perhaps explaining their common occurrence in this area.

Summary

Rift propagation on scales ranging from overlapping spreading centers with a few kilometers offset up to several hundreds of kilometers at microplate tectonic scales, and indeed all the way up to several thousands of kilometers at continental rifting scales, appears to be the primary mechanism by which Earth's accretional plate boundary geometry is reorganized.

Although conceptually simple, the propagating rift hypothesis has important implications for plate tectonic evolution. It explains the existence of several classes of structures, including pseudofaults, failed rifts, and zones of transferred lithosphere, that are oblique to ridges and transform faults and thus previously seemed incompatible with plate tectonic theory. These are all quantitatively predictable consequences of rift propagation. It explains why passive continental margins are not parallel to the oldest seafloor isochrons, but instead are pseudofaults, bounding lithosphere created on propagating spreading centers and indicating the direction of the continental breakup propagators. It explains the large-scale reorganization of many seafloor spreading systems, including both the origination and termination of many fracture zones, as well as the formation of some transient microplates which appear to be the modern analogs of large-scale spreading center jumps. This hypothesis provides a mechanistic explanation for the way in which many (if not all) spreading center jumps occur and why they occur in systematic patterns. It explains how spreading centers reorient when the direction of seafloor spreading changes, and the origin of large areas of petrologically diverse seafloor, including the major abyssal ferrobasalt provinces. The common occurrence of rift propagation over a wide range of spreading rates and tectonic environments indicates that it represents an efficient mechanism of adjustment of extensional plate boundaries to the forces driving plate motions.

See also

Mid-ocean Ridge Geochemistry and Petrology. Mid-ocean Ridge Tectonics, Volcanism and Geomorphology.

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PROTOZOA, PLANKTONIC FORAMINIFERA

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doi:10.1006/rwos.2001.0192

Introduction

Planktonic foraminifers are single celled organisms (protozoans) sheltered by a test (shell) made of calcite, with an average test diameter of 0.25 mm. They

live in surface waters of all modern open oceans and deep marginal seas, e.g., Mediterranean, Caribbean Sea, Red Sea, and Japan Sea, and are almost absent from shelf areas including the North Sea and other shallow marginal seas. Planktonic foraminifers constitute a minor portion of the total zooplankton, but are the main producers of marine calcareous particles deposited on the ocean floor and form the so-called 'Globigerina ooze.'

Planktonic foraminifers (Greek: foramen = opening, ferre = carry) first appeared in the middle Jurassic, about 170 million years ago (Ma), and spread since the mid-Cretaceous over all world oceans. Times of main appearance of new species in the Aptian (120 Ma), the Turonian (90 Ma), the Paleocene (55 Ma), and the Miocene (20 Ma), alternate with phases of main extinction in the Cenomanian (95 Ma), at the Cretaceous/Tertiary boundary (60 Ma), and in the Upper Eocene (40 Ma). Modern planktonic foraminifers have evolved since the early Tertiary, when first spinose species occurred directly after the Cretaceous/Tertiary boundary. Approximately 450 fossil and 50 Recent species are known, not including species based on molecular biology investigations. The appearance and radiation of new species seem to correlate with the development of new realms and niches, linked to plate tectonics and paleoceanographic changes. The geographical distribution and main events in planktonic foraminiferal evolution are associated in general with water mass properties, e.g., availability of food or temperature. The reproductive strategies depend highly on their life habitat in the photic zone or slightly below. The life span of planktonic foraminifers varies between 14 days and a year, mostly linked to the lunar cycle. Most living species bear symbionts requiring a habitat in the upper to middle photic zone. Their feeding habit depends on the spinosity (spinose versus nonspinose species) in respect to the size and class of prey. Predators that are specialized on planktonic foraminifers are not known.

