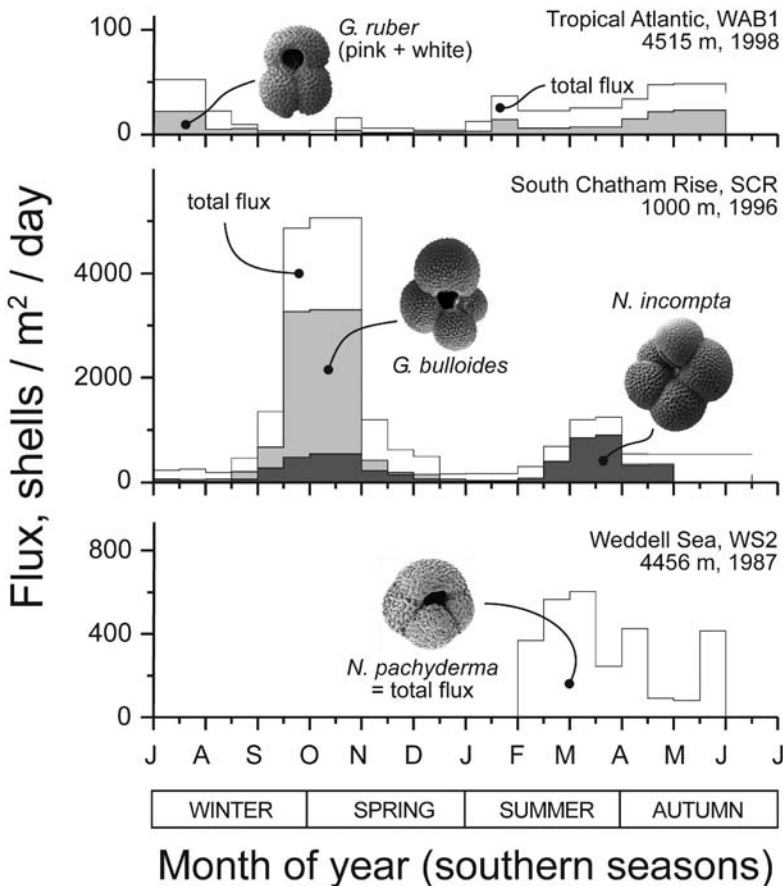


Figure 6 Typical patterns of annual cycle of planktonic foraminifera shell flux in polar, temperate, and tropical oceans. The flux in the polar ocean is limited to ice-free conditions; in temperate oceans it is typically focused into two seasonal peaks, each dominated by different species, and the oligotrophic tropical waters are characterized by extremely low and even fluxes throughout the year. Flux data are from different studies as reported in the compilation by Zaric et al. (2005). Note that all sediment-traps are from the southern hemisphere.

flux peak is observed during the summer, whereas in temperate oceans the spring flux maximum is often followed by a smaller autumn peak. Tropical and subtropical oceans are characterized by a steady rain of foraminiferal shells throughout the year (Figure 6).

Within the range of normal marine conditions (33–36‰), salinity does not appear to exert any significant influence on planktonic foraminifera (Hemleben et al., 1989). Laboratory experiments indicate that some species can tolerate a remarkable range of salinities (*G. ruber*: 22–49‰) and that salinity tolerances differ among species (Bijma et al., 1990b). In nature, no planktonic foraminifera are known to live under hyposaline conditions. *N. pachyderma* is known to avoid low salinity (<32‰) surface layers in the Arctic (Carstens, Hebbeln, & Wefer, 1997; Simstich, Sarnthein, & Erlenkeuser, 2003; Hillaire-Marcel, De Vernal, Polyak, & Darby, 2004) and the low-salinity surface water associated with the Zaire River plume is inhabited by a distinct assemblage dominated by *G. ruber* pink and *Neogloboquadrina dutertrei* (Ufkes, Jansen, & Brummer, 1998). At the other end of the spectrum, planktonic foraminifera inhabiting the Red Sea live at salinities in excess of 40‰ and the Antarctic *N. pachyderma* live in sea-ice where brine salinities exceed 80‰ (Dieckmann, Spindler, Lange, Ackley, & Eicken, 1991; Spindler, 1996). The upper salinity limit for tropical foraminifera determined by laboratory experiments seem to correspond well with observations from glacial Red Sea sediments, where planktonic zones correspond with paleosalinities determined from hydrological models (Fenton, Geiselhart, Rohling, & Hemleben, 2000; Siddall et al., 2003). The influence of ecological factors other than temperature, salinity, and fertility is difficult to disentangle, because most surface-water properties are strongly inter-correlated.

3. PLANKTONIC FORAMINIFERAL PROXIES

Many properties of individual organisms and whole ecological systems are affected by the physical and chemical parameters of their habitat. If we knew how the environment modifies the basic genetic design of organisms and how it controls their spatial and temporal distribution, we could use the fossil record of such organisms to reconstruct the state and variation of past environments. The various signals locked in fossils are only rarely directly related to individual environmental parameters. Therefore, paleoenvironmental reconstructions rely on recipes and algorithms describing ways of how to relate measurements and observations made on fossils and other geological material to past environmental variables.

Planktonic foraminifera are by far the most important signal carriers in paleo-oceanography. The physical and chemical properties of foraminiferal shells provide a multitude of paleoproxies, based on the chemical composition and morphology of their shells as well as species abundance patterns. This chapter will deal with the physical properties of foraminiferal shells and proxies that can be derived from them (Table 2). Chemical properties of foraminiferal shells and their use as proxies are treated in detail in chapters on stable isotopes and trace elements. Unlike their

Table 2 Physical Properties of Foraminiferal Shells that can be Used for Paleoproxies.

Census	Counts of taxa, ecological or functional types
	Presence/absence Semi-quantitative abundance estimates Absolute abundances Relative abundances
Biometry	Measurements made on individual specimens
	Morphology — size, shape Shell ultrastructure Colour and weight
Modification	Changes to fossils incurred after deposition
	Preservation indices Fragmentation

chemical composition, the physical properties of foraminiferal shells can be determined relatively easily and with high precision. In addition, physical and chemical properties of foraminiferal shells follow different taphonomic pathways and proxies based on these properties can be used to derive independent estimates of paleo-oceanographic parameters from the same fossil assemblage, thus providing a unique opportunity to assess the robustness of such paleoenvironmental reconstructions. However, the processes that contribute to the physical form of a foraminiferal shell are very complex, and, as a result, reconstructions based on physical proxies are often considered less reliable and more difficult to interpret.

In an ideal world, one would wish to have a full mechanistic understanding of why and how each proxy works. In reality, mechanistic understanding of most paleoproxies is rare, particularly of those based on fossils and their physical form. As soon as life with all its complexities enters the equation, paleoceanographers have to resort to the process of empirical calibration. Here, the relationship between a physical parameter of a fossil and an environmental variable is derived by observing and describing the distribution of taxa and their properties in the present-day ocean. This process is methodologically relatively simple but it involves a number of assumptions that limit the applicability of each empirically calibrated proxy.

An empirical calibration requires a database of measurements or recordings of a physical parameter of an extant organism, with simultaneous observations of the desired environmental variable(s) associated with its habitat and a mathematical tool or algorithm to determine the form of the relationship between the two types of data. In paleoceanography, this relationship is then applied on data extracted from the fossil record. The main assumptions of this process are that the target environmental variable exerts a significant influence on the measured property, and that the mathematical tool is able to describe this relationship effectively.

There are two additional issues that need to be considered when applying an empirical calibration to a fossil sample: how far back in time can a calibration be used, and how do we recognize that a proxy is extrapolating into the unknown, yielding reconstructions of unknown reliability? Both issues reflect the basic assumption of empirical calibration: the stationarity principle. This principle states that the properties of fossils and the relationships among them and the environment must remain identical throughout the range of the application of the proxy.

The exact range in time of each calibration depends on the rate of evolution in the group of fossils on which the calibration is based. The reliability is highest in samples derived from the same time frame as the calibration data set and decreases until the time when the signal carrier or its components first evolved (Figure 7). Molecular-clock ages of the most recent divergences among cryptic species in planktonic foraminifera (Darling et al., 2003, 2004; de Vargas et al., 1999, 2001), as well as morphometric observations on changes in their ecological preferences (Schmidt, Renaud, & Bollmann, 2003), suggest that an ecological calibration based on modern planktonic foraminifera can be used with high confidence during the last glacial cycle, while its application in samples older than 1 Myr would very likely suffer significantly from the breakdown of the stationarity assumption. For example, Kucera and Kennett (2002) discovered a small but distinct shift in the morphology of Pacific *N. pachyderma* at ~ 1 Myr and showed that this inconspicuous event coincides with a major change in the habitat of this species. A similar example from the Neogene *Fohsella* lineage is given by Norris, Corfield, and Cartlidge (1996). Apparent taxonomic uniformity of Cenozoic planktonic foraminifera has led to attempts to apply calibrated proxies in deep time (e.g., Andersson, 1997). However, morphological similarity does not imply ecological similarity, and morphology alone is clearly not sufficient to describe the true diversity in planktonic foraminifera. Therefore, caution has to be exercised whenever observations and assumptions derived from extant species are transferred to the fossil record.

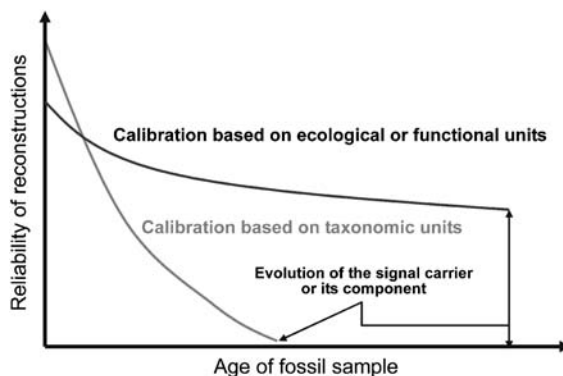


Figure 7 Gradual decrease with time of the reliability (accuracy) of a calibration based on taxonomic units and a calibration based on ecological or functional units. The reason for the decrease is the increasing possibility that ecological preferences of the constituent units of the calibration may have changed. Significant shifts in habitat and ecology within planktonic foraminiferal lineages can occur without noticeable changes to shell morphology.

Recognition of situations where a proxy yields unreliable reconstructions is a more difficult issue. In the case of transfer functions (see below), this uncertainty is embodied in the concept of the no-analog condition (Hutson, 1977). Such conditions occur when the measured value of a fossil property (size of a shell, abundance of a species) exceeds the variation in the calibration data set, or when the oceanographic situation in the past has no analog in the present. The latter is particularly difficult to detect and thus it is fair to say that all paleoceanographic reconstructions based on fossils have to be critically scrutinized. If in doubt, one should abstain from interpreting the absolute value of the proxy signal and use only its qualitative content (like the sign of a change). For obvious reasons, proxies delivering only qualitative information (warmer, colder) are much more robust and can be applied further back in time than rigorous quantitative proxies.

