LIFE HISTORY OF FORAMINIFERA: STABLE ISOTOPIC AND ELEMENTAL PROXIES*

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ABSTRACT

Foraminifera are morphologically and ecologically a most diverse group of single-celled organisms. They have been major constituents of the marine biomass as observed in the modern seas and in the marine rock records of the Phanerozoic times. For practical reasons, the biology and life history of foraminifera is not known in detail, particularly for a vast number of extinct species that have no living representatives for comparison. Coincidentally, the mineralized shells of foraminifera preserve the records of life conditions and life history of the organism. The incorporation of stable isotopes and trace elements in foraminiferal shells is known to be dependent on physical and chemical conditions of the ambient environment and biological processes of the organism. These geochemical data may therefore act as proxy of life conditions and life history including temperature of the habitat, temperature tolerance, reproduction, depth distribution, life span, calcification and photosymbiosis. It must be emphasized that the stable isotopes and trace elements in foraminiferal carbonate should be first understood well in modern foraminiferal taxa before using them as proxy data in palaeobiology. Improvements in analytical techniques, higher sampling resolution and better understanding of biomineralization processes are opening new possibilities in palaeobiological research in foraminifera.

Keywords: Foraminifera, Life history, stable isotopes, Mg/Ca ratio

INTRODUCTION

Foraminifera are remarkably diverse group of microscopic life belonging to single-celled protista. They occupy various niches of modern oceans and often form the bulk of the sediments in deep sea and in tropical coral reef settings. Over 55% of the Arctic biomass and over 90% of deep sea biomass in modern oceans are composed of foraminiferid tests (Armstrong and Brasier, 2005, p. 142). They were equally widespread in the geologic past since the Cambrian times and episodically formed thick sequences of limestone including the fusulinid limestone in Permian and nummulitic limestone in Eocene. The early micropalaeontological studies largely focused on the biostratigraphy of foraminifera. Although the biology of this group of micro-organism is somewhat better understood today due to several observations in natural environments and laboratory cultures, most aspects of foraminiferan biology are still not known (Lee and Anderson, 1991). It is particularly true for the fossil taxa which have no living representatives. For living forms too, there are limitations of making direct observations in the natural habitat and laboratory culture and, therefore, proxy data need to be used in the interpretation of life history and palaeobiology of foraminifera.

Urey et al. (1951) for the first time demonstrated that oxygen isotopic composition of *Belemnite* shells hold the key to seasonal cycles of temperature and as a result the life span of the organism can be inferred. This led Emiliani (1954, 55) to analyze oxygen isotopic composition of foraminifera from deep sea cores to infer Pleistocene temperature, establish the cyclic nature of Pleistocene glaciations and infer the depth habitat of planktic foraminifera. A number of workers since then have tried to study the stable isotopic composition of foraminifera and to relate it with seawater temperature, depth habitat, life cycle, food and symbiosis. The past decade has also seen a large number of research contributions on trace element compositions of biogenic carbonates, particularly corals and foraminifera. These studies have provided considerable information about the dependence of trace elements on environmental and biological factors (Lea, 1999; Raja et al., 2005, 2007). This paper discusses how stable isotopic and trace element composition of shells can be used as proxy of palaeobiology of foraminifera.

BIOLOGY AND CALCIFICATION

Foraminifera are characterized by a protoplasmic mass, differentiated into ectoplasm and endoplasm. The ectoplasm surrounds the test as thread-like or branching extensions, called pseudopodia. The organism uses pseudopodia for several life functions including capture of food, digestion, locomotion and construction of the test. Nutrition is obtained in various ways, although direct observations are largely limited to shallow water species and in laboratory cultures where they are mostly found to feed on algae. Suspension feeding, scavenging, uptake of dissolved organic matter and symbiosis are other methods of intake of food.

Some of the benthic and planktic foraminifera harbor algae in their cytoplasm. A variety of algae are found as symbionts including diatoms, chlorophytes, rhodophytes and dinoflagellates (Table 1). Foraminifera obtain all or part of their nutritional requirements from the endosymbionts. The symbiont photosynthesis helps in calcification and it is seen that the rate of calcification of the test is directly related to the rate of photosynthesis. Algal symbiosis is energetically advantageous in oligotrophic environment (Hallock, 2000) and the host–microalgae system benefits both the partners.

