Isotopic composition of a laboratory cultured planktonic foraminifer *O. universa* Implications for paleoclimatic reconstructions

Foraminifères
Isotopes stables
Paléoclimatologie
Fractionnement isotopique

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ABSTRACT

Laboratory cultured and superficial water plankton tow specimens of the foraminiferal species *O. universa* fractionate oxygen isotopes according to an experimental relationship close to isotopic equilibrium with the ambient water. By contrast, a significant enrichment in ^{18}O is observed in Holocene sediment *O. universa* shells, as compared to the expected values for their living surface waters counterparts. This enrichment could be explained by gametogenic calcification, which extracts calcite from deeper and cooler waters, during the sinking of the shell below the euphotic zone. Consequently, the isotopic record of planktonic foraminifera from deep sea sediment does not only reflect the variations of surface water conditions and is partly biased by those of the water below the euphotic zone.

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RÉSUMÉ

Composition isotopique d'un foraminifère élevé en laboratoire *Orbulina universa*. Implications pour les reconstitutions paléoclimatiques

Des spécimens du foraminifère planctonique *Orbulina universa*, élevés en laboratoire et échantillonnés dans les eaux superficielles à l'aide de filets à plancton, fractionnent les isotopes de l'oxygène selon une relation expérimentale proche de celle correspondant à l'équilibre isotopique avec l'eau ambiante au cours de la réaction de précipitation de la calcite.
Les tests d'*Orbulina universa* du sédiment récent présentent un enrichissement significatif en ^{18}O par rapport aux valeurs mesurées dans les tests collectés dans les eaux de surface. Celui-ci est expliqué par le fait que les coquilles trouvées dans les sédiments présentent une calcification secondaire qui est liée à la gamétogénèse. Pendant cette phase reproductive, l'animal tombe dans la colonne d'eau et dépose une couche superficielle de calcite qui enrobe la coquille formée en surface. La calcite gémétogénique présente les caractéristiques isotopiques d'une calcite déposée en eaux froides et est donc plus riche en ^{18}O que celle formée dans les eaux chaudes de surface.
Les courbes isotopiques obtenues dans les carottes marines sur des foraminifères plantoniques ne reflètent donc pas seulement les variations des conditions ayant régné dans les eaux de surface et sont aussi influencées par les modifications subies par les eaux en dessous de la couche euphotique.

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INTRODUCTION

Oxygen isotopic analyses of fossil foraminifera have become an increasingly important tool in paleoclimatology. They serve to determine paleotemperatures (Emiliani, 1955; Duplessy *et al.*, 1980), paleosalinities (Duplessy, 1982) and provide an accurate stratigraphy for the Pleistocene epoch (Shackleton, Opdyke, 1973; 1976). In order correctly to interpret the variations of isotopic composition of foraminifera from deep-sea cores, it is necessary to identify the most important set of factors which determine the $^{18}O/^{16}O$ ratio of different species.

Since scuba diving became a collecting technique for living specimens (Bé *et al.*, 1977), the biology of several living planktonic foraminifera species has been studied in the laboratory (Bé, 1982; Bé *et al.*, 1981; Caron *et al.*, 1982). Only one laboratory cultured species *G. sacculifer*, has been isotopically analysed (Erez, Luz, 1983). Results showed that the calcite secreted in the laboratory fractionates oxygen isotopes according to the equilibrium scale, while young specimens collected alive in the Gulf of Aqaba were systematically depleted in ^{18}O. Similarly, analyses of plankton tow *G. sacculifer* from the Indian Ocean surficial mixed layer showed its isotopic composition to be systematically poorer in ^{18}O then the expected mollusc equilibrium values by about 0.6 ‰ (Duplessy *et al.*, 1981 *a*).

The problem appeared even more complicated when it was found that living species collected with plankton tow show significant deviations from equilibrium (Shackleton *et al.*, 1973; Kahn, 1979), whereas material from sediment traps and bottom sediments does not (Curry *et al.*, 1983; Emiliani, 1971). These contradictions raise the questions whether the present state of knowledge of living planktonic foraminifera permits the accurate simulation of natural conditions in the laboratory or the correct interpretation of analyses of plankton tow samples.