3.1. Census Data

Deep-sea sediments deposited above the calcite compensation depth abound with shells of planktonic foraminifera. Typically, one gram of deep-sea calcareous ooze contains thousands to tens of thousands of specimens larger than 0.150 mm. Such high abundances combined with the ease of their extraction from the sediment make planktonic foraminifera particularly suitable for quantitative analyses. In addition, as we have shown in Section 2.3, species composition of foraminiferal assemblages is extremely sensitive to surface-water properties, particularly SST (Morey et al., 2005). Data from laminated sediments from the California Margin (Field, Baumgartner, Charles, Ferreira-Bartrina, & Ohman, 2006) show that even inter-annual SST variations are recorded in the composition of foraminiferal assemblages deposited onto the sea floor. Thus it is not surprising that the analysis of census counts of species abundances and assemblage composition is the most common source of planktonic foraminiferal proxies.

The determination of a foraminiferal assemblage census typically involves the counting of 300–500 specimens in random sub-samples of the >0.150 mm fraction. This standard procedure has been developed within the CLIMAP project and was motivated on the one hand by the need for rapid acquisition of large amounts of census data, and on the other hand by statistical reproducibility (CLIMAP, 1976). Subsequent studies validated this optimization (e.g., Pflaumann, Duprat, Pujol, & Labeyrie, 1996; Fatela and Taborda, 2002) and the continuation of this method can be safely recommended for routine data acquisition in normal environments. However, if a particular rare species is of interest, the census size has to be increased in order to be able to distinguish statistically significant changes in the relative abundance of that species (Pflaumann et al., 1996). Alternatively, the absolute abundance of a rare species can be expressed in terms of its accumulation rate (Kucera, 1998), rather than its proportion in the total assemblage.

Smaller-sized planktonic foraminifera are generally difficult to identify and time-consuming to count. In order to minimize errors due to taxonomic uncertainty, CLIMAP project members (1976) recommended the use of the >0.150 mm size fraction. This practice has been followed ever since and enormous quantities of data continue to be generated using this procedure (Kucera et al., 2005). Although

such a standard is essential for studies using environmental calibration based on species abundance, such as transfer functions (see below), many planktonic foraminiferal shells are smaller than 0.150 mm and the introduction of this artificial size limit inevitably biases the assemblage composition. Planktonic foraminiferal size decreases toward the poles (Schmidt et al. 2004a) and the use of the same lower size limit thus leads to an artificial decrease in diversity in high-latitude assemblages. The loss of information in census counts from such regions based on the >0.150 mm fraction led some researchers to consider the use of smaller sieve sizes (normally >0.125 mm). The value of analyzing smaller size fractions has been demonstrated for plankton samples from the Fram Strait (Carstens et al., 1997), as well as for reconstructions of the glacial–interglacial palaeoceanography of the polar Arctic Ocean (Kandiano & Bauch, 2002). Although there can be no doubt that the use of smaller fractions affords a more appropriate characterization of polar and subpolar assemblages, the use of counts based on this procedure in established environmental calibrations requires additional assumptions (Hendy & Kennett, 2000), or the development of new calibration datasets (Niebler & Gersonde, 1998).

The quality of census data relies on correct identification of the counted taxonomic units. Given the low overall number of planktonic foraminifera species and the common practice of lumping similar forms (e.g., *G. tumida* and *G. menardii*; Pflaumann et al., 1996; Kucera et al., 2005), there is no *a priori* reason to doubt the general applicability of environmental calibrations based on data generated by a range of researchers. Taxonomic schemes that are commonly used to generate census counts of planktonic foraminifera (Kucera et al., 2005) reflect a compromise between accuracy, speed, and reproducibility. However, no objective analysis of the errors resulting from different taxonomic opinions has ever been performed and every practitioner would agree that some species, such as *G. bulloides* and *G. falconensis*, are easily confused. Authors producing census counts are thus encouraged to consider their taxonomic concept carefully and note explicitly which species were recognized and which taxa were not being distinguished.

3.1.1. Indicator species and assemblages

The simplest types of foraminiferal proxies are based on abundances of ecologically significant (indicator) species. For example, the deep-dwelling *G. truncatulinoides* exhibits a yearly reproductive cycle during which it descends to considerable depth in the ocean (Schiebel & Hemleben, 2005). It can only complete its reproductive cycle if the waters at all depths it passes through are oxygenated. Following this argument, Casford et al. (2003) interpreted the presence of *G. truncatulinoides* in eastern Mediterranean sapropels as evidence for intermittent relaxation of intermediate-water anoxia during the sapropel-deposition events. Similarly, the affinity of *Globorotalia scitula* for sub-thermocline waters rich in organic debris allowed Schiebel, Schmuker, Alves, and Hemleben (2002) to trace the position of the Azores Front during the late Pleistocene.

The most commonly used index species is the shallow-dwelling opportunistic *G. bulloides*, which is known to thrive in high-productivity regimes, making it a good indicator of upwelling intensity (Thiede, 1975; Conan, Ivanova, & Brummer, 2002; Figure 8). Naidu and Malmgren (1995) and Gupta, Anderson, and Overpeck (2003)

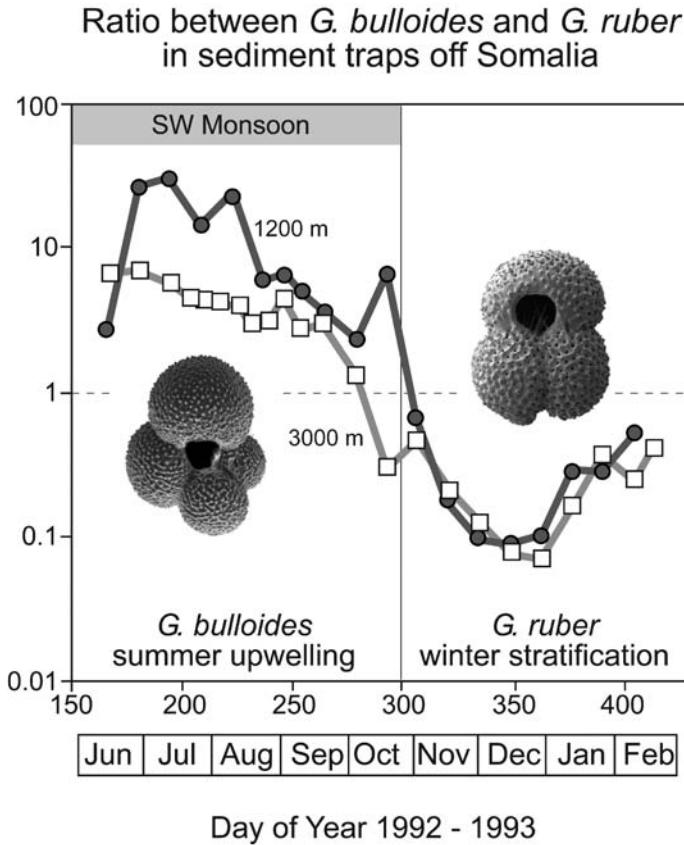


Figure 8 Increased flux of *G. bulloides* shells during upwelling off Somalia. Data from two sediment-traps moored at different depths show a consistent picture of dominance of this species during the south-western Monsoon, whereas *G. ruber* dominates the assemblage during the low-productivity winter period (modified from Conan et al., 2002).

used the abundance of this species to reconstruct sub-Milankovitch oscillations in Holocene monsoon-driven upwelling in the Arabian Sea, and Black et al. (1999) showed that its accumulation rate in laminated sediments from the Cariaco Basin correlates with historical records of wind strength and resulting upwelling in the region.

The ecology of individual species is often complex and poorly understood. Grouping ecologically similar species into “indicator assemblages” often provides a more robust approach. Indeed, the proportion between warm- and cold-water species could be used to track the thermal history of the ocean’s surface on geological time scales (Ingle, 1977), as well as with centennial resolution (Rohling, Mayewski, Hayes, Abu-Zied, & Casford, 2002). A specific fauna is known to be associated with the warm Agulhas Current off South Africa (Giraudeau, 1993) and past changes in the abundance of this “Agulhas fauna” can be used to reconstruct

the history of surface–water exchange between the Indian and Atlantic Oceans on glacial–interglacial time scales (Peeters et al., 2004) (Figure 9).

In the North Atlantic, planktonic foraminiferal assemblages allow an indirect reconstruction of sea-ice distribution. Kucera et al. (2005) showed that surface sediment samples deposited below the modern Arctic Domain surface water in the North Atlantic always contain a small but detectable fraction (0.3–1%) of subpolar species, including *T. quinqueloba*, *G. bulloides*, and *G. glutinata*, whereas in the perennially ice-covered regions these species are totally absent. The subpolar intruders are strictly bound to seasonally open conditions guaranteeing food and light supply, in particular the symbiont-bearing *T. quinqueloba* (Schiebel & Hemleben, 2005). Thus, presence of even small portions of subpolar species can be taken as a proxy of seasonally ice-free conditions. This approach has been used by Kucera et al. (2005) to reconstruct the extent of seasonally ice-free conditions in the Nordic Seas during the last glacial maximum (Figure 10).

Species and assemblage abundance proxies are simple and effective, but their main limitation is that they only deliver qualitative reconstructions. The understanding of many oceanographic processes requires knowledge of the absolute values of environmental parameters or the magnitudes of their changes. In order to derive such information from census data, the abundances of planktonic foraminiferal species have to be empirically calibrated to environmental variables. Such calibration is the subject of the so-called transfer functions.

3.1.2. Transfer functions

The strong relationship between environmental variables, notably SST, and assemblage composition of planktonic foraminifera has long tempted workers to make qualified guesses of absolute values of past environmental conditions (see review in Vincent & Berger, 1981). The art of qualified guessing eventually evolved into mathematical formalization of the ecological relationships. This transition can be exemplified by the weighted-average optimum temperature method of Berger (1969). This technique combines a somewhat intuitive ecological analysis of species with a rigorous formula:

$$T_{\text{est}} = \frac{\sum(p_i \cdot t_i)}{\sum p_i}$$

where p_i is the proportion of species i and t_i the “optimal” temperature for species i .