The life cycle of foraminifera is known to alternate between a sexually reproducing gamonts and asexually reproducing agamont generations. In some species, a third generation, schizont, is introduced between agamont and gamont although the succession of three generations is not obligate and foraminifera may undergo repetitive asexual generations before

Representative Genera	Symbiont Type
Benthic: *Peneroplis*	Unicellular red alga
Benthic: *Archaias, Cyclorbiculina, Androsina*	Chlorophyte
Benthic: *Sorites, Amphisorusi, Marginopora*	Dinoflagellate
Planktic: *Globigerinoides, Orbulina*	
Benthic: *Alveolinella, Borelis, Amphistegina,*	Diatom
Calcarina, Baculogypsina, Nummulites,	
Operculina, Heterostegina, Cycloclypeus	
Planktic: *Candeina, Pulleniatina,*	Chrysophyte
Hastigerina, Globorotalia, Neogloboquadrina,	
Globigerina	

producing sexually reproducing gamonts. The lifespan of foraminifera is variable from a few days to a few years. The typical lifespan of planktic foraminifera is two to four weeks and larger benthic foraminifera live for a few months to two years.

The test of foraminifera consists of one or more chambers, separated by a septum. During construction of chambers, foraminifera form a protective cyst by pseudopodia that is fixed temporarily at some distance from the apertural face and an organic template is constructed at the site of the future wall (Hottinger, 1986). Mineralization of the shell takes place on the organic template. In agglutinated foraminifera, the pseudopodia collects assorted grains from the surrounding environment and the grains are glued to the organic template but in hyaline and porcelaneous groups precipitated calcite is used for test construction.

The parent solutions for calcification in foraminifera are ambient seawater and cell-derived fluids (Bentov and Erez, 2006). Two modes of calcification are observed. In porcelaneous fora- minifera, the crystals are precipitated within intracellular vesicles and then carried to the site of chamber formation (Angell, 1980) and in radial hyaline foraminifera the precipitation is *in situ* and occurs in extra-cellular confined space (Angell, 1979). Experi- mental studies in recent years are refining our knowledge about biomineralization mechanisms in foraminifera. A novel experi- ment by Bentov and Erez (2005) has shown that in *Amphistegina lobifera*, a perforate foraminifera, the wall is composed of layers of calcite of different composition – a thin, primary layer of high- Mg calcite and inner and outer lamellae of low-Mg calcite on the two sides of the primary layer. Most of the modern foraminifera have bilamellar walls of this kind in which organic template is calcified both externally and internally.

Symbionts play an important role in calcification of symbiont-bearing benthic and planktic foraminifera. Rottger *et al.*(1980) noted that the growth rates of *Heterostegina depressa* and *Amphistegina lessonii* increased with the intensity of light and the optimal light intensity for growth was 400 – 800 lux. The growth stopped in dark but it continued without food when incubated in light. In another experiment, Duguay (1983) measured calcium incorporation and carbon fixation by microalgal symbionts in *Archaias angulatus, Sorites marginalis* and *Cyclorbiculina compressa* and found that the rates of calcification increased with the intensity of light and algal symbionts stimulate carbonate production.

PROXIES OF LIFE HISTORY

The life history of living foraminifera can be observed directly in their habitats and in laboratory cultures. Practically,

however, it is not possible to make observations in the entire spectrum of foraminiferal habitats, nor is it possible to simulate all environmental parameters of the habitats in laboratory. It is further challenging for a large number of fossil foraminifera in geological archives for which there is no living representatives. In such cases, it is indirectly inferred by proxies such as morphology and geochemical composition of the test. The oxygen and carbon isotopes and trace elements are incorporated directly from seawater during the process of precipitation of foraminiferal calcite. The skeletal composition reflects not only the seawater composition but also the physical and biological conditions prevailing at the time of the construction of the test. Several aspects of life history can be understood by stable isotopic and minor and trace element composition of the tests. These include temperature of the habitat, temperature tolerance, reproduction, depth distribution, lifespan and photosymbiosis. The temperature tolerance, relative depths of habitat, temperature and depth at which reproduction takes place and life span of individuals can be inferred directly or indirectly by temperature proxies such as $\delta^{18}O$ and Mg/Ca. Symbiosis is known to create a distinct microenvironment around the shell and affects carbonate chemistry particularly $\delta^{13}C$, Mg/Ca and possibly some other trace elements.

Depth habitat, Reproduction and Lifespan: $\delta^{18}O$ and Mg/Ca

Temperature is an important limiting factor in the distribution of organisms. Most organisms tolerate only a limited range of temperature. It regulates various life processes including metabolism, growth rate and reproduction. An understanding of temperature of the habitat of foraminifera is significant in this context. Emiliani (1954, 55) pioneered the use of oxygen isotopic ($\delta^{18}O$) variations in foraminifera to infer palaeotemperature. It subsequently became a routine analysis on the samples from the deep sea cores and led to reconstruction of the Cenozoic climate. The $\delta^{18}O$ composition of different foraminiferal species would therefore give a direct indication of the temperature of the seawater of their habitat. The temperature dependence of Mg/Ca and Sr/Ca ratios in foraminiferal carbonates has been demonstrated in many studies (Nurnberg *et al.*, 1996; Lea *et al.*, 1999). But, unlike $\delta^{18}O$, unambiguous relationship between growth temperature and Mg/Ca or Sr/Ca is not yet established (Delaney *et al.*, 1985; Raja *et al.*, 2007). In general, Mg/Ca in planktic foraminifera is found to vary from 0.5 to 5 mmol/mol in which the surface dwelling spinose species have higher Mg than deeper dwelling non-spinose (Lea, 1999).