History

With the technological improvement of microscopes d'Orbigny in 1826 was able to describe the first planktonic foraminiferal species, *Globigerina bulloides*, from beach sands, and classified it as a cephalopod. In 1867 Owen described the planktonic life habit of these organisms. Following the Challenger Expedition (1872–1876) the surface-dwelling habitat of planktonic foraminifers was recognized. Rhumbler first described the biology of foraminifers in 1911. In the first half of the twentieth century, foraminifers were widely used for stratigraphic purposes, and many descriptions were published, mainly by Josef A. Cushman and coworkers. Studies on the geographic distribution of individual foraminiferal species are based on samples from the living plankton since the work of Schott in 1935. Planktonic foraminifers have been used since the beginning of the twentieth century to date marine sediments drilled by oil companies, and later on obtained through the Deep-Sea Drilling and Ocean Drilling Programs. In addition, extensive studies on distribution, ecology of live and fossil faunas were carried out to understand the changing marine environment. The ecological significance has been applied in paleoecological and paleoceanographic settings and yielded subtle information on ancient oceans and the Earth's climate. Recent investigation still focuses on evolution and population dynamics. Modern techniques, e.g., polymerase chain reaction (PCR), are being used to reveal the genetic code, and their relation to morphological classification tests needs to be checked.

Methods

Planktonic foraminifers are sampled from the water column by plankton nets of various design, with a mesh size of 0.063–0.2 mm, by employing plankton recorders, water samplers, pumping systems, or collection by SCUBA divers. To study faunas from sediment samples or consolidated rock, the surrounding sediment has to be disaggregated by hydrogen peroxide, tensids, acetic acid (pure), or physical methods, and washed over a sieve (0.03–0.063 mm). Shells may be studied under a binocular microscope, or with a scanning electron microscope for more detail. Transmission electron microscopy is suited to the study of cytoplasm at high resolution. Some species have already been cultivated under laboratory conditions. For faunistic analysis live and dead specimens are distinguished by their content of cytoplasm. For statistical significance on average 300 individuals have to be classified and counted.

According to the distribution and ecology of modern planktonic foraminifers, and due to the fact that their calcitic tests contribute substantially to the microfossil faunal record of marine sediments, planktonic foraminifers are used in reconstructing the climatic, ecological, and geological history of the Earth. Physical factors that determine the modern faunal composition are related to the fossil assemblages by multiple regression statistical techniques (transfer functions) to yield a confident estimate on ancient environmental parameters.

Stable isotopic ($^{18/16}O$ and $^{13/12}C$) and trace element ratios of the calcareous (calcite) shell display mostly the composition of the ambient water. These so-called proxies of the physical, chemical, and biological state of modern and ancient oceans are used to reconstruct productivity, temperature, and salinity of paleo-water masses, and to determine the relative age of marine sediments. Laboratory experiments and field calibration are carried out for synoptical evaluation of physical and chemical controls over the geochemical composition of foraminiferal calcite. The metabolic fractionation of isotopes (vital effect) that are included in the foraminiferal shell, varies between species, and depends on water temperature and carbonate (CO_3^{2-}) concentration. The radioactive ^{14}C isotope gives an absolute age of the shell, limited to the last approximately 40 000 years.

Molecular biology methods have recently been used to investigate foraminiferal rRNA genes (rDNA) after DNA extraction, amplification by PCR and normally automated sequencing.

Cellular Structure

Planktonic foraminifers have a single cell that builds calcareous shells and forms chambered tests. Chamber formation, resulting from deposition of calcite, takes place within a cytoplasmic envelope produced by rhizopodia that also secrete a primary organic membrane. A calcitic bilamellar wall is formed at the primary organic membrane. The only exception is the monolamellar genus *Hastigerina* (**Figure 1**). The proximal side of the POM consists of two to three calcite layers whereas the distal (outer) layer reveals as many layers as there are chambers. Layered pustules are built within the outer layers of the wall, concurrent with successive stages of calcite lamination. Spines are not layered and are lodged as plugs within the wall.

Intrashell cytoplasm is differentiated from a reticulate or rhizopodial type on the outer shell. Planktonic foraminiferal cell organelles, e.g., nucleus, mitochondria, peroxisomes, Golgi complex, endoplasmic reticulum, annulate lamellae, vacuolar system (**Figure 2**), are typical of those observed in other eukaryotic cells. A fibrillar system seems to be unique among known protozoa, and is suspected to be a floating device or calcifying organelle. Food in the form of lipids and starch is stored in special vacuoles.