The choice of t_i is informed by the distribution of foraminiferal assemblages in modern oceans and sea-floor samples and represents a simple kind of empirical calibration. Such multi-dimensional empirical calibrations of species abundances and environmental parameters are called “transfer functions” in paleoceanography. Generally speaking, transfer functions can be defined as empirically calibrated mathematical formulas or algorithms that serve to optimally extract the general relationship between faunal composition in sediment samples and environmental conditions reflected by the fauna. This relationship is then applied to census data from fossil samples (Figure 11). Like any other empirical calibration, transfer functions rely on a number of assumptions. For more details, the

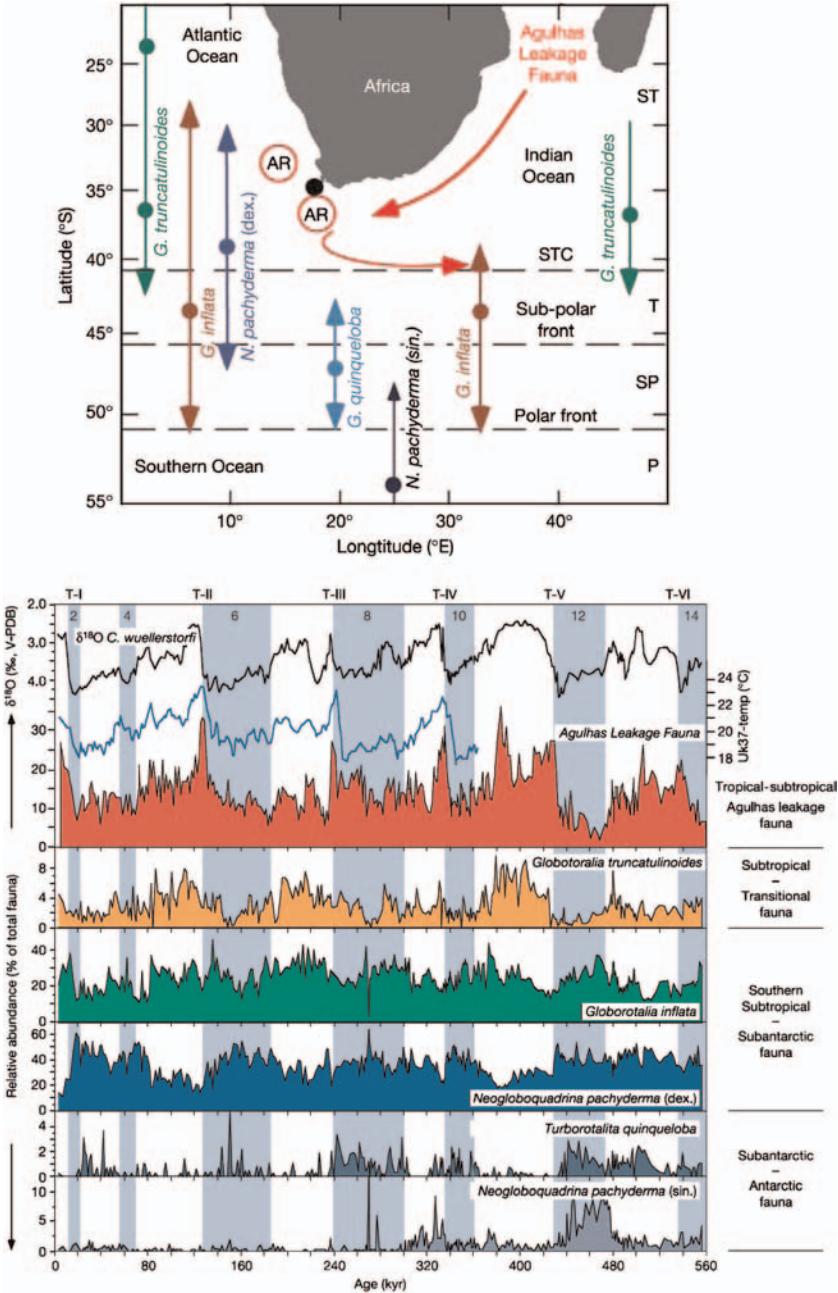


Figure 9 Changes in the abundance of assemblages of planktonic foraminifera in a core taken off Cape of Good Hope (solid circle). Present-day distribution of individual species is shown by vertical arrows in the upper panel; AR = Agulhas Rings. Subtropical species are carried into the region by the warm Agulhas Current and their abundance reflects the intensity of the current in the past (after Peeters et al. (2004). Copyright 2004, Nature).

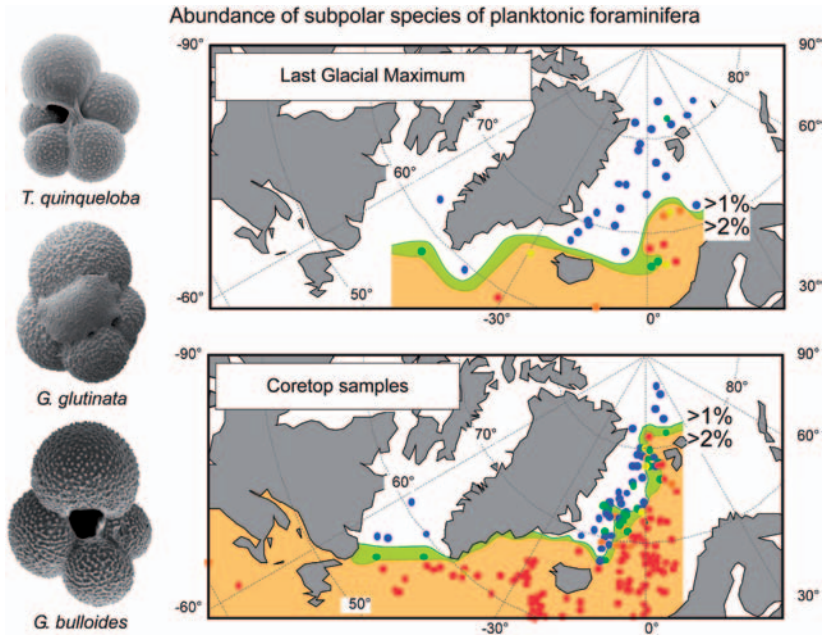


Figure 10 Distribution of subpolar species of planktonic foraminifera in modern and glacial North Atlantic sediments. The presence of subpolar species in glacial Norwegian Sea indicates that this region must have been seasonally ice-free during the glacial period. Yellow, orange and red colours indicate samples with more than 2, 5 and 10% of subpolar species, respectively (data from Kucera et al., 2005).

reader is referred to the reviews in Birks (1995), Kucera et al. (2005), and Chapter 13 of this book.

The struggle for improvement in the precision of transfer function reconstructions has caused researchers to resort to more complex, often computer-intensive methods. A good review of early work on planktonic foraminiferal transfer function techniques is given by Hutson (1977). A true breakthrough in this field came with the so-called Imbrie-Kipp Transfer Function method (Imbrie & Kipp, 1971) which used Q-mode principal component analysis to decompose the variation in the faunal data into a smaller number of variables that were then regressed upon the known physical parameters. The Imbrie-Kipp method was the foundation for the pivotal effort of the CLIMAP group to reconstruct the sea-surface temperature field of the last glacial maximum ocean (CLIMAP, 1976). Foraminiferal transfer functions have seen a recent revival, fuelled mainly by the development and application of new computational techniques (Kucera et al., 2005, Chapter 13). Despite its caveats and limitations, the method is extremely important since its reconstructions are independent of geochemical proxies.

Although most planktonic foraminiferal transfer functions have dealt with SST, there is no reason to exclude the possibility that other environmental variables can be meaningfully extracted from the census data. Anderson and Archer (2002) used the modern analog technique (see Chapter 13) to reconstruct calcite saturation of

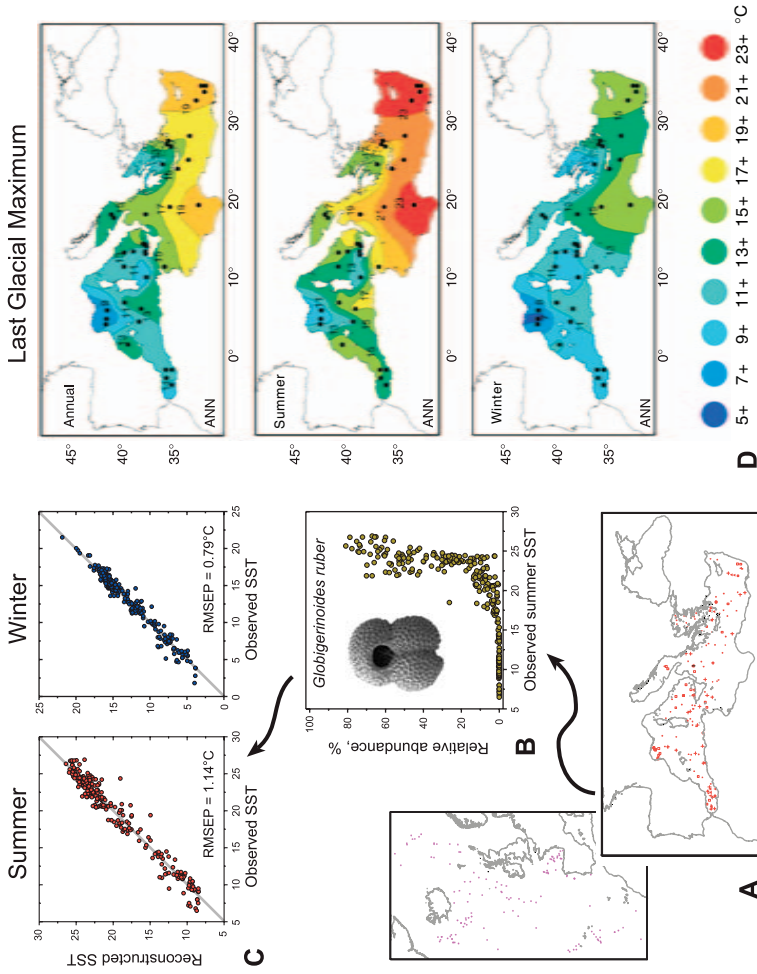


Figure 11 Foraminiferal transfer function for reconstruction of sea surface temperature in the Mediterranean. The calibration is based on 145 Mediterranean and 129 Atlantic core-top samples (A). In each sample, the abundance of 23 species of planktonic foraminifera was determined (B) and an artificial neural network algorithm was used to extract the relationship between species abundance and SST (C). The strong relationship between species abundance and SST is exemplified by the tropical species *G. ruber*. The estimated errors of SST reconstruction (RMSEP) range around 1°C. The algorithms were then used to reconstruct SST in 37 cores representing the Last Glacial Maximum (D) (modified from Hayes, Kucera, Kallel, Sbaifi, & Rohling, 2005).

glacial bottom waters, and Ivanova et al. (2003) reconstructed paleoproductivity in the Arabian Sea using a variant of the Imbrie–Kipp method. The reason why most of the focus has been on SST is clearly shown in the analysis of Morey et al. (2005). These authors used a multivariate statistical technique known as canonical correspondence analysis in order to determine which of a series of 35 environmental parameters showed a strong and independent relationship with assemblage composition. SST came out as the single most significant factor, followed by a weak and diffuse relationship with a combination of parameters that Morey et al. (2005) interpreted as indicative of surface-water fertility.

The greatest challenge of foraminiferal transfer functions is generalization. Through a combination of increasing size of calibration data sets and increasing complexity of mathematical techniques, the apparent prediction errors of transfer functions have been brought to below 1°C. However, it is imperative to constantly remind ourselves that transfer functions are not developed to reproduce present-day faunal patterns. They are being devised to describe the general relationship between fauna and environmental forcing. Only those transfer functions that are capable of extracting the general relationship between fauna and environment will be robust to no-analog situations and can be meaningfully applied to the past (Hutson, 1977; Kucera et al., 2005).