Although geochemical data may not provide the absolute depth habitat of foraminifera, vital information on relative depth ranking can be obtained by oxygen isotopic composition due to depth related change in seawater temperature. Again, Emiliani (1954) for the first time analyzed the oxygen isotopic composition of multiple species of planktic foraminifera from the same core and inferred their depth habitats. *Globigerinoides ruber* and *Globigerinoides sacculifer* were interpreted to live close to surface waters and *Globorotalia* in deeper waters. The depth stratification data from plankton tows are in good agreement with the isotopic depth rankings of planktic foraminifera (Hecht, 1976; Table 2). Saraswati (2004) carried out high-resolution stable isotopic analysis of two species of larger benthic foraminifera and found that the shallow

Table 2: Depth ranking of planktonic foraminifera based on plankton tow and oxygen isotope data (compiled from Hecht 1976, table 2).

Plankton Tow Data	Oxygen Isotope Data
0 – 150 m	0 – 50 m
G. ruber, G. sacculifer,	G. ruber, G. sacculifer,
G. conglobatus	G. conglobatus
50 – 100 m	0 – 100 m
O. universa, N. dutertrei,	N. dutertrei
P. obliqueuloculata, G. menardii	
> 150 m	50 - >100 m
G. bulloides, C. nitida,	P. obliqueuloculata,
S. dehiscens, G. tumida,	G. menardii, G. truncatulinoides
G. truncatulinoides	

water species, *Marginopora kudakajimaensis,* show a higher scatter of $\delta^{18}O$ through ontogeny compared with deeper water *Cycloclypeus carpenteri* (Fig.1).

Morphological features are often used to infer depth habitats of fossil foraminifera. Glassy pustules on surface of many larger benthic foraminifera are believed to act as lenses to concentrate light for symbiotic algae in deeper waters (Hottinger, 1983). The modern day planktic foraminifera are broadly classified as globular, spinose "globigerinids" and flattened, non-spinose "globorotaliids". The globigerinids live in shallow water and globorotalids in deeper water. For the Palaeogene planktic foraminifera, however, the morphological depth-rankings do not match with the isotopic depth rankings

Fig.1. Comparison of ontogenetic variation in $\delta^{18}O$ and $\delta^{13}C$ between a shallow water larger foraminifer *Marginopora kudakajimaensis* (A) and deeper water *Cycloclypeus carpenteri* (B). The shallow water species has a higher scatter of $\delta^{18}O$ as compared with the species from deeper water (after Saraswati, 2004).

(Pearson, 1998). The "globorotaliid" form *Morozovella* showed lightest $\delta^{18}O$ and the "globigerine" form *Subbotina* gave heavier $\delta^{18}O$ values. This is inverse of the expected values and misinterpretation of the depth habitat. It is stated that palaeontologists would not have regarded the angular keeled Palaeogene planktic foraminifera as shallow dwelling without the isotopic information (Pearson, 1998).

For oxygen isotopic analysis, usually a number of individuals of foraminifera are necessary to yield a requisite quantity of carbonate for analysis. The data at best represents an average temperature during the growth of the species. The growth time of species varies, from a few weeks for planktic and smaller benthic species to a few years for some of the larger benthic species. The foraminifera having longer lifespan are likely to preserve a record of seasonal variation of the temperature of the ambient environment. And, therefore, seasonal temperature variation can be extracted from these foraminifera by adopting a suitable sampling technique. The records of seasonality can give important information about the temperature tolerance, lifespan and reproduction in foraminifera. With improvements in mass spectrometry and requirements of lesser amount of carbonate for analysis, many studies have attempted analysis of dissected chambers of foraminifera to obtain isotopic data at different growth stages (Wefer and Berger, 1980; Houstan and Huber, 1998; Saraswati, 2004; Saraswati *et al.*, 2004).