Chambers are connected by openings (foramen) between them and have sealed pores in the chamber wall which faces the external environment. Gas exchange between cell and the ambient sea water takes place through these pores; the aperture(s) serves for cytoplasmic contact with the surrounding water, mainly to exchange food particles and waste products. Different types of spines, pores, wall structures, and test morphology may adapt the species to certain environments and are of taxonomic significance. Spines allow anastomosing cytoplasm to stretch far out of the test, to form rhizopodial nets for capturing prey, and to carry prey and symbionts as on a conveyor belt to support the cell.

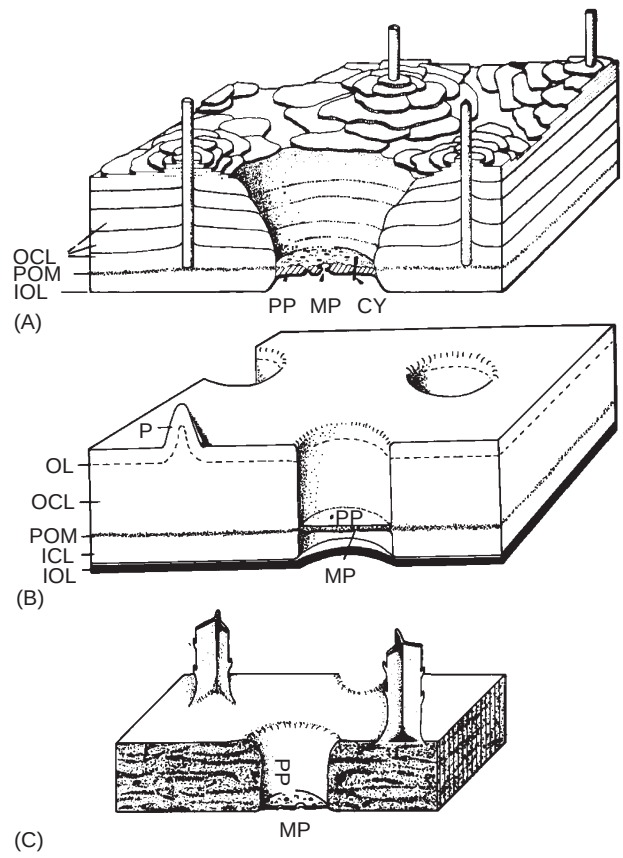

Figure 1 Schematic diagrams of wall structures and pores in bilamellar spinose (A), bilamellar nonspinose (B), and monolamellar (C) planktonic foraminifera (courtesy Cushman Foundation). CY, foraminiferal cytoplasm; ICL, inner calcite layer; IOL, inner organic lining; MP, micropore; OCL, outer calcite layer; OL, outer organic layer; POM, primary organic membrane; P, pustule; PP, pore plate.

Reproduction and Ontogeny

Planktonic foraminifers probably display only sexual reproduction without the diploid generation. Shallow-dwelling species have been shown to reproduce once per month (*Globigerina bulloides*), or within two weeks (*Globigerinoides ruber*), triggered by the synodic lunar cycle. During reproduction

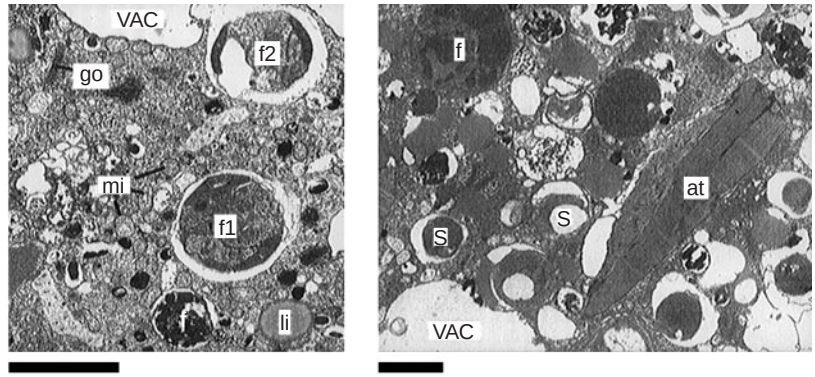

Figure 2 Transmission electron microscopical sections of *Globigerinella siphonifera* cytoplasm including cell organelles. at, animal tissue; f, food vacuole; f1, food vacuole including fresh green algae; f2, food vacuole including partly digested green algae; go, Golgi complex; li, lipid droplet; mi, mitochondria; s, symbiont; vac, empty vacuole. Scalebar = 3 μm.