3.2. Shell Morphology

All organisms are affected during growth by the state of their physical environment. The phenotype of each species thus reflects the combined action of the genetically stored information overprinted by ecological effects. If the nature of the action of environment on the phenotype was known, the morphology of an organism could be used to reconstruct the environmental conditions to which it was exposed during its life. This is the basic premise of proxies based on the morphology of planktonic foraminiferal shells. Because of the inherent complexity of the factors affecting shell morphology, quantitative empirical calibrations of morphological properties are rare and often imprecise. On the other hand, physical properties of foraminiferal shells can be determined unambiguously and accurately. Normally, measurements made on 20–50 specimens are enough to characterize the average state of a morphological variable in a fossil assemblage. This leads to the curious situation whereby morphological variability can be reconstructed with great accuracy but the resulting interpretations remain qualitative (Renaud & Schmidt, 2003; Schmidt et al., 2003). The difficulty in developing quantitative morphological proxies is also the reason why such proxies are rarely applied, especially when compared to the widespread use of transfer functions.

3.2.1. Shell size

The dimensions of planktonic foraminiferal shells found in sediments may vary by as much as two orders of magnitude. Some of the variation can be attributed to ontogenetic growth, but shells vary in size considerably even among adult individuals. In part, this variation is linked to taxonomy: the tiniest modern species build shells consistently smaller than 0.1 mm, while the giants can reach sizes well

over 1 mm (Figure 1). Larger size is typically associated with warm-water species and Schmidt et al. (2004a) showed how this relationship is manifested in a spectacular expansion of the size range in foraminiferal assemblages from the poles toward the equator (Figure 12). The exact cause of this pattern is difficult to disentangle, as most of the involved variables are highly inter-correlated. Most likely a combination of higher carbonate saturation, faster metabolic rates, higher light intensity, and greater niche diversity (due to stronger stratification) can promote growth to larger and heavier shell sizes in the warm subtropical and tropical oceans (Schmidt et al., 2004a; de Villiers, 2004).

Temperature-related effects appear to control shell size in planktonic foraminifera even at the species level. Kennett (1976) and Hecht (1976) noticed that abundance and size maxima of many taxa tend to occur at specific temperatures. B e, Harrison, and Lott (1973) documented a marked decrease in shell size of *O. universa* south

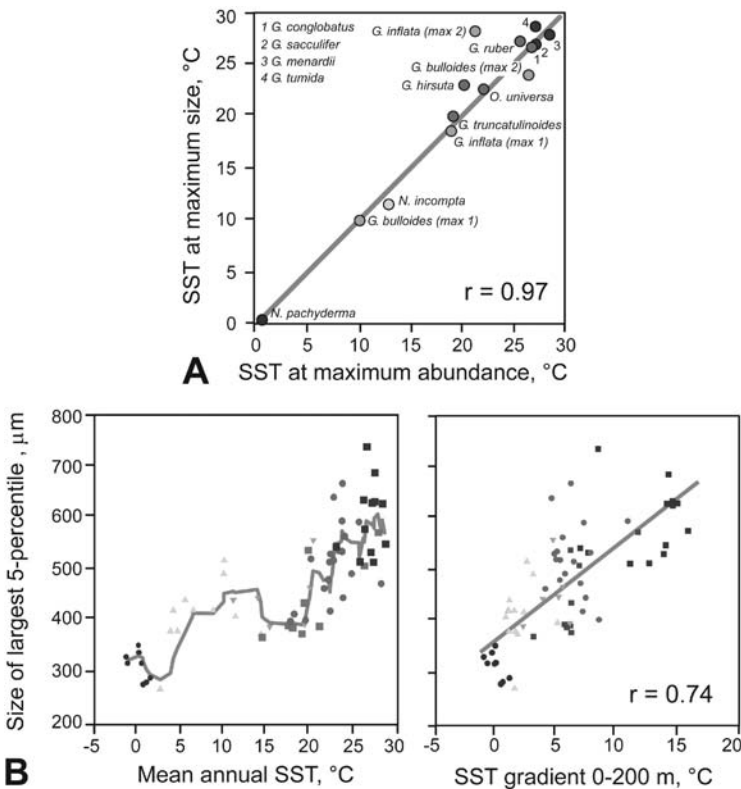


Figure 12 Relationship between shell size and temperature in planktonic foraminifera. Individual species achieve maximum size where they are most abundant (A), indicating that large size signals optimum ecological conditions. Size of the entire assemblage, expressed as the value dividing the 5% largest specimens from the rest, shows a gradual increase toward the tropics, interrupted at oceanographic fronts (B). Large assemblage size correlate with stronger vertical gradients in SST, indicating a greater number of niches. Symbols and shading distinguish samples representative of the five bioprovinces shown in Figure 5 (modified from Schmidt et al., 2004a).

of 30°S in the Indian Ocean and Hecht (1976) showed that in the North Atlantic, *G. bulloides* reach their largest sizes around 50°N, whereas in the subtropical to tropical *G. ruber*, maximum sizes occur around 10°N. The fact that temperature ranges leading to the largest size coincide with the highest relative abundance of individual species indicates that the largest size is reached under optimum environmental conditions, facilitating faster growth (Figure 12, Schmidt et al., 2004a). This model appears robust: it has been reproduced in all other oceanic basins and confirmed by laboratory experiments (Hemleben, Spindler, Breiting, & Ott, 1987; Caron, 1987a).

Malmgren and Kennett (1978a, 1978b) pioneered the use of shell size as a proxy for SST. Their records from the southern Indian Ocean (Figure 13) revealed systematic shifts in mean shell size of *G. bulloides* that followed isotopically and faunally defined glacial stages. In these records, size was negatively correlated with temperature. However, one must realize that this is only because these cores are located near the present-day ecological optimum of this species and during glacial times surface ocean conditions shifted toward colder temperatures, away from the ecological optimum. If the core was located in a water mass which was warmer than the ecological optimum of *G. bulloides*, glacial cooling would have caused the ambient water mass to appear closer to the ecological optimum, leading to larger shell sizes (Figure 13). The range of possible responses of shell size as well as assemblage size to environmental forcing has been documented and extensively discussed by Schmidt et al. (2003).

An additional factor affecting size is food availability. Intuitively, a greater availability of food particles should lead to less energy being spent on foraging resulting in faster growth. However, Schmidt et al. (2004a) showed that this relationship only holds up to an “optimum primary productivity” of about 150 gC/m²/yr. At high primary productivity, the shell size decreases. This pattern is mirrored in assemblage size range data, which show distinct minima at the position of major frontal systems (Figure 12), a finding consistent with the observation of Ortiz, Mix, and Collier (1995). Large, warm-water species are adapted to oligotrophic open ocean conditions. As discussed in the previous section, in high-productivity regimes, such species are outcompeted by generalists such as *G. bulloides*, which tend to be smaller. In sediments from the Arabian Sea, Naidu and Malmgren (1995) found a relationship between Holocene upwelling intensity and the shell size of four planktonic foraminiferal species, and speculated that this relationship may reflect changes in primary productivity rather than SST.

The study of Schmidt et al. (2003) showed that for the analyzed species, the relationship between shell size and SST remained stationary throughout the last 300 kyr. However, on evolutionary time scales, it appears that assemblage size of planktonic foraminifera followed the development of thermal gradients in the oceans and that late Neogene (including current) tropical oceans harbor unusually large planktonic foraminifera (Schmidt, Thierstein, Bollmann, & Schiebel, 2004b).

In summary, shell size is a potentially interesting variable, since it is objective, easy to determine and existing records show that it is highly sensitive to environmental forcing. Although the interpretation of the observed changes could be complex, the possibility of simultaneously analyzing several species as well as entire

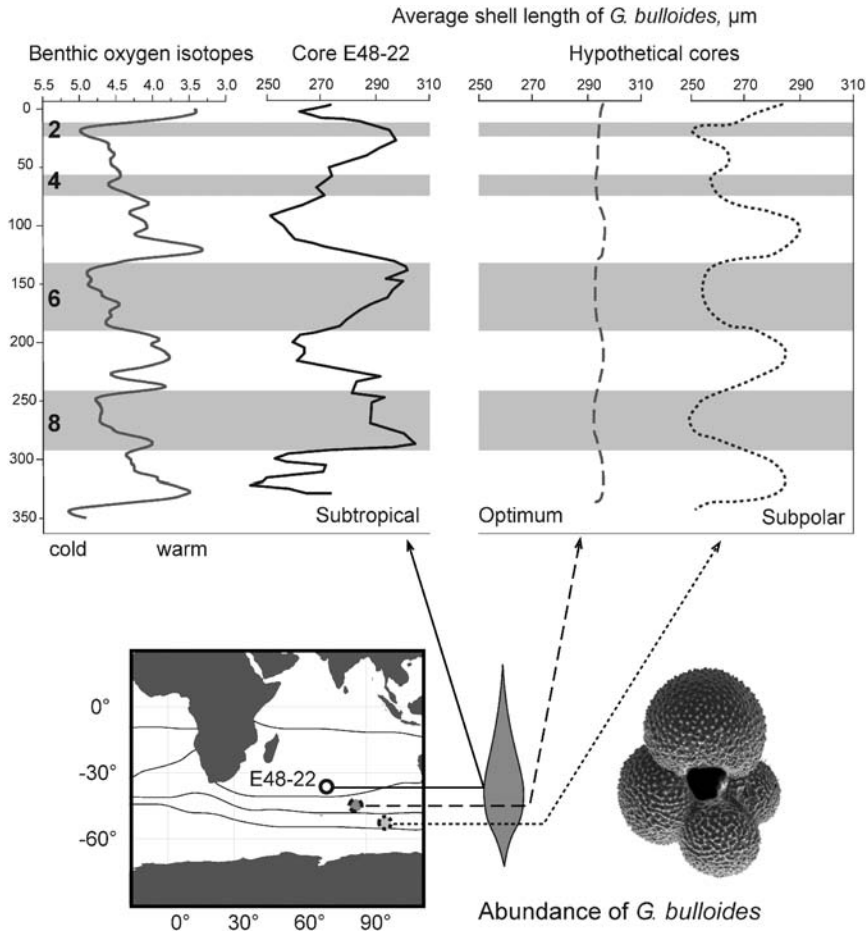


Figure 13 Variation in shell size of *G. bulloides* during the late Quaternary. The record from Core E48-22 (data from Malmgren & Kennett, 1978a, 1978b) in the subtropical province shows that larger sizes occurred during glacial periods (marine isotope stages 2, 4, 6, and 8), when the colder water masses expanded. This reflects the phenomenon that largest sizes correspond to ecological optimum: a change away from the optimum results in smaller sizes. Hypothetically, a core located near the ecological optimum would show a muted signal, whereas a core located in colder water should record largest sizes during warm intervals and smaller sizes during glacial periods. The boundaries between present-day foraminiferal bioprovinces are indicated in the map.

assemblages highlights the potential of foraminiferal shell size as a proxy for surface-water conditions throughout the late Quaternary.