MATERIAL AND METHODS

We analysed specimens of a planktonic foraminifera *O. universa*, a common spinose species, as cultured in the laboratory, sampled by plankton tows and found in core top sediments. Young trochospiral *O. universa* obtained off Curaçao were cultured in the laboratory under controlled feeding, light, and salinity conditions at different water temperatures (Bé *et al.*, 1981; Bé, 1982). The specimens were kept in the laboratory from the trochospiral stage through the spherical stage until the occurrence of genetogenesis in almost all cases. As there is a progressive loss or resorption of the trochospiral chambers during the reproductive stage (Bé *et al.*, 1973), no correction of the measured $^{18}O/^{16}O$ ratio for the original isotopic composition of the trochospiral stage was needed.

Both plankton tow and laboratory culture samples were roasted first in a low temperature asher. All the samples were then roasted under vacuum at 400°C, and analysis according to the procedure used in the laboratory at Gif (Duplessy, 1978). Results are expressed using the traditional $\delta^{18}O$ fashion.

The plankton tow specimens originate from the same tropical and subtropical Indian Ocean surficial mixed layer tows as the *G. sacculifer* specimens mentioned above (Duplessy *et al.*, 1981 *a*). They were taken along a N-S transect at about 75°E. Water temperature variations in this area are small (Wyrtki, 1971). As the

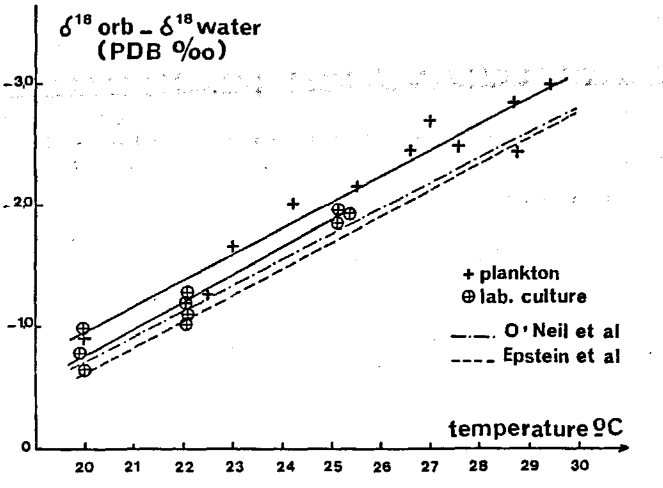

Figure 1

Variations of the oxygen isotopic composition of O. universa *calcite with water temperature. Seawater* $\delta^{18}O$ ($\delta\omega^{18}$) *has been measured for each samples.*
The best fit lines are:
δ_c^{18}-$\delta\omega^{18}$ = 3.194-0.208 *t* (*r* = 0.97) *for plankton tow samples.*
δ_c^{18}-$\delta\omega^{18}$ = 3.502-0.214 *t* (*r* = 0.98) *for laboratory culture samples.*
Statistical comparisons were made between:
— the two best fit lines, yielding t test values of:
t slope = 0.255, *t intercept* = 2.480 *at x* = 24°C,
t p = .980 = 2.376 *for* 21 *d.f.;*
— the laboratory cultured samples and the O'Neil et al. *relationships, yielding:*
t slope = 0.064, *t intercept* = 3,307 *at x,*
t p = .980 = 2.681 *for* 12 *d.f.;*
— the plankton tow samples and the O'Neil et al. *relationships, yielding:*
t slope = 0.349, *t intercept* = 4.393 *at x,*
t p = .980 = 2.821 *for* 9 *d.f.*