adults release gametes (several hundred thousand) to form offspring with a first calcified chamber (proloculus), which is 8–34 μm in size. The prolocular ontogenetic stage consists of a first (protoconch) and second chamber (deuteroconch). First juvenile chambers are formed on a subdaily rate. During ontogeny the rate of chamber formation gradually decreases. The neanic stage is marked by substantial changes in morphology, and occasional changes in selection of diet and depth habitat, which might explain the relative enrichment of $\delta^{13}C$ with increasing test size. Maturity is reached when the adult stage is reached and tests consist of 10–20 chambers, with a size of 0.1–2 mm (about 0.25 mm on average). The terminal stage is related to reproduction and marked by chamber alterations such as shedding of spines and partial wall thickening. The empty adult test sinks towards the seafloor forming the 'Globigerina Ooze.'

Symbionts, Commensals, and Parasites

Species that bear symbionts (mostly spinose species) are bound to light and live in the euphotic zone of the ocean. Some species without symbionts live in the deep ocean, and only ascend to the sea surface once a year to reproduce (e.g., *Globorotalia truncatulinoides*). Symbionts associated with spinose (**Figure 3**) and occasionally with nonspinose species are dinoflagellates and chrysophycophytes, which may contribute photosynthetic compounds to the host and provide energy to drive the calcification process. This is especially important for the use of $\delta^{13}C_{SHELL}$ in paleo-reconstructions because the $\delta^{13}C$, among other parameters, is determined by the symbiont activity, which is directly correlated to the light level in the water column.

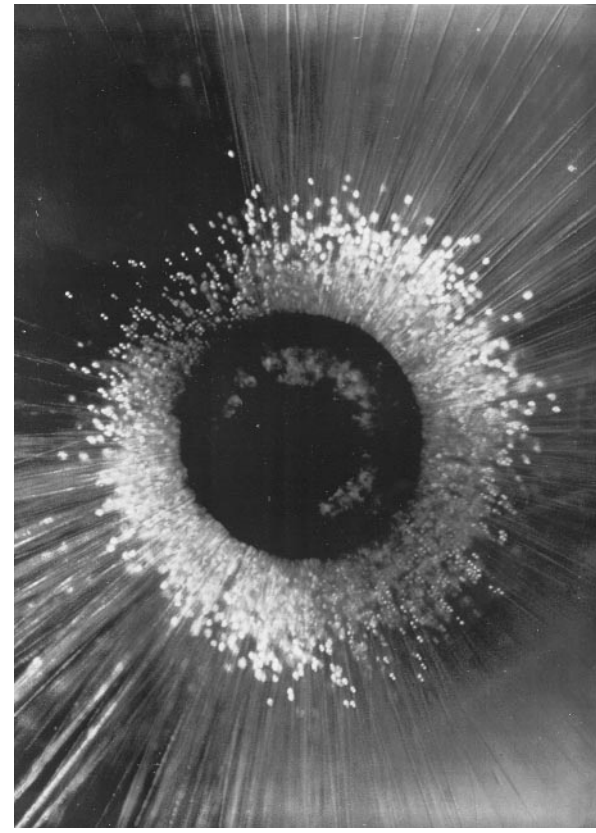

Figure 3 Spinose planktonic foraminifer *Orbulina universa*. Spines allow cytoplasm to stretch far out of the test, to form a rhizopodial net. Symbionts are carried out by cytoplasm streaming during the light period, and are withdrawn into the test during darkness. Diameter of the test is about 0.5 mm (without spines).

Commensalistic dinophytes acquire nutrients as metabolic by-products from the host. Parasites, such as sporozoans, may dart in and feed on foraminiferal cytoplasm.