3.2.2. Coiling direction

Planktonic foraminiferal shells with trochospirally arranged chambers can exhibit either dextral (right-handed) or sinistral (left-handed) coiling (Figure 14). Some species show a strong preference (bias) for either right-handed or left-handed

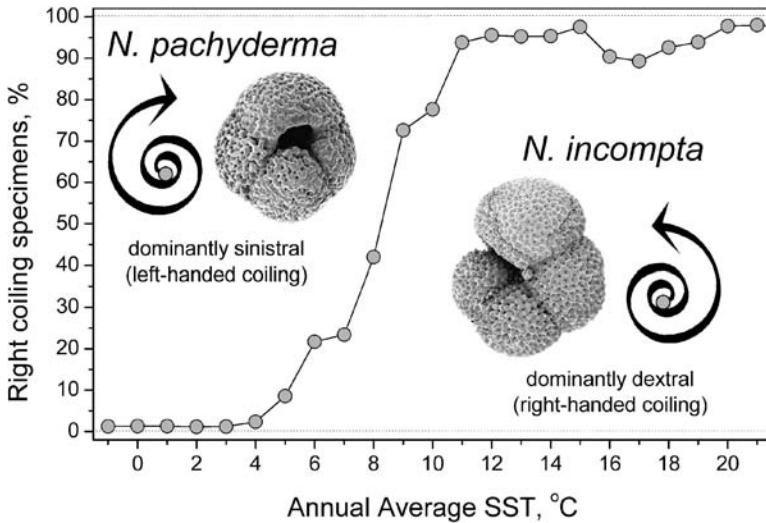


Figure 14 Changes in coiling direction of shells of the high-latitude species of *Neogloboquadrina*. The proportion of right-coiling specimens increases dramatically between 6 and 10°C, reflecting the replacement of *N. pachyderma*, which produces mainly sinistral shells by *N. incompta*, which produces mainly dextral shells (modified from Darling et al., 2006).

coiling, while other species exhibit mixed coiling proportions. Brummer and Kroon (1988) noticed that biased coiling is associated with non-spinose macro-perforate species, whereas proportionate coiling was typical for spinose species and microperforate species.

The ratio between the two coiling types of a species can vary through time and/or space. Patterns of distinct shifts in coiling preference have been recognized and quantitatively characterized among several species of modern planktonic foraminifera (Table 3). Assuming that coiling direction in such species reflected ecophenotypic response to environmental parameters, mainly sea-surface temperature (Ericson, 1959; Ericson, Wollin, & Wollin, 1954; Boltovskoy, 1973), coiling ratios became an important early tool to reconstruct past marine environments. The determination of coiling ratios is rapid, accurate, and reproducible. A census of 50–100 specimens is normally sufficient to detect environmentally significant changes in coiling direction. Useful reviews of earlier work on coiling direction in planktonic foraminifera are given in Kennett (1976), Vincent and Berger (1981), and Hemleben et al. (1989).

Ericson (1959) and Bandy (1960) developed the most widely used coiling direction proxy. It is based on the remarkably strong and consistent relationship between coiling direction and sea-surface temperature in high-latitude species of the genus *Neogloboquadrina* (Figure 14). Earlier workers explained this behavior by temperature controlling the coiling direction in a single species, *N. pachyderma*, but Darling et al. (2000, 2004, 2006) demonstrated that the pattern reflects the presence of two distinct species with opposite coiling preferences. Polar waters of both hemispheres are inhabited by *N. pachyderma*, with dominantly sinistral shells, whilst

Table 3 Coiling Direction Proxies in Late Cenozoic Planktonic Foraminifera.

Species	Application	References
<i>Neogloboquadrina pachyderma</i>	Sinistral coiling associated with cold temperatures	Ericson (1959); Bandy (1960)
<i>Globorotalia truncatulinoides</i>	Sinistral coiling associated with cold temperatures or low salinity	Ericson et al. (1954); Thiede (1971)
<i>Globigerina bulloides</i>	Holocene biostratigraphy in the North Atlantic	Pujol (1980); Zaragosi et al. (2000)
	Sinistral coiling associated with colder temperatures or higher fertility	Boltovskoy (1973); Naidu and Malmgren (1996)
<i>Globorotalia hirsuta</i>	Holocene biostratigraphy in the North Atlantic	Duprat (1983); Zaragosi et al. (2000)
<i>Pulleniatina</i> spp.	Neogene biostratigraphy of tropical Atlantic and Pacific	Saito (1976)

the dominantly dextrally coiled *N. incompta* thrives in subpolar and temperate regions (Figure 14).

Similarly, Ericson et al. (1954) noted the presence of distinct regions in the North Atlantic characterized by different coiling directions of *G. truncatulinoides*. Early interpretations of this pattern again focused on phenotypic response to water temperature, but a molecular genetic study by de Vargas et al. (2001) revealed that dextral coiling in this species is associated with one of the four distinct genetic types they identified; the remaining three types showing sinistral coiling. These recent discoveries support earlier work by Brummer and Kroon (1988), who concluded that coiling direction in planktonic foraminifera is likely to be a genetically determined binary trait and that coiling direction changes were not driven by environmental factors.

The discovery of a link between coiling preference and genetic distinction implies that any qualitative or quantitative proxy based on coiling direction in planktonic foraminifera is only applicable as long as the ecological and coiling preferences of the genetic types remain unchanged. Morphological and molecular genetic data suggest that in the case of high-latitude *Neogloboquadrina*, coiling direction can only be used as a proxy for sea-surface temperature during the last 1 Myr (Kucera & Kennett, 2002; Darling et al., 2004). In contrast, the ecophenotypic hypothesis allowed a more extensive application of the proxy throughout the geological past.

As in other organisms, the genetic control on body (shell) symmetry is not 100% efficient. Darling et al. (2006) showed that a low level (<3%) of aberrant coiling is associated with both *N. pachyderma* and *N. incompta*, indicating that coiling direction cannot be taken as an absolute discriminator among genetic types. While species

with biased coiling seem to deliver a consistent picture, the control on coiling direction in species with proportionate coiling remains unclear. Boltovskoy (1973), Malmgren and Kennett (1976), and Naidu and Malmgren (1996) showed that *G. bulloides* exhibits a significant bias toward sinistral coiling which seems to be linked to temperature. Darling et al. (2003) confirmed the presence of this bias, which does not seem to be linked to genetic distinction, but no relationship between coiling direction and temperature was observed.

In summary, shifts of coiling ratios in planktonic foraminifera species are almost certainly a signature of distinct genetic types, which are revealed through their opposite coiling directions. If such genetic types are linked to different ecological preferences, the coiling ratio can be used as a meaningful paleoenvironmental signal. The abundance of coiling types in species exhibiting systematic shifts in coiling preference should thus be recorded separately for the purpose of environmental calibration and where foraminiferal calcite is used as substrate for geochemical proxies.

3.2.3. Shape

Compared to other groups of marine microzooplankton, planktonic foraminifera show a surprisingly low diversity. However, all of the ~50 living species exhibit a remarkable degree of morphological plasticity. The origin of this morphological plasticity has been traditionally attributed to ecophenotypic response to environmental forcing. Scott (1974) and Kennett (1976) give excellent summaries of early work on planktonic foraminiferal morphology and its relationships with environmental parameters. Kennett (1968a) documented a morphological gradation in *N. pachyderma* in surface sediments from the South Pacific. Shell morphology of this species, including variables such as the number of chambers in the last whorl, was shown to follow surface ocean hydrography in the region. Malmgren and Kennett (1972) later reanalyzed the same data using multivariate statistics and identified four distinct latitudinal clusters. Similarly, Kennett (1968b) showed compelling evidence for the relationship between shell morphology and SST in *G. truncatulinoides* (Figure 15), while Hecht (1974) found that the rate of chamber expansion in *G. ruber* from the North Atlantic appears correlated with surface salinity. Malmgren and Kennett (1976) noted a systematic relationship between SST and shell compression and aperture size in *G. bulloides* from the southern Indian Ocean.

Two factors hamper the application of foraminiferal morphological variation in reconstructions of Quaternary paleoceanography. First, virtually nothing is known about the functional morphology of planktonic foraminiferal shells, and thus any environmental calibration inevitably remains a black box. Secondly, the assumption that morphological variability is linked to ecophenotypy must be supported by independent means. Although the former constraint remains, advances in molecular genetics of foraminifera have made it possible to test the latter assumption. Recent molecular genetic studies have shown a high level of genetic diversity among morphospecies of planktonic foraminifera and suggested a significant genetic component in the morphological variation of planktonic foraminiferal species. Darling et al. (2004) showed that the southern ocean is inhabited by a series of distinct genetic types of *N. pachyderma*, whose distribution follows that of the

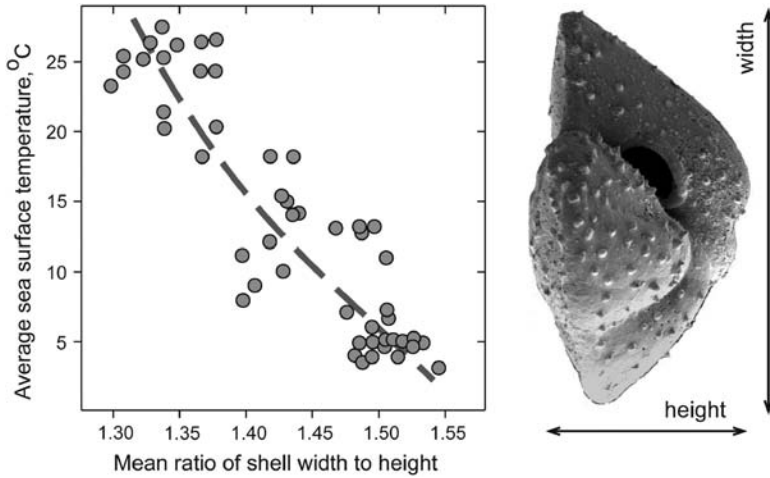


Figure 15 Variation in shell morphology of modern *G. truncatulinoides* (modified from Kennett, 1968a). The apparent ecophenotypic increase in shell height toward the tropics in fact reflects the varying proportions of four different genetic types (de Vargas et al., 2001).

morphological clusters identified by Kennett (1968a) and Malmgren and Kennett (1972). Even stronger evidence was presented in the study of *G. truncatulinoides* by de Vargas et al. (2001), who found a direct link between genetic distinction and shell morphology in this morphospecies. This discovery provides an elegant explanation for the presence of morphological and stable isotopic “subpopulations” in this species (Healy-Williams et al., 1985). Similarly, the pattern of changes in the morphology (including coiling direction) of this species in late Quaternary Atlantic sediments (Lohmann & Malmgren, 1983) can be explained in terms of habitat tracking among cryptic species with different ecological preferences (Renaud & Schmidt, 2003).

