Non-equilibrium oxygen and carbon isotopic fractionation in tests of living planktonic foraminifera

^{18}O
^{13}C
Non-equilibrium
Foraminifera
Equatorial Atlantic
^{18}O
^{13}C
Hors d'équilibre
Foraminifères
Atlantique équatorial

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ABSTRACT

Oxygen and carbon isotopic analyses were performed on 9 species of planktonic foraminifera collected from known depth intervals of the eastern equatorial Atlantic Ocean. *In situ* temperature and salinity, as well as local and regional stable isotopic, oceanographic, and faunal data were used in the interpretation of the results. Depletion in both ^{18}O and ^{13}C was found in the calcite tests of many species relative to calcite precipitated in equilibrium with ambient seawater. Minimum estimates of the departures from isotopic equilibrium range from $\sim 0^0/_{00}$ in *Pulleniatina obliquiloculata* to $-1.57^0/_{00}$ in *Neogloboquadrina dutertrei* for $\delta^{18}O$, and from $-0.69^0/_{00}$ in *N. dutertrei* to $-3.48^0/_{00}$ in *Globigerinella aequilateralis* for $\delta^{13}C$. Comparison between larger and smaller size groups of the same species reveals the existence of ontogenetic decreases in the vital effect for either $\delta^{18}O$, $\delta^{13}C$, or both. The ontogenetic decreases in vital effect maybe caused by decreases in metabolic rate with age in the utilization of metabolic CO_2 in test secretion. Fair agreement was found between the relative depth habitats estimated using plankton tow counts, and oxygen and carbon isotopic data of the larger size groups, and the oxygen isotopic ratios of the smaller and larger size groups combined. There was no agreement when only populations of smaller size groups were considered. The hypothesis that planktonic foraminifera kummerform chambers develop due to environmental stress is not supported by the isotopic data of the study. Bias in paleotemperature determinations may be minimized if isotopic analysis are performed on limited size ranges.

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RÉSUMÉ

Fractionnement hors d'équilibre des isotopes de l'oxygène et du carbone dans les tests des foraminifères planctoniques vivants

Les compositions isotopiques de l'oxygène et du carbone des tests de 9 espèces de foraminifères planctoniques, collectés à différentes profondeurs connues dans l'est de l'océan Atlantique équatorial, ont été comparées aux paramètres océanographiques (température et salinité *in situ*, teneur en ^{18}O et ^{13}C) en tenant compte des données sur la répartition des faunes. Par rapport à l'eau de mer ambiante, la calcite des tests de plusieurs espèces est appauvrie à la fois en ^{18}O et ^{13}C. Les estimations minimales des écarts à l'équilibre isotopique sont comprises, pour ^{18}O, entre $0^0/_{00}$ chez *Pulleniatina obliquiloculata* et $-1,57\ ^0/_{00}$ chez *Neogloboquadrina dutertrei* et pour ^{13}C, entre $-0,69\ ^0/_{00}$ chez *N. dutertrei* et $-3,48\ ^0/_{00}$ chez *Globigerinella aequilateralis*. La comparaison entre les différents groupes de taille au sein d'une même espèce révèle l'existence d'une diminution ontogénétique de l'effet vital sur $\delta^{18}O$ ou $\delta^{13}C$ ou les deux. Ceci peut être une conséquence d'une diminution avec l'age du régime métabolique qui contrôle l'utilisation du CO_2 métabolique dans le processus de sécrétion du test. Comparées aux relevés des filets à

plancton, les profondeurs relatives d'habitat des différentes espèces sont estimées de manière satisfaisante à partir des teneurs en ^{18}O et ^{13}C des formes de grande taille ou à partir des teneurs en ^{18}O des groupes de petite et grande taille combinés. Une telle estimation n'est pas possible à partir des formes de petite taille seules. Les données isotopiques ne supportent pas l'hypothèse selon laquelle les chambres « kummerform » des foraminifères planctoniques se développeraient dans des conditions d'environnement défavorable. Les biais dans les déterminations de paléotempératures peuvent être minimisés en effectuant les analyses isotopiques dans des gammes de taille limitées.