Molecular Biology

Most recently, methods widely used in molecular biology have also been applied to planktonic foraminifers. A general question is based on the bipolar distribution of the group, and the genetic relationships of species in both hemispheres, especially those clearly distributed in both arctic and antarctic cold waters. Species diversity, based on molecular genetics, is greater than would be expected by applying the traditional concept of morphotaxa. This points towards a larger variety of genetically defined populations, which may permit these to be classified as cryptic sibling species. In addition, the most recent results indicate a polyphyletic origin linked to benthic foraminifers. The molecular methods being used explore the small and large subunits of ribosomal DNA (SSU and LSU rDNA) sequence variability. The results achieved by these molecular methods are manyfold and as yet cannot be explained consistently. However, the large potential of this new field will certainly aid in unraveling the distribution pattern, ecological adaption, speciation, and phylogeny of planktonic foraminifers.

Trophic Demands

Planktonic foraminifers are basically omnivorous. Spinose species prefer a wide variety of animal prey, including larger metazoans such as copepods, pteropods, and ostracods. Cannibalism has also been reported and bacteria are suspected to form part of the diet. Nonspinose species are largely herbivorous. However, in addition to diatoms, which seem to be the major diet, dinoflagellates, thecate algae, and eukaryotic algae, and also muscle tissue and other animal tissue has been found in food vacuoles. The position of planktonic foraminifers in the marine food web is, therefore, different compared to other protozoans, and occasionally ranges above the basic level of heterotrophic consumers. Predators specialized on planktonic foraminifers are not known, but tests have been found in pteropods, salps, shrimp, and other metazooplankton. Species are spatially and temporally distributed according to diet and temperature and are sensitive to environmental impacts.

Ecology and Distribution

Different faunal groups are characteristic of various oceanic realms. Species are bound to their typical depth habitat in the water column, permitting separation of potentially competing species, and faunal composition changes on a temporal and spatial scale. The vertical separation of the habitats of different species is more evident in warmer than in colder waters; physical and biotic conditions between the sea surface and bathyal depth vary more in subtropical and tropical regions than at high latitudes. Faunal provinces roughly follow a latitudinal pattern, displaying the water temperature and salinity. However, on a finer scale the amount and quality of light, turbidity of the ambient water, trophic state, and distribution of predators play an important role. Only two Recent species (*Neogloboquadrina pachyderma* and *Turborotalita quinqueloba*) are frequent in polar regions. In general, assemblages of planktonic foraminifers occur in five major faunal provinces: (1) polar, (2) subpolar, (3) transition, (4) subtropical, and (5) tropical. Faunal mixing occurs due to hydrodynamic features (e.g., upwelling or current systems) and additional provinces are (6) upwelling, (7) subtropic/tropic, and (8) transitional/subpolar (**Figure 4**). Special environments like the upwelling of nutrient-rich water masses are characterized by high numbers of *Globigerina bulloides*. Typical faunas exist along the margins of the subtropical gyres and at hydrographic frontal systems. The highest diversity is recorded from temperate to subtropical waters (**Figure 5**). A seasonal distribution pattern of planktonic foraminifers is most pronounced in high and midlatitudes, displaying the phytoplankton succession and associated food chain. Due to meso-scale and local features and a certain reproduction pattern, the distribution of planktonic foraminifers is patchy on various temporal and spatial scales.

The highest numbers (> 1000 specimens per m^3) of adult tests (> 0.1 mm) are recorded in areas and during times of highest primary production, which are upwelling areas and seasonal blooms in the temperate and polar oceans (**Figure 6**). High numbers of individuals correlate with maximum amounts of chlorophyll in the upper ocean and to the deep chlorophyll maximum at the base of the surface mixed layer of the ocean. In the mesotrophic to oligotrophic ocean 1–50 specimens per m^3 occur, and from blue waters (e.g., eastern Mediterranean) less than one specimen per m^3 is reported.