Most geochemical proxies rely on species-specific empirical calibrations. The specificity reflects the interference of metabolic processes and ecological behavior with the incorporation of chemical signals into foraminiferal calcite. If morphological variation is linked to genetic distinction, different morphotypes of planktonic foraminiferal species could be used to detect the presence of genetic diversity and assist in the interpretation of geochemical signals. This potential is not a theoretical conjunction; Bijma, Hemleben, Huber, Erlenkeuser, and Kroon (1998) found geochemical differences between the two genetically distinct types of *G. siphonifera* and recent studies link apparent intraspecific variability to different stable isotopic signatures in *G. bulloides* (Bemis, Spero, Lea, & Bijma, 2000) and isotopic and trace-element differences in *G. ruber* (Wang, 2000; Steinke et al., 2005). Both of these morphospecies are known to consist of several distinct genetic types (Kucera & Darling, 2002). Clearly, an understanding of the origin and significance of the morphological variation in individual species has a great potential for increasing the capacity of planktonic foraminifera to produce accurate and reliable information on past sea-surface conditions.

3.2.4. Wall ultrastructure

Several features of planktonic foraminiferal shell wall have been considered to be related to environmental parameters; thorough reviews of this topic are given in Kennett (1976), Vincent and Berger (1981), and Hemleben et al. (1989). Kennett (1968a, 1970) noted an increase in wall thickness of several globorotalid species in colder waters and Srinivasan and Kennett (1974) showed that surface ornament in *N. pachyderma* varied in pace with Neogene climate oscillations in temperate waters of the South Pacific. Although the final thickness of the shell wall appears to be controlled chiefly by carbonate ion concentration, both during life and after the deposition (see Section 4.2.2 “Shell weight”), the functional significance of changes in surface ornament in planktonic foraminifera remains obscure. Vincent and Berger (1981) caution against the use of surface ornament. Given the exposure of this part of the shell, and its particularly large surface-to-volume ratio, the preservation of the ornament ought to be particularly prone to dissolution. Indeed, Dittert and Henrich (2000) were able to devise an SEM-based wall-texture index for *G. bulloides* that could have been used to measure calcite dissolution intensity.

Of all properties of the shell wall, by far the maximum attention has been given to porosity. The size and frequency of pores is easy to measure and a number of studies have shown a close relationship between porosity and temperature in surface sediments both among species (Figure 16; Bé, 1968) and within species of macroperforate planktonic foraminifera (Frerichs, Heimann, Borgman, & Bé, 1972; Bé et al., 1973). Wiles (1967) and Hecht, Bé, and Lott (1976) showed that porosity could be used to trace Quaternary climatic cycles. Based on experimental observations and

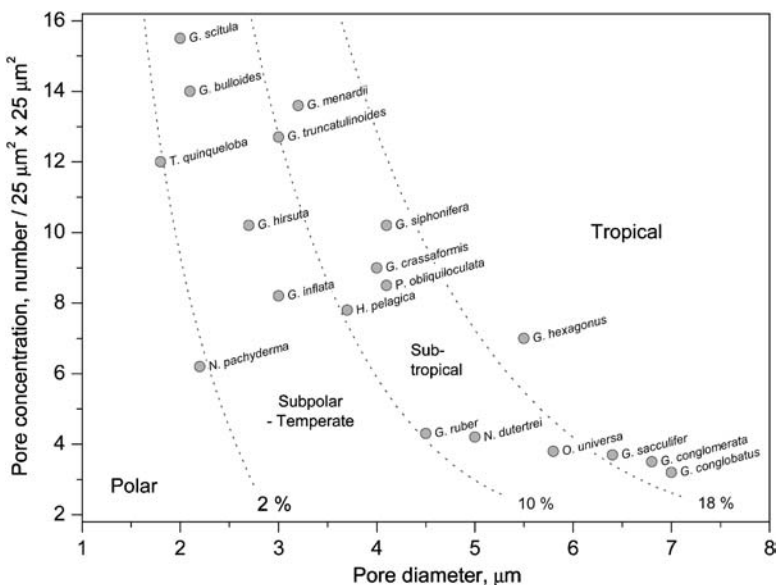


Figure 16 Variation in shell porosity among 19 macro-perforate extant planktonic foraminifera species. Tropical species show the highest porosity values whereas polar species show the lowest porosities (modified from Bé, 1968).

mitochondrial distribution (Hemleben et al., 1989), it appears that pores are related to gas exchange. This hypothesis is supported by laboratory experiments which indicate that increase in temperature correlates with larger pore diameter in *G. sacculifer* and *Orbulina universa* (Caron, Faber, & Bé, 1987a, 1987b; Bijma et al., 1990b): lower gas solubility under higher temperature promotes the growth of larger pores.

The use of shell porosity as a proxy of surface-water properties is complicated by several factors. Porosity in planktonic foraminifera changes dramatically during ontogeny (e.g., Huber et al., 1997) implying that a meaningful comparison is only possible among individuals of the same maturity. Next, calcite dissolution leads to an apparent increase in pore diameter (Bé, Morse, & Harrison, 1975), although pore density is immune to this effect. Finally, although the environmental relationship between porosity and temperature is undisputed, it is clear that some of the variation in porosity is linked to cryptic genetic diversity. Huber et al. (1997) have shown that porosity is the only morphological character discriminating genetic Types I and II of *G. siphonifera*. Interestingly, in a survey of porosity in five species of planktonic foraminifera from sedimentary samples, Frerichs et al. (1972) found no relationship between latitude and porosity in this species. Similarly, a link between shell porosity in *O. universa* (Bé et al., 1973; Hecht et al., 1976) and genetic diversity has been proposed by de Vargas et al. (1999), although this hypothesis remains to be verified by direct observations on genotyped specimens. Despite these limitations, pore properties in planktonic foraminifera in well-preserved sediments are an underestimated source of useful environmental information, particularly because of the known functional significance of these structures and the verification of environmental observations by laboratory experiments.

3.3. Planktonic Foraminifera as Substrate for Geochemical Studies

Foraminiferal calcite has been used as a passive recorder of surface-water composition, as well as for the monitoring of kinetically and metabolically mediated fractionations (Henderson, 2002). Isotopic and trace element proxies have been treated comprehensively in the reviews by Rohling and Cook (1999), Lea (1999), and Schiebel and Hemleben (2005), and are the subjects of Chapters 18, 16, and 17 of this book. The use of planktonic foraminifera as substrate for geochemical proxies increasingly relies upon a detailed knowledge of the ecology of the signal carrier (Rohling et al., 2004). It may be useful to remind ourselves of the main factors influencing the incorporation of geochemical signatures into foraminiferal shells.

The chemical composition of foraminiferal shells derives primarily from the chemistry of the ambient seawater. Proxies that are known to be passively incorporated into the shells, require knowledge of the habitat and ecology of the analyzed species. The fossil assemblage is biased toward shells deposited during the time of maximum production. Depending on the species and the ecological circumstances, a signal measured on a group of specimens may either represent the yearly average, the spring, the summer, or the autumn (Figure 6). The vertical migration pattern and depth of calcification determine what level in the water column the chemical signal represents. Size may be used to estimate the ontogenetic stage indicating what part of the vertical migration cycle the analyzed specimens represent.

Proxies monitoring kinetic or metabolic fractionations must further consider the microhabitat of the analyzed species. Symbionts alter the chemical microenvironment of the foraminifera, while changes in growth rates related to food availability or sub-optimum ecological conditions affect the rate of metabolic processes and associated fractionations. All proxies using species-specific ecology require correct identification of taxa whose behavior does not change through their geographical range. It is increasingly obvious that the presence of multiple cryptic genetic types in common species of planktonic foraminifera has been an underestimated source of noise in paleoceanographical reconstructions.

Like physical proxies, geochemical proxies can only be applied as far back in time as the relationship between species ecology and biology and the target chemical process remain stationary. Even if the metabolic or biochemical pathway responsible for incorporation of the chemical signal remains the same, any change in calcification depth or production season will alter the meaning of the reconstructed record. As we have shown in Section 3, planktonic foraminiferal species may have kept to a similar niche for several hundreds of thousands of years. Environmental calibrations derived from extant species cannot be applied to foraminifera extracted from early Quaternary and Neogene sediments, without considering the possibility of non-stationary behavior. Such applications are possible in principle, but require elaborate matching and cross-calibration of the ecology of fossil species.

4. MODIFICATIONS AFTER DEATH

4.1. Settling through the Water Column

Unlike ciliates or flagellated protozoans, planktonic foraminifera have no active means of propulsion. Their calcite shells cause negative buoyancy, which is compensated for by the production of low-density lipids or gasses during metabolism and which allows the foraminifera to control their vertical position in the water column. Subsequent to premature death or following sexual reproduction, the positive buoyancy is lost and planktonic foraminiferal shells, empty or filled with residual cytoplasm, begin to descend to the sea floor. Schiebel (2002) estimated the global export production of foraminiferal calcite at 100 m depth to 1.3–3.2 Gigatonnes/yr, equivalent to 25–50% of the total pelagic carbonate flux. Of this amount, 0.36–0.88 Gigatonnes/yr arrive on the sea floor, making up 30–80% of the deep-sea biogenic carbonate (Figure 17).

Clearly, a large amount of foraminiferal calcite is lost during settling. This loss is attributed to biogeochemical cycling in the water column. The intensity of these processes is a function of the residence time of individual shells in the water column, which is directly proportional to settling velocity. Berger and Piper (1972) conducted the first modern settling experiments, followed by the work of Fok-Pun and Komar (1983) and Takahashi and Bé (1984). Furbish and Arnold (1997) investigated in detail the effect of spine geometry on sinking. All studies show that the majority of foraminiferal shells have Reynolds numbers larger than 0.5 and that

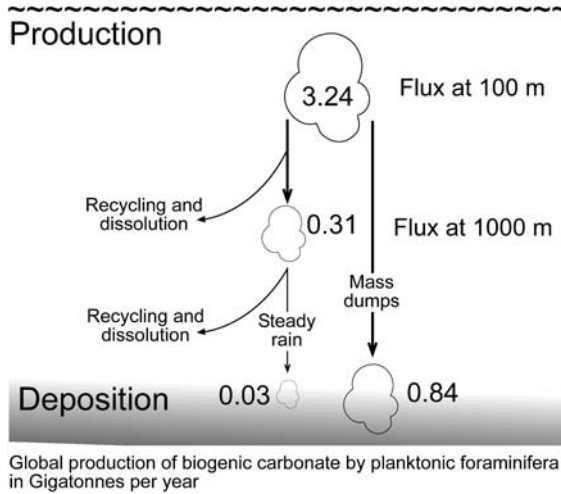


Figure 17 The contribution of planktonic foraminifera to global biogenic carbonate flux in the ocean. Note that only about one-quarter of the export flux from the surface layer is deposited on the sea floor. A majority of this carbonate is transported to the sea floor during mass deposition events (blooms). Modified from Schiebel (2002).

they consequently do not settle in the Stoke's region. Further, it was shown that the settling velocity of empty shells of planktonic foraminifera depends on the shell size, weight, shape, and presence of residual cytoplasm, and on the physical properties of ambient seawater. In general, large, spineless, gametogenic specimens are expected to sink at speeds between 500 and 3,000 m/day, i.e., reaching the sea floor within a week, while small specimens and specimens with spines sink more slowly (>200 m/day), with a residence time of two weeks or more.