Variations de la composition isotopique de l'oxygène de la calcite d'*Orbulina universa* en fonction de la température de l'eau. Le rapport $^{18}O/^{18}O$ de l'eau de mer ($\delta^{18}\omega$) a été mesuré pour chaque échantillon.
Les droites de régression ont pour équation :
δ^{18}-$\delta\omega^{18}$ = 3,194-0,208 t (r = 0,97) pour les échantillons des filets à plancton.
δ^{18}-$\delta\omega^{18}$ = 3,502-0,214 t (r = 0,98) pour les échantillons élevés au laboratoire.
Des comparaisons statistiques ont été faites entre :
— les deux relations; les valeurs du t de Student sont :
t pente = 0,255, t intercept = 2,480 à 24°C,
t p = 0,980 = 2,376 pour 21 degrés de liberté;
— la relation obtenue pour des échantillons élevés au laboratoire et celle d'O'Neil *et al.*, les valeurs étant :
t pente = 0,064, t intercept = 3,307 à la température moyenne des échantillons,
t p = 0,980 = 2,681 pour 12 degrés de liberté;
— la relation obtenue pour des échantillons pris à l'aide de filet à plancton et celle d'O'Neil *et al.*, les valeurs étant :
t pente = 0,349, t intercept = 4,393 à la température moyenne des échantillons,
t p = 0,980 = 2,821 pour 9 degrés de liberté.

life span of foraminifera is assumed to be only a few weeks (Bé *et al.*, 1981), the comparison between measured sea surface temperature and towed *O. universa* $\delta^{18}O$ permits evaluation of temperature.

The oxygen isotopic composition of *O. universa* is, however, very slightly but systematically lighter than the equilibrium values according to the O'Neil *et al.* carbonate-water temperature scale (1969). This systematic depletion is on the average 0.1 ‰ for the cultured *O. universa* (and about 0.2 per mil for the plankton tow samples) introducing an error of 1°C at the most in water temperature estimates according to that equilibrium scale. This departure from isotopic equilibrium may be due to the activity of symbiotic algae, Table

Comparison of the oxygen isotopic composition (‰ vs PDB) of O. universa *specimens from Holocene sediments and from the mixed layer.* Δ *represents the* $\delta^{18}O$ *difference between the sediment shell values and the annual maximum* $\delta^{18}O$ *calculated for the mixed layer shells. When more than one sample was analysed (number of samples in bracket), we reported the mean value* ± *the mean standard error.*

Comparaison de la composition isotopique de l'oxygène (‰ vs PDB) d'échantillons d'*Orbulina Universa* du sédiment récent (Holocène) et d'échantillons des eaux superficielles. Δ représente la différence entre les valeurs de $\delta^{18}O$ des échantillons du sédiment et la valeur maximale de $\delta^{18}O$ calculée pour la calcite déposée dans la couche d'eau superficielle mélangée. Lorsque plusieurs échantillons ont été analysés (nombre d'échantillons entre parenthèses), nous avons reporté la valeur moyenne ± l'erreur moyenne à σ.

		Living specimens		Annual $\delta^{18}O$ range in the mixed layer			Δ (fossil-living)
Station	Location	depth -m)	$\delta^{18}O$	min.	max.	Fossil samples from Holocene sediment	the living value being the annual maximum
10-19	06°23'5N 78°39'5E			—2.97	—1.99	—1.47 ± 0.18 (3)	+0.52
10-26	12°05'4N 73°54'0E			—2.85	—2.21	—1.58 ± 0.18 (3)	+0.63
10-28	14°59'8N 72°19'8E	0-50 m	—2.49	—2.73	—1.73	—1.39 ± 0.07 (2)	+0.34
10-30	16°59'4N 71°30'8E			—2.61	—1.85	—1.42 ± 0.14 (6)	+0.41
13-67	19°13'3N 60°40'9E			—2.49	—0.97	—0.98 ± 0.13 (2)	—0.01
13-68	20°41'9N 59°34'1E			—2.28	—0.97	—0.87 ± 0.16 (2)	+0.10
						X = +0.34 O=0.23 σ_X=0.11	

O. universa being known to have symbiotic zooxanthellae in its cytoplasm (Bé, 1982; Hemleben, Spindler, 1983). Their activity is important since a single large *O. universa* is 20,000 times more productive in oligotrophic waters than the entire phytoplanktonic population present in an equivalent volume of sea water (Spero, Parker, 1985). Nevertheless, the resulting isotopic effect seems to be quite moderate (Bouvier-Soumagnac, Duplessy, 1985).