Sedimentation

Global calcite production of planktonic foraminifers amounts to about two Gigatons per year, from which only 1–2% reaches the deep sea floor. Planktontic foraminiferal shells dissolve while settling through the water column. Preservation of tests depends on the biogeochemistry of the ambient water and on the resting time of tests in the water column. Due to the low sinking velocity and long time of

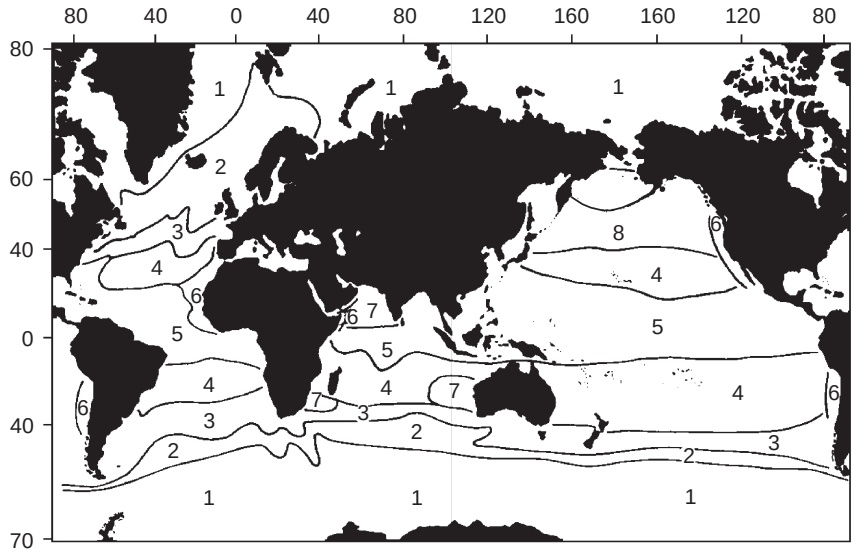

Figure 4 Foraminiferal provinces. 1, polar; 2, subpolar; 3, transitional; 4, subtropic; 5, tropic; 6, upwelling; 7, subtropic/tropic; 8, transitional/subpolar (after Hemleben *et al.*, 1989).

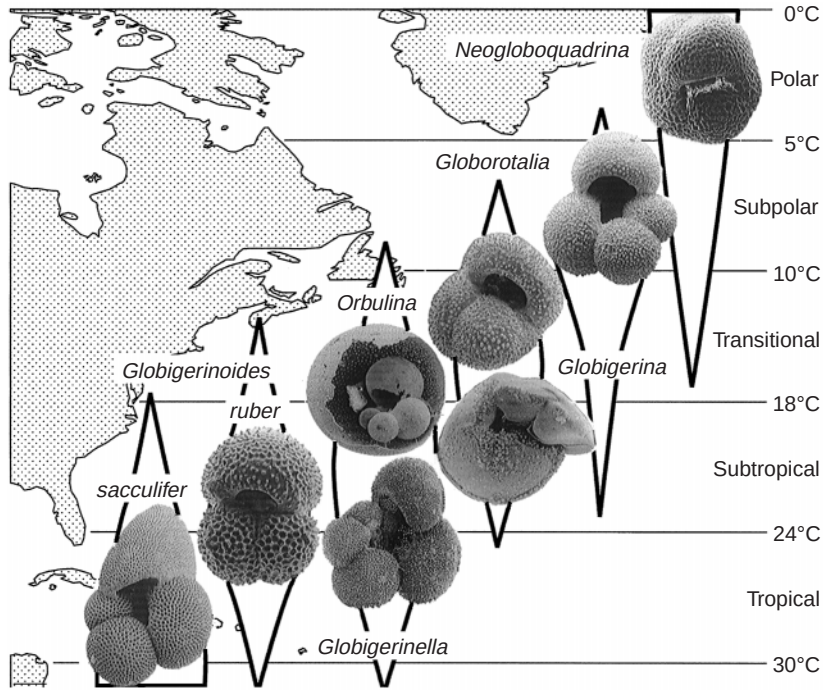

Figure 5 Schematic distribution pattern of modern planktonic foraminifers exemplified for the North Atlantic (according to Hemleben *et al.*, 1989). Species from the lower left to the upper right are *Globigerinoides sacculifer*, *Globigerinoides ruber*, *Globigerinella siphonifera*, *Orbulina universa* (spherical stage cracked open to show the interior preadult test), *Globorotalia truncatulinoides*, *Globorotalia inflata*, *Globigerina bulloides*, and *Neogloboquadrina pachyderma*.

exposition, small and thin-walled tests (about 100 m per day) are preferentially removed from the settling assemblage, and mainly large and fast sinking tests (up to 1500 m per day) are deposited at the seafloor. Mass sinking of aggregates (marine snow) during seasons of enhanced biological productivity includes planktonic foraminiferal test, which balances the fossil faunal record towards species assemblages that reflect high productivity, e.g., seasonal upwelling and spring blooms (**Figure 6**). A substantial amount of planktonic foraminiferal shells is remineralized far above the calcite lysocline, between 200 and 700 m water depth. Below the calcite compensation depth virtually no calcareous particles are preserved.