The varying settling velocities of foraminiferal shells imply that the time of deposition on the sea floor, or in sediment traps, lags behind the time of reproduction and growth. Prolonged exposure during settling of small specimens leads to their preferential dissolution and disproportionate amounts of adult shells thus appear to accumulate in deep-sea sediments (Peeters et al., 1999; Schiebel & Hemleben, 2005). Schiebel (2002) argues that mass dumping of fast-settling particles during export production peaks is in fact responsible for the majority of foraminiferal shells that reach the sea floor (Figure 17). In addition, fast-sinking specimens are less likely to be expatriated during settling. Expatriation is a process of lateral advection of passively floating organisms associated with surface or subsurface currents (Berger, 1970b; Weyl, 1978) or storm events (Schiebel et al., 1995). Expatriation affects living specimens as well as empty shells and leads to an apparent expansion of the geographical ranges of species away from their ecological optima. This effect is particularly obvious in sediments deposited near major fronts or margins of biogeographical provinces. Increasing steepness of surface ocean gradients, such as during the glacial expansion of polar waters, may be manifested in unusual "mixed" faunal assemblages that may prevent environmental reconstructions using transfer functions (see Section 3.1 "Census Data").

4.2. Calcite Dissolution

The deep waters of the world oceans are undersaturated with respect to calcium carbonate (Berger, 1970a), and the decomposition of organic matter during settling and the acidic environments in predator guts create corrosive microenvironments conducive to calcite dissolution throughout the water column (Schiebel, 2002). Therefore, empty shells of planktonic foraminifera settling onto the sea floor are subject almost immediately after death to dissolution (Berger, 1971). The intensity of dissolution depends upon the final settling depth and residence time in the water column and on the sea floor. Although recent estimates suggest that only about 25% of planktonic foraminiferal shells reach the sea floor (Schiebel, 2002), the rate of water-column dissolution is too low in comparison with the rate of carbonate supply, and the weight loss to dissolution is not manifested in the carbonate content of the sediment (Berger, Bonneau, & Parker, 1982). However, several hundred meters above the calcite compensation depth (CCD), the dissolution intensity rapidly increases and begins to affect the bulk composition of the sediment in favor of insoluble constituents (clay, opal). This level is known as the foraminiferal lysocline (Berger 1970a, Figure 18). In regions with high primary productivity, degradation of excess organic carbon delivered to the sea floor causes increased CO₂ concentration in pore waters that may result in carbonate dissolution above the lysocline (Peterson & Prell, 1985; Adler, Hensen, Wenzhöfer, Pfeifer, & Schulz,

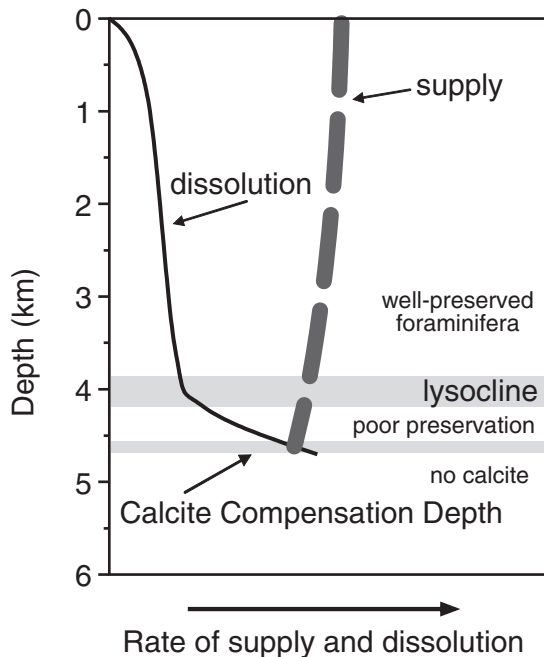


Figure 18 The relationship between calcite supply, dissolution, and preservation on the sea floor. The lysocline is defined by a sudden increase in dissolution rate, reflected by poor preservation of planktonic foraminifera in surface sediments (modified from Berger, 1970a).

2001). The position of the lysocline and the CCD reflect bottom water carbonate ion concentration, which varies in response to changes in oceanic circulation and redistribution of carbon among the main global reservoirs. Although changes in the position of the CCD cannot be effectively monitored in one sediment core, the proximity of the lysocline and the intensity of dissolution are well reflected in the preservation of planktonic foraminiferal shells. Therefore, preservation of planktonic foraminifera can be used as a proxy for bottom water chemistry and indirectly for deep circulation and carbon cycling.

4.2.1. Quantifying dissolution intensity

In order to reconstruct dissolution intensity, we need to devise an effective quantitative measure of foraminiferal preservation. Following studies by Ruddiman and Heezen (1967) and Berger (1968, 1970a) based on core-top samples from depth transects, as well as experimental investigations by Bé et al. (1975), the effects of dissolution on foraminiferal shells are well understood (Figure 19, Table 4). With increasing dissolution, the thickness of the shell decreases, corresponding to the mass of calcite lost to dissolution. Early stages of dissolution are seen as distinct etching patterns (Bé et al., 1975; Dittert & Henrich, 2000), but eventually, thinner, or more exposed parts of the shell become so weakened that the shell disintegrates into fragments. In pelagic oozes, where planktonic foraminiferal shells are the main constituent of the coarse fraction, this process leads to a gradual decrease in the sand content of the sediment. Due to the different morphology of their shells some planktonic foraminifera species are more prone to dissolution (Ruddiman & Heezen, 1967; Berger, 1968). This means that assemblages affected by dissolution are enriched in species resistant to dissolution (Table 1). This effect can be used to quantify dissolution intensity by determining the excess abundance of resistant species. Similarly, deep-sea benthic foraminifera have normally thick and smooth shells that are more resistant to dissolution than those of planktonic foraminifera and the ratio between whole shells of the two groups (the P/B ratio) decreases with

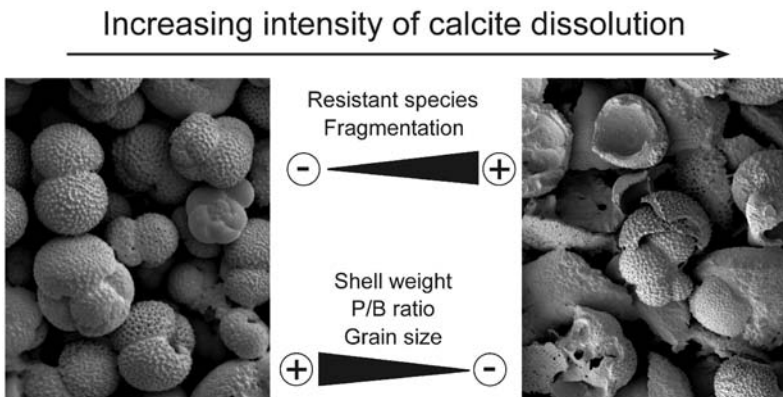


Figure 19 A well-preserved assemblage of planktonic foraminifera compared to an assemblage affected by calcite dissolution and a summary of the various effects of calcite dissolution on foraminiferal shells.

Table 4 Common Indices Used for Estimating Calcite Dissolution Intensity from Planktonic Foraminifera.

Index	Remarks
<p>Degree of fragmentation $F(\%) = 100 \times F/(C+F)$; F = number of fragments; C = number of complete shells; Berger (1970a)</p> <p>$F_{LS}(\%) = 100 \times (F/8)/((F/8)+C)$; Le and Shackleton (1992)</p>	<p>The most commonly used dissolution index, considered to be reliable and robust. Its determination is subjective and it is therefore not suitable for quantitative calibrated reconstructions.</p> <p>A modification used to improve the linearity of the relationship of the index with dissolution intensity.</p>
<p>Shell weight $\Delta\text{CO}_3^{2-} = [G. \textit{sacculifer} (355\text{--}425 \mu\text{m}) \text{ shell weight } (\mu\text{g}) - 20.27]/0.70$; Broecker and Clark (2001a)</p> <p>$\Delta\text{CO}_3^{2-} = [G. \textit{ruber} (300\text{--}355 \mu\text{m}) \text{ shell weight } (\mu\text{g}) - 12.6]/0.22$; de Villiers (2005)</p> <p>ΔCO_3^{2-} = Calcite saturation state at the sediment–water interface</p>	<p>Both calibrations are based on data from Indian and Pacific Ocean coretops and assume that all of the shell weight variation is due to calcite dissolution. Unlike fragmentation, this index is objective and thus better suited for quantitative calibration.</p>
<p>Percentage of resistant species $\text{res}(\%) = 100 \times r/(r+s)$; r = number of shells of resistant species; s = number of shells of susceptible species; Ruddiman and Heezen (1967)</p>	<p>Requires regional calibration and an <i>a priori</i> knowledge of species dissolution susceptibility. It is only sensitive at low dissolution intensity.</p>
<p>Assemblage dissolution index $\text{FDX} = \Sigma(p_i R_i)/\Sigma p_i$; R_i = rank of species i; p_i = percentage of species i; Berger (1968)</p>	<p>Requires regional calibration and an <i>a priori</i> knowledge of species dissolution susceptibility. It has a wider sensitivity range than the previous index.</p>
<p>Loss of susceptible species $L(\%) = 100 \times (1 - r_o/r)$; r_o = percentage of resistant species in an unaltered sample; r = percentage of resistant species in a sediment sample; Berger, 1971</p>	<p>Requires one unaltered sample from the investigated region and an <i>a priori</i> knowledge of species dissolution susceptibility. It is only sensitive at low dissolution intensity.</p>
<p>P/B — plankton to benthos ratio $B(\%) = 100 \times B/(B+P)$; B = number of benthic foraminiferal shells; P = number of planktic foraminiferal shells (Arrhenius, 1952)</p>	<p>Shells of benthic foraminifera are more resistant to dissolution than those of planktic foraminifera, but there are many other factors influencing the abundance of both groups. This index is robust and sensitive even at high dissolution intensity, but it can be difficult to interpret unambiguously.</p>

Source: Modified from Conan et al., 2002.

increasing dissolution. The latter can be used as a dissolution proxy only in abyssal sediments. In shallower settings, the P/B ratio is primarily controlled by food availability.

The phenomena described above have been used to devise a number of numerical or ordinal indices (Table 4). Although they may differ in their sensitivity at various intervals of the dissolution intensity range, their reproducibility, and their spatial and temporal applicability, all of these indices are often highly correlated, and the choice is thus primarily guided by the specific circumstances of each application. Below, we will discuss two measures of dissolution intensity. For a more thorough review of other indices, the reader is referred to the volume by Sliter, Bé and Berger (1975) and to the reviews in Thunell (1976), Berger et al. (1982), Hemleben et al. (1989), Dittert et al. (1999), and Conan et al. (2002).