COMPARISON WITH SEDIMENT SHELLS

We analysed *O. universa* specimens from core tops for which the Holocene age had been checked by oxygen isotopic stratigraphy (Duplessy, 1982). The results (Tab.) show a systematic enrichment in ^{18}O relative to the expected values for surficial water specimens. Moreover in five out of six stations the sediment samples have heavier isotopic composition than the calculated one for *O. universa* calcite if secreted in the overlying surficial waters during the coolest and saltiest month of the year (Fig. 2). This rules out the possibility that selective dissolution of the inner well of the thinner warmer water specimens (Berger, 1971) is the only cause for the enriched $\delta^{18}O$ values observed in the sediment shells.

Gametogenic calcification has been proposed as an explanation for a similar enrichment observed in *G. sacculifer* shells from the surface sediment as compared to living specimens (Duplessy *et al.*, 1981 *b*), because an additional calcite crust is secreted over the last formed chambers of the shell during the gametogenesis. In the laboratory, this deposition coincides with a spine loss and a sinking of the animal to the bottom of the culture vessel. Under natural conditions, gametogenic calcification is believed to occur below the euphotic zone, producing a calcite enriched in ^{18}O relatively to that deposited in the surficial mixed layer (Bé, 1980). Similar laboratory observations have been made for *O. universa* (Bé *et al.*, 1977). Observations of *O. universa* from the Indian Ocean show that on the average, sediment core tops shells have a thicker test than shells from 0-300 m plankton tows (Bé *et al.*, 1973). An increase of weight of sediment *O. universa* relatively to plankton tow samples has also been reported for the Central North Atlantic. The increase has been evaluated at 36% (Erez, Honjo, 1981). These data suggest that gametogenic calcification below the euphotic zone in cold waters is responsible for the observed enrichment in ^{18}O of *O. universa* shells from the sediment as compared to living specimens.

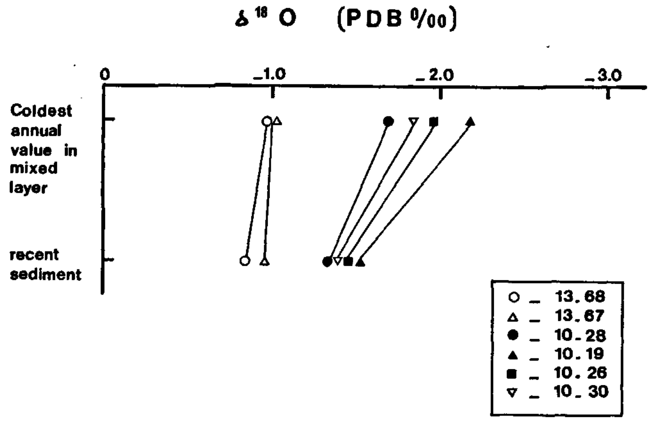

Figure 2

Comparison of the oxygen isotopic composition of Holocene sediment and mixed layer O. universa *specimens. The mixed layer* $\delta^{18}O$ *is the annual heaviest value calculated for calcite secreted in surface waters.*

Comparaison de la composition isotopique de l'oxygène d'échantillons d'*Orbulina universa* provenant du sédiment récent avec celle d'échantillons collectés dans les eaux superficielles. La valeur de $\delta^{18}O$ pour les eaux superficielles est la valeur annuelle la plus élevée calculée pour la calcite déposée dans la couche de mélange (et correspondant aux conditions les plus froides).

We therefore conclude that the planktonic foraminifer *O. universa* cultured in the laboratory or sampled by plankton tow fractionates oxygen isotopes with changing water temperature close to the isotopic equilibrium values. When shells recovered from the sediment are considered, only part of the calcite shell is found to have been secreted in the mixed layer, the remainder having been secreted in deeper and colder waters during gametogenesis at the end of the life of the foraminifer.

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REFERENCES

Bé A. W. H., 1980. Gametogenic calcification in a spinose planktonic foraminifer, *Globigerinoides sacculifer (Brady)*, *Mar. Micropaleontol.*, **5**, 283-310.

Bé A. W. H., 1982. *Studies in geology*, edited by T. W. Broadhead, Univ. Knoxville, Tennessee, 85-92.

Bé A. W. H., Harrison M., Lott L., 1973. *Orbulina universa d'Orbigny* in the Indian Ocean, *Micropaleontology*, **19**, 150-159.

Bé A. W. H., Hembleden C., Anderson O. R., Spindler M., Hacunda J., Tuntivate-Choy S., 1977. Laboratory and field observations of living planktonic foraminifera, *Micropaleontology*, **23**, 155-179.