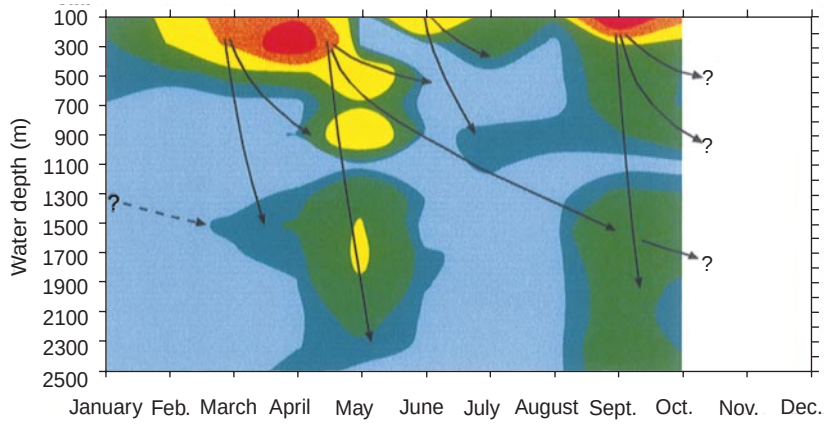

Figure 6 The calcite flux of planktonic foraminiferal shells from the upper water column to the deep sea is determined by population dynamics and settling velocity of empty tests. In the eastern North Atlantic maximum standing stocks of more than 400 specimens per m^3 occur in the upper 300 m during the phytoplankton spring bloom (March through May). A minor maximum in abundance during fall (September to October) is due to redistribution of chlorophyll and entrainment of nutrients and resulting phytoplankton growth in surface waters. During summer and winter the number of specimens may not exceed 10–50 per m^3. Most species live in surface waters. Only a few species live at a depth of 100–500 m. Abyssal species are rare in the transitional North Atlantic and more frequent in the subtropical realm. As a result of population dynamics and differential settling velocity of tests (100–1500 m day^{-1}), the test flux occurs in pulses (arrows), being highest during spring and fall exceeding 60 mg $m^{-2} d^{-1}$ (red; orange = 30–60; yellow = 10–30; dark green = 3–10; light green = 1–3; blue = < 1 mg $m^{-2} d^{-1}$). Remineralization of tests is highest between 200 and 700 m depth. Below 700 m major $CaCO_3$ flux is restricted to mass sinking events during high-productivity periods. November and December have so far not been sampled.

Application

As major contributors to the vertical $CaCO_3$ flux, planktonic foraminiferal shells cause a substantial portion of $CaCO_3$ burial in deep-sea sediments. As a component of the marine carbon turnover and vertical flux, planktonic foraminifers are of major interest for paleoclimatologists, because their tests carry fossil information on climates since the mid-Cretaceous. Their faunal composition, details of the test morphology, and their stable isotope and element ratios, provide detailed information on paleotemperature ($\delta^{18}O$, Mg/Ca, Sr/Ca, $\delta^{44}Ca$), paleoproductivity ($\delta^{13}C$), paleo-pH ($\delta^{11}B$), nitrate (NO_3^-) concentration of seawater ($\delta^{15}N$), and paleo-CO_2 levels by estimating the vertical flux and burial rates of $CaCO_3$ of planktonic foraminiferal and other marine calcite-sequestrating organisms (mainly coccolithophorids and pteropods). Their role in the marine and global carbon budget which still needs to be quantified, provides great potential information on marine biogeochemistry.

See also

Benthic Foraminifera. Calcium Carbonates. Conservative Elements. Plankton and Climate. Freshwater Transport and Climate. Geophysical Heat Flow. Large Marine Ecosystems. Marine Snow. Pelagic Biogeography. Protozoa, Planktonic Foraminifera. Upwelling Ecosystems.

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