4.2.2. Shell weight

The use of size-normalized weight of planktonic foraminiferal shells as an indicator of dissolution intensity was first proposed by Lohmann (1995); a recent review of the method is given by de Villiers (2005). Broecker and Clark (2001a, 2001b) showed that the weight loss of foraminiferal shells due to dissolution is strongly correlated with bottom water carbonate ion concentration and showed how this relationship could be used to reconstruct past ocean chemistry. The method is based on empirical calibration of bottom water carbonate ion concentration with average weight of clean, empty shells of selected species picked from narrow size ranges in core-top sample transects (Figure 20). The application of this proxy rests on the assumption that the “initial weight” of foraminiferal shells of a certain size is

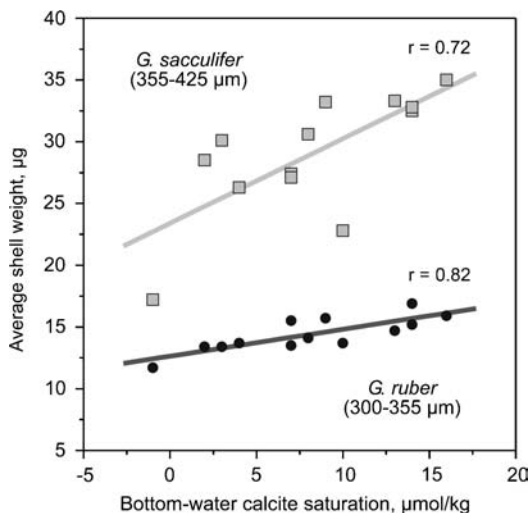


Figure 20 Progressive decrease in average shell weight of two species of planktonic foraminifera with decreasing calcite saturation of ambient bottom waters in Pacific and Indian Ocean core-top samples. The decrease in shell weight reflects gradual thinning of the shell wall. The relationship can be used to reconstruct bottom-water chemistry in the past (data from de Villiers, 2005).

constant through both time and within the geographical range of each species. However, Barker and Elderfield (2002) noticed a significant variability in the size-normalized weight of foraminiferal shells and attributed it to the influence on shell growth of carbonate saturation in the surface waters. This conclusion is supported by laboratory experiments (Spero, Bijma, Lea, & Bemis, 1997) and by glacial–interglacial shell weight variability consistent with lowered glacial atmospheric CO₂ (Barker & Elderfield, 2002).

The shell weight technique is elegant in its simplicity and potentially powerful, but one must not forget that its applicability is limited by the assumptions of the species-specific empirical relationships upon which it is based. Core-top calibrations may be valid for the modern ocean, but their application in the geological past and across evolutionary time scales is questionable. In addition, the technique is still in its infancy, and a considerable number of additional factors that potentially influence shell weight remain to be explored (de Villiers, 2004, 2005).

4.2.3. Fragmentation

The proportion between fragments and complete shells of planktonic foraminifera is the most commonly used proxy for calcite dissolution intensity. It is based on visual identification and counting of the abundance of fragments and complete shells, typically out of 300 particles. Because every researcher has to develop one's own criteria for discrimination between fragments and whole shells, the index is highly subjective and not easily reproducible. This subjectivity is particularly significant when the index is used for quantitative calibration with bottom water carbonate ion concentration (de Villiers, 2005). Nevertheless, the degree of fragmentation of planktonic foraminifera has been used in numerous studies, which indicates that in low-to-moderate dissolution regimes it represents an excellent index of calcite dissolution (Thunell, 1976; Le & Shackleton, 1992). This proxy has a number of advantages: it is rapid and simple to determine, independent of species composition of the analyzed assemblage, and as a semi-quantitative index it can be applied to pelagic sediments with planktonic foraminifera of any age.

4.2.4. Effect of calcite dissolution on foraminiferal proxies

Calcite dissolution has the potential to modify the chemical composition of foraminiferal shells and affect proxies using foraminiferal calcite as substrate. The most significant effect is seen in the Mg/Ca ratio of foraminiferal calcite. The Mg-rich carbonate phase is more soluble than pure calcite and foraminiferal shells that are subject to dissolution will thus appear depleted in Mg. This effect is discussed in detail by Brown and Elderfield (1996) and a recent review is given in Barker, Cacho, Benway, and Tachikawa (2005). A similar effect is to be expected for other trace elements, especially as many of these are not distributed evenly throughout the foraminiferal shell (Eggins, DeDecker, & Marshall, 2003, 2004). Progressive solution of outer layers can thus alter the bulk composition of the entire shell even if the studied trace element dissolves out at the same rate as Ca. Berger and Killingley (1977) showed that calcite dissolution may influence even the carbon and oxygen stable isotopic composition of foraminiferal calcite. In this case, a shift in the isotopic composition can be linked to preferential removal of outer layers of the shell that store

geochemical and isotopic signatures of the adult habitat of each species. The effects of calcite dissolution on geochemical proxies become most apparent at depths approaching the foraminiferal lysocline. At such depths, calcite dissolution must be considered as a potential source of noise in any paleoceanographic application.

The effects of calcite dissolution are not limited to geochemical proxies. Dissolution increases fragmentation and alters the size spectrum of the assemblage. In addition, the abundance of dissolution-prone species becomes gradually reduced and the residual assemblages appear to represent colder conditions (Berger, 1968; Vincent & Berger 1981; Thunell & Honjo, 1981). This phenomenon reflects the tendency of dissolution-prone species to be more common in tropical faunas (Figure 21). Although there have been attempts to compensate for dissolution-related assemblage composition bias, the best recommendation would seem to refrain from basing environmental reconstructions on samples that bear signs of moderate to severe dissolution. Although calcite dissolution has a potentially significant impact on foraminiferal proxies, it is easy to recognize and its effects are understood. Paleocyanographers are well aware of this problem and take great care to limit their studies to appropriately preserved fossil material. As a result, dissolution is rarely an issue when considering the reliability of foraminiferal proxy results.

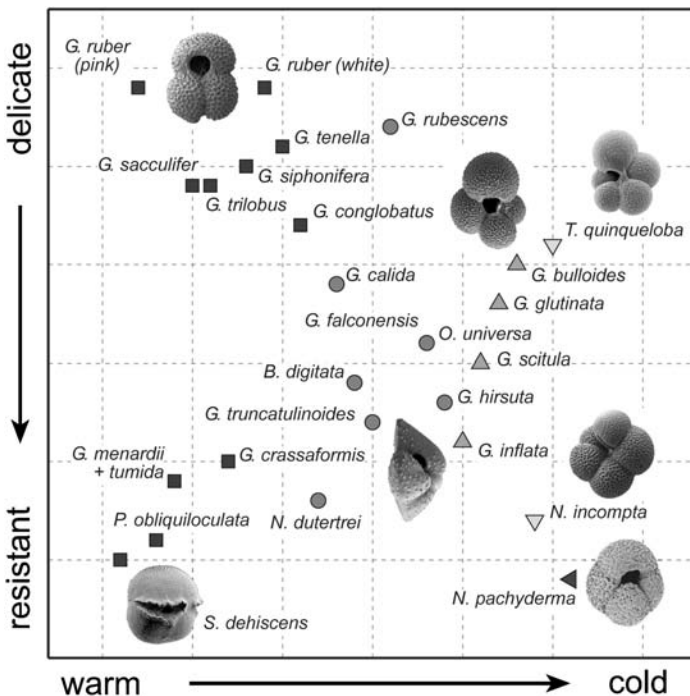


Figure 21 A comparison of temperature and dissolution susceptibility ranking of 26 extant species of planktonic foraminifera. Symbols and shading indicate species characteristic of the five foraminiferal bioprovinces as shown in Figure 5. Warm-water species tend to be delicate and easily dissolved, whereas most cold-water species are resistant (data from Figure 5 and Hemleben et al., 1989).

5. PERSPECTIVES

Planktonic foraminifera are the main provider of paleoceanographic proxies and there is every reason to believe that they will continue to represent our main source of information on the state of past oceans. The enormous research effort of the last two decades has helped to elucidate many aspects of foraminiferal life, ecology, and shell chemistry, so that the proxies we are using today are more precise and reliable than ever. At the same time, the huge progress that has been made in the research on planktonic foraminifera over the last 20 years has also helped to highlight a number of basic issues that continue to hamper the use of these organisms for paleoceanographical applications. It is especially the increasing effort to achieve a more mechanistic understanding of proxies that calls for urgent action in the three following areas:

- It is increasingly obvious that further development of geochemical proxies is only tenable if the mechanism of foraminiferal biomineralization is understood. The studies of Erez (2003) and Bentov and Erez (2005) reveal how little we know, and how many of our assumptions may need to be revised, and the necessity to clarify nanoscale mineralogy of foraminiferal shells is highlighted in the analyses made by Eggins, Sadekov, and De Deckker (2003, 2004).
- Geochemical and physical proxies alike suffer from our insufficient knowledge of the microhabitat and natural behavior of planktonic foraminifera, including the functional morphology of their shells. This ignorance is epitomized in our inability to have these organisms reproduce in laboratory cultures, a technical constraint that severely restricts work on geochemical calibrations, ecological experiments, and genetic analyses.
- As if there were not enough other issues to tackle, molecular genetics seems to have shattered the very basis of foraminiferal proxies — morphologically defined species are hiding a manifold of cryptic genetic types that appear to have distinct ecologies (de Vargas et al., 1999; Darling et al., 2004) and introduce noise into environmental calibrations (Kucera & Darling, 2002). The nature, origin, and ecological significance of this cryptic diversity have to be clarified, so that proxies requiring species-specific calibration can be adjusted and applied appropriately.

WWW RESOURCES

<http://www.emidas.org/>

The Electronic Microfossil Image Database System (EMIDAS) offers access to digital images of planktonic foraminifera and includes an annotated key to their modern species.

<http://www.maureenraymo.com/taxonomy.php>

The taxonomic plates from Bé (1977), reprinted with permission from Elsevier.

<http://www.nmnh.si.edu/paleo/foram/>

The foraminiferal site of the Smithsonian Institution, including access to the largest collection of type specimens.

<http://portal.chronos.org/>

The Chronos project provides electronic access to stratigraphic distributions of species through the Neptune database and includes excellent taxonomic tools for identification of fossil planktonic foraminifera.

<http://www.pangaea.de/Projects/MARGO/>

The MARGO project houses the definitive collection of quantitative counts of planktonic foraminifera from core-tops and last glacial maximum samples. It includes the CLIMAP data set and the Brown University Foraminiferal database.

<http://www.ngdc.noaa.gov/mgg/geology/hh1996.html>

A useful graphical compilation of the relationships between extant planktonic foraminiferal species and surface-water properties in the Atlantic and Indian Oceans, using the CLIMAP data set.

<http://www.cushmanfoundation.org/>

The official site of the Cushman Foundation for Foraminiferal Research, which publishes the *Journal of Foraminiferal Research*.

<http://www.tmsoc.org/>

The official site of The Micropalaeontological Society, which promotes research on all microfossils, including foraminifera, and publishes the *Journal of Micropalaeontology*. The site contains an excellent collection of links to online resources.

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