Based on $\delta^{18}O$ composition of the dissected embryonic chambers of larger foraminifera, Saraswati *et al.* (2004) interpreted that *Sorites orbiculus* and *Peneroplis planatus* reproduce in late autumn while *Amphisorous hemprichii* and *Heterostegina depressa* reproduce in early summer. *Marginopora kudakajimaensis* is found in two size-groups and the $\delta^{18}O$ compositions of the two sizes are distinctly different. One group has a distinctly higher $\delta^{18}O$ value compared with the other. It was inferred that one group (having higher $\delta^{18}O$) was reproduced in late autumn and the other (having low $\delta^{18}O$) in early summer. The interpretation is consistent with the field observations of Fujita *et al.* (2000) who observed two cohorts of *Marginopora kudakajimaensis*, one releasing megalospheric juveniles in winter and the other in late spring (May). Most investigations indicate that miliolids reproduce at distinct periods, the main in late spring/early summer and a second in late fall/early winter, and the rotaliids reproduce continuously, peaking in late spring (Hohenegger, *personal communication*). The consistency in the isotopic interpretation with field data suggests that this aspect of foraminiferan palaeobiology can be reliably understood by geochemical proxy data.

The lifespan of an individual foraminifer can also be indirectly estimated by oxygen isotopic variation with ontogeny. The cyclical change within a single test of *Marginopora kudakajimaensis* indicates that it lived for little over a year (Fig.2). This approach was also used for an extinct Eocene *Nummulites obtusus* (Saraswati *et al.*, 1997) and it suggests a lifespan of one and a half years (Fig.3). Purton and Brasier (1999) analyzed *N. laevigatus* from England and inferred that it lived for at least 5 years and speculated that some of the very large species such as *N. millecaput* would have lived for more than 100 years. This technique to indirectly infer lifespan has great potential to know about the longevity of fossil foraminifera, particularly those which nave no modern counterparts for comparison. Due to practical problems of
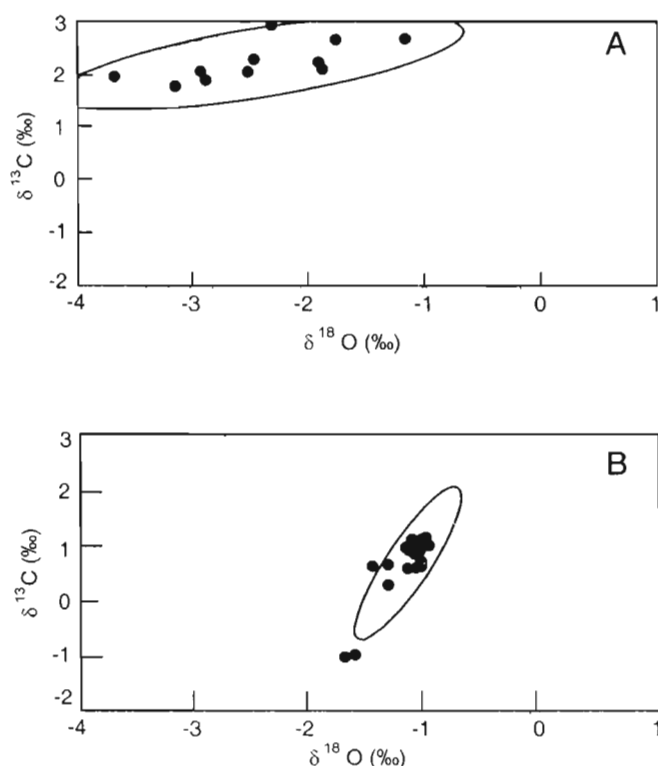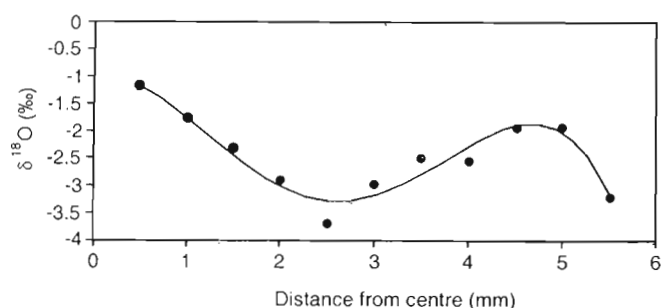
Fig.2. Variation in $\delta^{18}O$ from proloculus to final chamber of a modern foraminifer *Marginopora kudakajimaensis* showing cyclical change in the isotopic composition reflecting seasonal variation in the temperature of the ambient seawater (after Saraswati *et al.*, 2004).

dissecting chambers in small-sized foraminifera, this method can only be applied successfully in larger foraminifera. The laser ablation technique is becoming more accessible and it is possible in future to study ontogenetic variation in isotopic composition of smaller benthic and planktic foraminiferal species.