Bé A. W. H., Caron D. A., Anderson O. R. J., 1981. Effects frequency on life processes of the planktonic foraminifera *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. UK*, **61**, 257-277.

Berger W. H., 1971. Sedimentation of planktonic foraminifera, *Mar. Geol.*, **11**, 325-358.

Bouvier-Soumagnac Y., Duplessy J.-C., 1985. Carbon and oxygen isotopic composition of planktonic foraminifera from laboratory culture, plankton tows and redent sediment: implications for the reconstruction of paleoclimatic conditions and of the global carbon cycle, *J. Foram. Res.*, **15**, 302-320.

Caron D. A., Bé A. W. H., Anderson O. R., 1982. Effects of variations in light intensity on life processes of the planktonic foraminifera *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. UK*, **62**, 435-451.

Curry W. B., Thunell R. C., Honjo S., 1983. Seasonal changes in the isotopic composition of planktonic foraminifera collected in Panama Basin sediment traps, *Earth Planet. Sci. Lett.*, **64**, 33-43.

Duplessy J. C., 1978. Isotope studies, in: *Climatic change*, edited by J. Gribbin, Cambridge Univ. Press, London, 46-67.

Duplessy J. C., 1982. Glacial to Interglacial contrast in the Northern Indian Ocean, *Nature*, **295**, 494-498.

Duplessy J. C., Moyes J., Pujol C., 1980. Deep water formation in the North Atlantic Ocean during the last ice age, *Nature*, **286**, 479-482.

Duplessy J.-C., Bé A. W. H., Blanc P. L., 1981 *a*. Oxygen and carbon isotopic composition and biogeographic distribution of planktonic foraminifera in the Indian Ocean, *Palaeogeogr. Paleoclimatol. Palaeoecol.*, **33**, 9-46.

Duplessy J.-C., Blanc P. L., Bé A. W. H., 1981 *b*. Oxygen 18 enrichment of planktonic foraminifera due to gametogenic calcification below the euphotic zone, *Science*, **213**, 1247-1250.

Emiliani C., 1955. Pleistocene temperatures, *J. Geol.*, **63**, 538-578.

Emiliani C., 1971. Depth habitats of growth stages of pelagic foraminifera, *Science*, **173**, 1122-1124.

Erez J., Honjo S., 1981. Comparison of isotopic composition of planktonic foraminifera in plankton tows, sediment traps and sediments, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **33**, 129-157.

Erez J., Luz B., 1983. Experimental paleotemperature equation for planktonic foraminifera, *Geochim. Cosmochim. Acta*, **4**, 1025-1031.

Khan M. I., 1979. Non-equilibrium oxygen and carbon isotopic fractionation in tests of living planktonic foraminifera, *Oceanol. Acta*, **2**, 2, 195-200.

O'Neil J. R., Clayton R. N., Mayeda T. K., 1969. Oxygen isotope fractionation in divalent metal carbonates, *J. Chem. Phys.*, **51**, 5547-5558.

Shackleton N. J., Opdyke N. D., 1973. Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale, *Quat. Res.*, **3**, 39-55.

Shackleton N. J., Opdyke N. D., 1976. Oxygen-isotope and paleomagnetic stratigraphy of Pacific core V28-239 Late Pliocene to Latest Pleistocene, *Geol. Soc. Am. Mem.*, **145**, 449-464.

Shackleton N. J., Wiseman J. D. H., Buckeley H. A., 1973. Non-equilibrium isotopic fractionation between seawater and planktonic foraminiferal tests, *Nature*, **242**, 177-179.

Spero H. J., Parker S. L., 1985. Photosynthesis in the symbiotic planktonic foraminifer Orbulina Universa", and its potential contribution to oceanic primary productivity, *J. Foram. Res.*, **15**, 273-281.

Williams D. F., Bé A. W. R., Fairbanks R. G., 1981. Seasonal stable isotopic variations in living planktonic foraminifera from Bermuda plankton tows, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **33**, 71-103.

Wyrtki K., 1971. *Oceanographic atlas of the international Indian Ocean expedition*, N.S.F., Washington DC.