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INTRODUCTION

Emiliani (1954, 1955 *a*, 1955 *b*) first used oxygen isotope analyses of fossil foraminiferal tests to determine their average depth habitats and to derive paleotemperatures for the Pleistocene oceans. These investigations involved the assumption that foraminifera secrete their tests in isotopic equilibrium with the surrounding sea water. It is now known that species-dependent departures from oxygen isotopic equilibrium exist in both benthic (Duplessy *et al.*, 1970; Vinot-Bertouille, Duplessy, 1973; Buchardt, Hansen 1977) and planktonic foraminifera (van Donk, 1970; Shackleton *et al.*, 1973; Vergnaud-Grazzini, 1976; Kahn, 1977 *b*), and that an understanding of non-equilibrium (biological) fractionation ("vital effect"; Urey *et al.*, 1951) in foraminifera is needed before we can use isotopic analyses to deduce depth habitats, obtain paleotemperature estimates, and estimate the isotopic composition of seawater. In some cases isotopic differences between subspecies, phenotypes, and even individuals at different growth stages may be significant (Oba, 1969; Horibe *et al.*, 1969; Hecht, Savin, 1970, 1971, 1972; Emiliani, 1971; Weiner, 1972, 1975; Vergnaud-Grazzini, 1976, Kahn, 1977 *b*).

Most recently $^{13}C/^{12}C$ ratios of foraminiferal tests have received much attention as a potential tool in determining depth habitats in planktonic foraminifera (Duplessy, 1972; Sommer, Matthews, 1975; Williams, Sommer, 1975; Vincent, Shackleton, 1975; Weiner, 1975; Kahn, 1977 *a*). $^{13}C/^{12}C$ ratios of foraminiferal tests may also provide spatial and temporal information regarding the $^{13}C/^{12}C$ composition of seawater (Broecker, 1971; Duplessy, 1972; Douglas, Savin, 1973; Shackleton, Kennett, 1975; Williams *et al.*, 1977). Little has been published regarding the magnitude of the vital effect on the $^{13}C/^{12}C$ ratios in forminiferal tests (Craig in Revelle and Fairbridge, 1957; Vinot-Bertouille, Duplessy, 1973; Weiner, 1975; Kahn, 1977 *b*; Williams *et al.*, 1977) and only a single work containing $\delta\,^{13}C$ determinations on tests of living planktonic foraminifera has been published (Vergnaud-Grazzini, 1976). The purpose of the present study is to examine in greater detail the magnitude and significance of non-equilibrium oxygen and carbon isotopic fractionation in living planktonic foraminifera at the specific, phenotypic, and growth stage levels. The study also investigates the use of the carbon isotopic composition of planktonic foraminiferal tests as a means of determining the depth habitats of these organisms. The samples used in this study were collected from extremely limited, known depth intervals in the eastern equatorial Atlantic Ocean in which environmental parameters such as temperature and salinity were measured simultaneously. In addition, information is available regarding the distribution, ecology, and population dynamics of the foraminifera in the area (Jones, 1967, 1969; Boltovskoy, 1968), the local and regional physical oceanography (Metcalf *et al.*, 1962; Neuman, Williams, 1965; Rinkel *et al.*, 1966; Mazeika, 1968; National Oceanographic Data Center, unpub. data), as well as the oxygen (Craig, Gordon, 1965) and carbon (Duplessy, 1972) isotopic composition of the water at nearby locations.

AREA OF STUDY

The samples utilized in the present investigation were collected from a portion of the eastern Equatorial Atlantic Undercurrent and adjacent water masses (Fig. 1). The Undercurrent is a shallow easterly-flowing subsurface countercurrent which is about 300 km wide and is more or less symmetrically located about the equator (Metcalf *et al.*, 1962). The most outstanding feature of the Undercurrent is a core of high-salinity water which probably is associated with the main current axis (Rinkel *et al.*, 1966). The $35.7^{0}/_{00}$ isohaline has been used to define chemically the limits of the Undercurrent (Jones, 1969).