The whole-shell oxygen isotopic composition represents the average temperature and thereby average depths at which the bulk of carbonates of the shell were secreted. There are, however, multiple calcification events in the life span of an individual organism. It is observed in planktic foraminifera that many species secrete their shells continuously as they sink slowly through the water column (Be *et al.*, 1966) or they deposit a veneer of calcite on the surface of their shell at the end of the
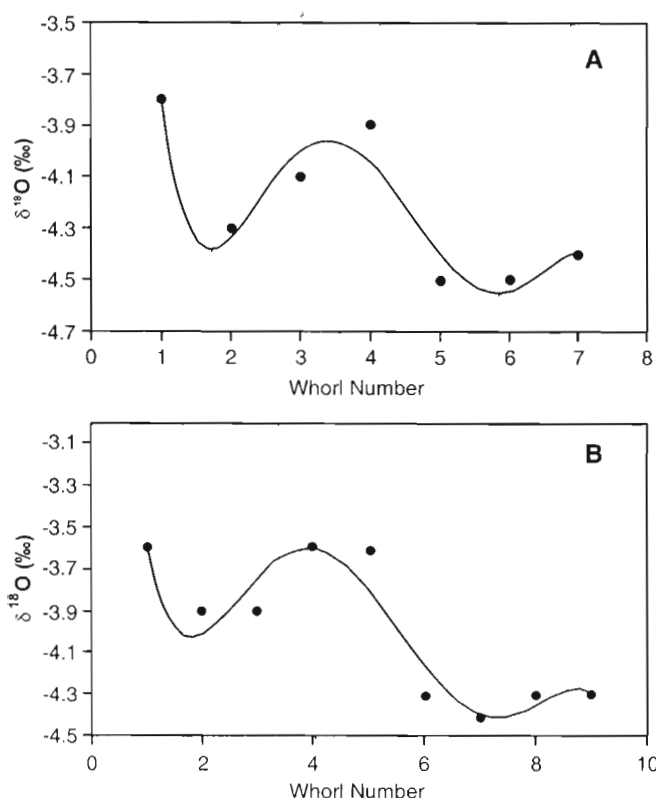

Fig.3. Variation in $\delta^{18}O$ from the first whorl to the final whorls of a megalospheric (A) and microspheric (B) forms of Eocene *Nummulites obtusus* indicating seasonal variation in temperature during the lifetime of the analyzed individuals (data after Saraswati *et al.*, 1997).

life cycle (Duplessy *et al.*, 1981). The geochemical proxies, $\delta^{18}O$ and Mg/Ca, can give important information about this life process of foraminifera. Bouvier-Soumagnac and Duplessy (1985) used $\delta^{18}O$ data to understand the formation of gametogenic calcite in *Orbulina universa*. They concluded that the species grows its shell in the surficial mixed layer but during gametogenesis it deposits an additional crust of calcite in colder waters. Spero and Lea (1993) also studied this species in laboratory and provided an alternative hypothesis that secretion of ^{18}O enriched gametogenic calcite occurs in the mixed-layer temperature itself and not in the cooler waters at greater depths. The mechanism of secretion of ^{18}O enriched gametogenic calcite needs to be investigated further. If the calcification-at-depth hypothesis of Bouvier-Soumagnac and Duplessy is valid it may be possible to infer water depths at which different planktonic foraminifera undergo reproduction.

Photosymbiosis: $\delta^{13}C$ and Mg/Ca

Both the benthic and planktic foraminifera host symbiotic algae comprising diatoms, dinoflagellates, chlorophytes, rhodophytes and chrysophytes. It helps foraminifera obtain energy in oligotrophic environments and promote calcification (Hallock, 2000). A similar symbiotic relationship is believed to have existed in the geologic past (Hottinger, 1983) that led to enhanced calcification and gigantic size of some benthic foraminifera in Permian, Cretaceous and Eocene times. Although there is no direct evidence of photosymbiosis, the architectural complexity of the test is considered as morphological adaptation for the benefit of algal symbionts. The spinose planktic foraminifera keep their symbionts inside the shell in the night time, when no photosynthetic activities take place, and move them outside to hang from the spines for photosynthesis in the day time. Thus, morphological as well as behavioral adaptations are noted in foraminifera having photosymbiosis.

Photosymbiosis has a marked effect on geochemistry of the foraminifera shells. It is particularly true for carbon isotopes. ^{12}C enriched CO_2 is preferentially removed by the symbionts during photosynthesis and this enriches $^{13}C/^{12}C$ ratio of the calcifying microenvironment. The $\delta^{13}C$ of the shell will therefore be more in high light environment than in low light. *Orbulina universa*, maintained in laboratory at different light conditions, showed different $\delta^{13}C$ values (Fig.4): shells precipitated in dark or low light conditions were distinctly depleted in ^{13}C relative to those in high light conditions (Spero, 1998). Respiration, unlike photosynthesis, should decrease $\delta^{13}C$ due to addition of respired CO_2 which is enriched in ^{12}C. Micro-sensor studies have recognized distinct chemical microenvironment in the vicinity of symbiont-bearing foraminifera shells where the carbonate chemistry is quite different from the sea-water (Fig. 5). Calcification, respiration and symbiont photosynthesis change the pH, and shift the concentrations of CO_2, CO_3 and HCO_3 in this microenvironment (Kohler-Rink and Kuhl, 2001, 2005). The $\delta^{13}C$ of foraminiferal carbonates precipitated in this environment is a function of sea-water chemistry and "vital effects". The "vital effects" include (i) respiration of foraminifer (ii) respiration of symbiotic algae and (iii) photosynthesis of the symbiotic algae. Respiration produces CO_2 which is enriched in ^{12}C. Photosynthesis preferentially removes ^{12}C and therefore the foraminiferal microenvironment gets enriched in ^{13}C. The change in carbon isotopic composition of this environment will de-
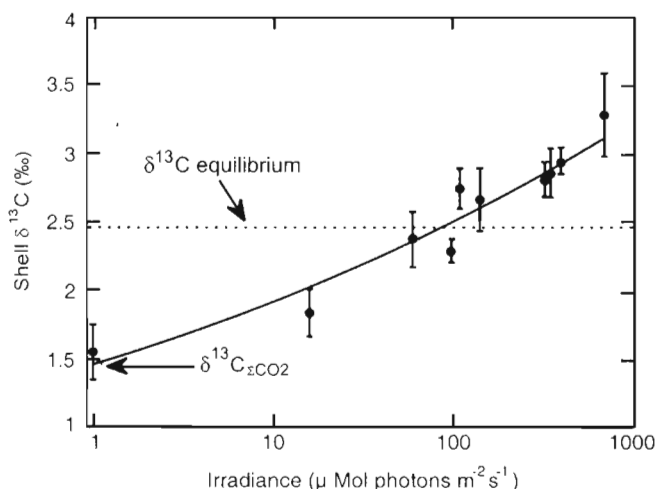
Fig. 4. $\delta^{13}C$ variation in planktonic foraminifer *Orbulina universa* cultured at different light intensities. Shells precipitated in low light conditions are distinctly depleted in ^{13}C relative to those in high light conditions (after Spero, 1998).

pend on the relative contributions of respired and photosynthetically produced carbon flux. Symbiosis does not have a marked effect on oxygen isotopic composition of either planktic foraminifera (Spero and DeNiro, 1987) or benthic foraminifera (Saraswati *et al.*, 2004). Observations of some of the workers are, however, different and they found that both $\delta^{18}O$ and $\delta^{13}C$ are affected by "vital" effects including photosymbiosis and respiration (Erez, 1978; Williams *et al.*, 1981). It is known that in kinetic fractionation, oxygen and carbon isotopic ratios have good correlation but when there is an over-riding effect of metabolism the $\delta^{18}O$ - $\delta^{13}C$ correla-

tion is lost (McConnaughey, 1989). This is very well observed in modern, symbiont-bearing, benthic foraminifera (Fig. 6).

Due to marked effect of photosymbiosis on isotopic composition of the foraminiferal shells, $\delta^{13}C$ is recognized as a potential tool to infer photosymbiosis in fossil taxa. Norris (1996), Houston and Huber (1998) and Houston *et al.* (1999) suggested the following characteristics of photosymbiosis: (i) $\delta^{18}O$ values more negative than co-existing asymbiotic taxa (ii) relatively small size-related changes in $\delta^{18}O$ values (iii) a strong positive size-related shift in $\delta^{13}C$ values of 0.5‰ or more (iv) a poor co-variance between size-related changes in $\delta^{18}O$ and $\delta^{13}C$ values and (v) significant intra-specific variability in $\delta^{13}C$ values. On the above criteria, Maastrichtian taxa *Planoglobulina acervulinoides* and *Racemiguembelina fructicosa* were considered to be photosymbiotic (Houston *et al.*, 1999). The Palaeocene taxa *Acarinina* and *Morozovella* were also interpreted to be symbiont-bearing on stable isotopic criteria (D'Hondt *et al.*, 1994).