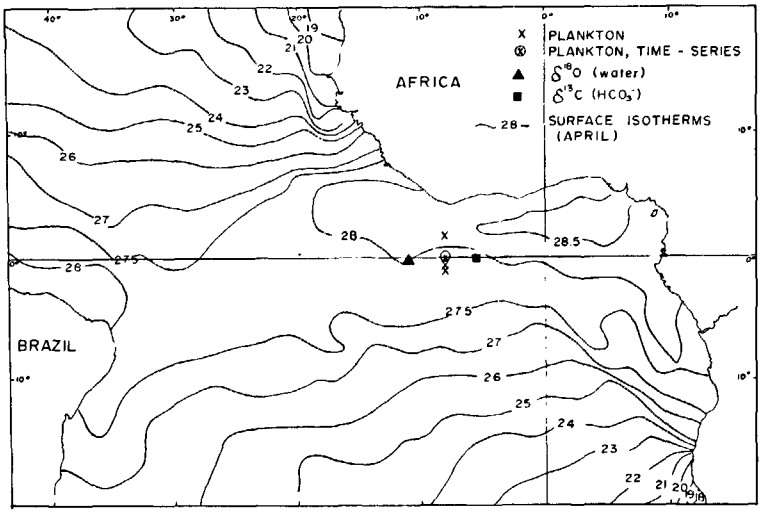
MATERIALS AND METHODS

Collection and storage procedures

The plankton samples and environmental data used in this study were obtained by J. I. Jones during *R. V. Pills-*

Figure 1

Map showing locations of plankton and water samples discussed in the text, with the mean surface water temperatures (°C) for April (isotherms after Mazeika, 1968).



bury cruise P6503 from April 16 to May 2, 1965, while at an anchored time-series station (samples # 10-# 43) located approximately on the equator (0°1'S) at long. 7°55'W, and during transects at nearby locations at the same longitude from 1°38'N to 0°58'S (Fig. 1). STD probe lowerings and hydrographic casts were alternated continuously with the plankton stations. The plankton collections were made with 200 micron mesh, opening-closing plankton nets, having a one-half-meter square mouth opening, equipped with flow meters and time-depth recorders. This sampling design provided quantitative plankton samples from limited depth intervals with no contamination from other water layers over a depth range of 30-260 m; a temperature range of 12.63-26.52°C; and salinity range of 35.19-36.12‰ (Table 1). Immediately following collection, the plankton samples were preserved in a seawater and formalin solution buffered with hexamethyalinetetramine (hexamine) and then refrigerated.

After separation (technique described by Bé, 1959 *a*), the high density fractions (the shelled plankton concentrates) were placed into plastic vials which then were filled with seawater-buffered formalin solution and sealed with plastic snap-caps. The sample vials were kept in a cool storeroom, and the pH of their solutions was checked periodically and maintained at 8-8.5. Several aliquots consisting of monospecific (or monophenotypic) foraminiferal populations were picked from the shelled plankton concentrates within a few months after their collection on April 28 and 30, 1965. These aliquots were rinsed with distilled water and placed in glass screw-cap vials. In November of 1973 the samples, kept in buffered formalin, were rinsed with distilled water, then switched to 70% ethyl alcohol. Preliminary isotopic analyses showed that preservation in buffered formalin or ethyl alcohol has no effect on the isotopic composition of the tests of living planktonic foraminifera (Kahn, 1977 *a*). Only specimens containing protoplasm, and therefore considered living at the time of capture, were included in the population counts or isotopic analyses.

Table 1
Environmental data of samples studied.