The stable isotopic characteristics of symbiont-bearing benthic foraminifera have some similarity with those of planktic foraminifera but differ in certain aspects (Table 3). The size-related change in $\delta^{18}O$ is small in planktic foraminifera but in larger foraminifera the trend is different. It is large in *Marginopora kudakajimaensis*, a shallow water species but small in deeper water species *Cycloclypeus carpenteri* (Saraswati *et al.*, 2004). This contrast in the isotopic signatures of planktic and benthic foraminifera could possibly be due to a longer lifespan of the latter foraminifera. The tests of larger foraminifera record a complete range of seasonal change, and therefore show a significant size-related change in $\delta^{18}O$. *Cycloclypeus carpenteri* although records the seasonal change, experiences a smaller variation in temperature in
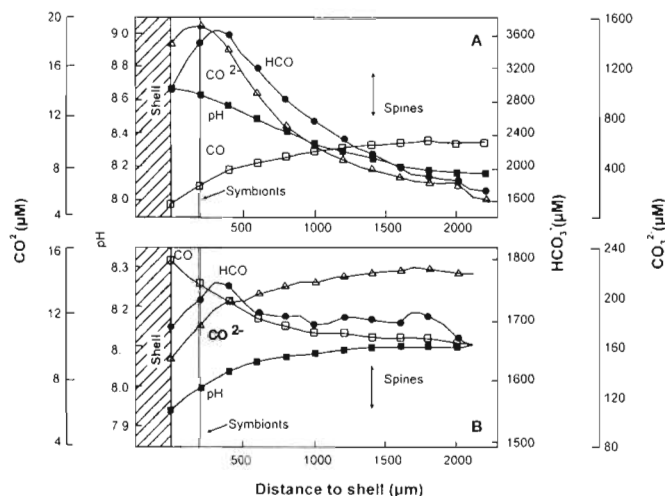

Fig. 5. Chemical microenvironment in the vicinity of the shell of symbiont-bearing foraminifer *Orbulina universa* as recorded in a micro-sensor study in laboratory culture. The concentrations of CO_2, CO_3 and HCO_3 shift in this microenvironment relative to the seawater concentration (after Kohler-Rink and Kuhl, 2005).
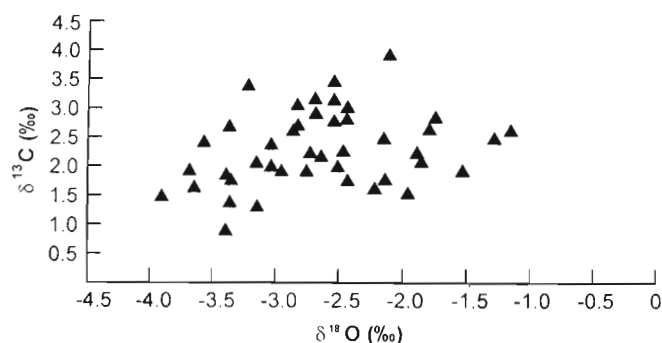
Fig. 6. Poor correlation between $\delta^{18}O$ and $\delta^{13}C$ of symbiont-bearing *Marginopora* from various localities.

Table-3: A comparison of oxygen and carbon isotopic signatures in the symbiont bearing planktonic and larger benthic foraminifera (after Saraswati *et al.*, 2004)

$\delta^{18}O$ - $\delta^{13}C$ signatures	Planktonic	Larger benthic
Value of ^{18}O as compared with co-existing asymbiotic taxa	More negative	In the same range
Size-related change in $\delta^{18}O$	Small	Large for shallow-water species and small for deeper water species
Size-related change in $\delta^{13}C$	Large	Large
$\delta^{18}O$ - $\delta^{13}C$ correlation	Poor	Poor
Intra-specific variability in $\delta^{13}C$	Significant	Significant

deeper water and therefore shows a minor variation in $\delta^{18}O$ with size.

A positive relationship between Mg/Ca and temperature is reported for foraminifera by many workers (Nurnberg, 1995; Rathburn and De Deckker, 1997; Rosenthal *et al.*, 1997). On the contrary, Eggins *et al.* (2004) found that in *Orbulina universa*, a symbiont-bearing planktic foraminifer, Mg/Ca composition of the calcite is strongly influenced by algal symbionts. Similar observation is made for several species of symbiont-bearing benthic foraminifera (Raja *et al.*, 2005, 2007) and it is suggested that (i) there is a large variation in Mg/Ca ratios between co-existing species and (ii) the intra-test spatial heterogeneity is of very high order in these foraminifera (Figs. 7 and 8). Eggins *et al.* (2004) could achieve a high resolution analysis of *Orbulina universa* using laser ablation ICP-MS that led them to identify high- and low- Mg growth-bands. These bands were interpreted to be of diurnal origin and caused by photosynthesis – respiration cycle of the algal symbionts. A strong influence of photosymbiosis is thus found on carbon isotopic ratio as well as Mg/Ca ratio of foraminiferal carbonates and these together could provide an unequivocal evidence of photosymbiosis in fossil foraminifera.

VALIDITY OF GEOCHEMICAL PROXIES

The isotopic or trace element composition of biogenic calcite is controlled by a number of physical and biological factors. An essential requirement in relating oxygen isotope values to temperature is to ensure that skeletal $CaCO_3$ is deposited in close isotopic equilibrium with the surrounding
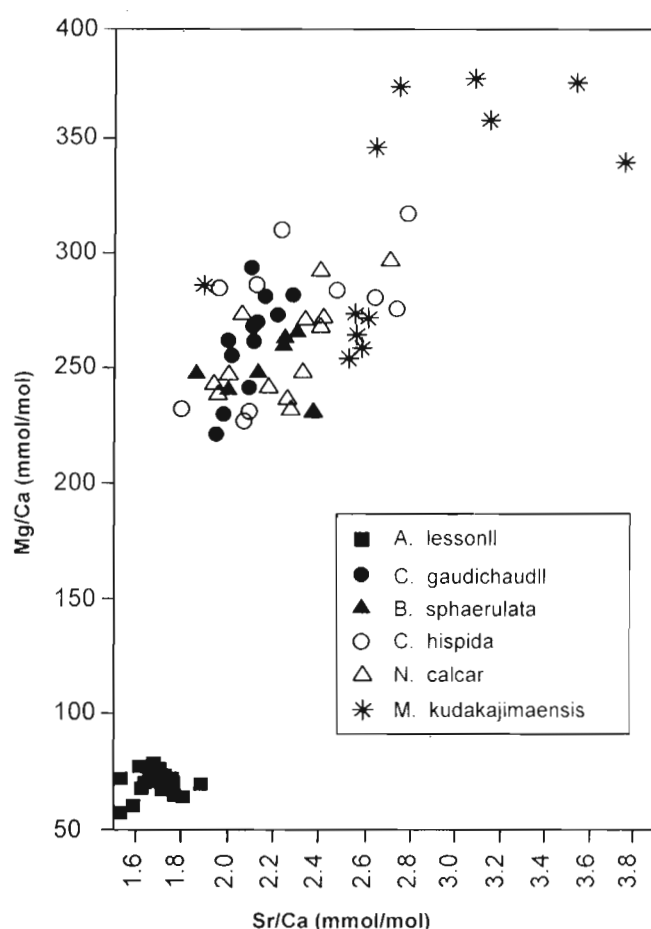

Fig. 7. Large inter-species variation in Mg / Ca and Sr / Ca ratios in symbiont-bearing modern benthic foraminifera (after Raja *et al.*, 2007).
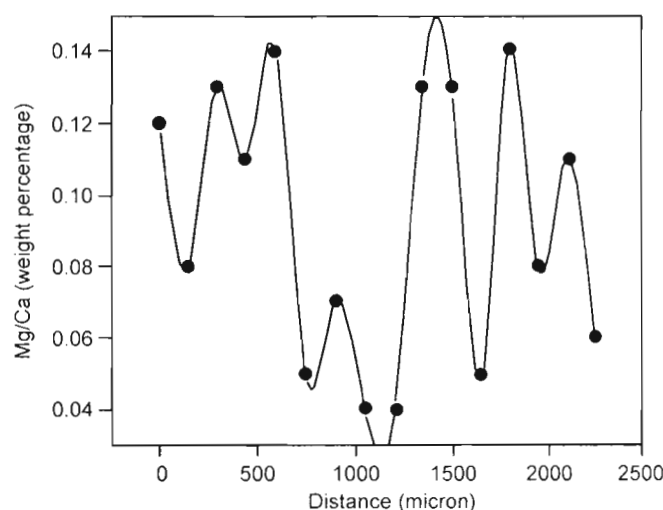

Fig. 8. A high intra-test variation in Mg/Ca ratio of *Marginopora* analyzed from centre to periphery (Raja *et al.*, 2005).

sea-water. Studies suggest that in foraminifera the deposition takes place in equilibrium (Smith and Emiliani, 1968) to near equilibrium (Berger *et al.*, 1981) or out of equilibrium (Vinot-Bertouille and Duplessy, 1973; Erez, 1978). Saraswati *et al.* (2004) analyzed several co-existing living larger foraminifera and found that in most modern species the oxygen isotopes are secreted

either in equilibrium or enriched up to 0.8 ‰ relative to equilibrium calcite. In carbon isotopes, the disequilibrium ranges up to 5‰ and it is believed to be largely due to physiological effects. The trace element composition is also found to be influenced by biological factors. Isotope and trace element incorporation in biogenic carbonate should be understood well in modern foraminifera before using them as proxy data in palaeobiology. Needless to say, pristine preservation of foraminifera tests is vital to all interpretations based on geochemical proxy data.

CONCLUSION

The $\delta^{18}O$, $\delta^{13}C$ and Mg/Ca ratio of foraminiferal shells provide important information about their life conditions and life history. The major life processes that can be inferred by these proxies include temperature of the habitat, temperature tolerance, reproduction, depth distribution, lifespan, calcification and photosymbiosis. There is a great scope for future work in this direction. New possibilities are opening up in view of improvements in analytical techniques, higher sampling resolution and better understanding of biomineralization process in foraminifera. New geochemical proxies are being developed for palaeoceanographic investigations which will be equally important in palaeobiology.

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