Sample	Depth (m)	Temp. (°C) (*a*)	Sal. (‰) (*a*)	$\delta^{18}O$ (eql) (*b*)	$\delta^{13}C$ (HCO_3^-) (*c*)	$\delta^{13}C$ (eql) (*e*)
35 B	30	26.52	35.64	−1.61	1.77 (*d*)	3.85
7 B	30	26.50	35.63	−1.60	1.77 (*d*)	3.85
43 B	45	25.17	36.01	−1.33	1.50	3.53
37 C	45	25.07	36.06	−1.31	1.50	3.53
—	50	—	—	—	1.40 (*d*)	≃3.43
8 B	55	25.15	36.11	−1.33	1.35	3.38
49 B	55	22.86	36.12	−0.85	1.35	3.30
5 B	70	17.38	35.66	0.35	1.31	3.07
34 D	75	18.44	35.66	0.11	1.30 (*d*)	3.10
36 D	85	17.88	35.85	0.23	1.33	3.11
7 C	100	15.37	35.55	0.82	1.35 (*d*)	3.04
6 C	105	15.74	35.63	0.73	1.35	3.05
6 D	200	13.07	35.30	1.38	1.35	2.96
4 D	260	12.63	35.19	1.48	1.35	2.94

(*a*) Measured *in situ*.
(*b*) Calcite equilibrium values relative to Chicago PDB-1, calculated from Horibe-Oba (1972) calcite-water equilibrium equation (see text) using $\delta_w^+ = 0.43$‰ from Craig and Gordon (1965).
(*c*) Data from Duplessy (1972, Fig. 48); values in per mille vs. PDB-1. Surface value = 1.87‰.
(*d*) Values of actual data points; other values estimated from best fit curve.
(*e*) Carbonate equilibrium values (vs. PDB-1), where $\delta^{13}C\,(eql) = \delta^{13}C\,(HCO_3^-) + 1.85 + 0.035\,(t-20)$ (after Emrich *et al.*, 1970). Surface value ≃4.03‰.

Isotopic analysis

Between 8-40 specimens were used in a single analysis. Each foraminiferal specimen was manually clean of adhering foreign material and crushed under AR grade methanol with a glass rod. The samples were then dried in an oven at 45° ± 3°C and vacuum roasted for 75 minutes at 450°C to remove volatile organic contaminants. Immediately after cooling to near room temperature *in vacuo*, the samples were reacted with concentrated phosphoric acid at 25.0° ± 1°C for ~ 12 hours. The evolved CO_2 gas was purified of water, then analyzed in a VG micromass 602 C mass spectrometer or in a Nuclide 6-60 mass spectrometer. The results are reported in δ notation as per mil (‰) deviations from the Chicago PDB-1 CO_2 (Urey *et al.*, 1951) where

$$\delta\,(‰) = \left(\frac{R_{sample}}{R_{PDB}} - 1\right) \times 10^3,$$

and R is the $^{18}O/^{16}O$ or $^{13}C/^{12}C$ ratio. Carbon isotope values are calibrated through the belemnite standard LJ-1 which has a value of −0.75‰ vs. PDB-1 (H. Linck, pers. comm., 1976). Oxygen isotope values are calibrated through LJ-2, the Scripps water standard, which has a δ value of −0.59‰ vs. PDB-1 (Craig, 1965, p. 4-5). The analytical precision at USC based on repeated preparations and analyses of foraminifera from the same sample is ±0.07‰ (1σ) for $\delta^{18}O$ and ±0.05‰ (1σ) for $\delta^{13}C$. The twenty-one pairs of duplicate foraminifera samples analyzed by the author at Brown University have precision of ±0.03‰ (average mean deviation) for $\delta^{18}O$ and ±0.09 (average mean deviation) for $\delta^{13}C$. Interlaboratory calibrations were made through analyses of the same CO_2 gas sample.

Calculations

In this study isotopic temperatures were calculated using the empirically derived equilibrium relationship

of Horibe and Oba (1972) for calcite and water. This relationship is:

$t = 17.04 - 4.34\,(\delta_s^+ - \delta_w^+) + 0.16\,(\delta_s^+ - \delta_w^+)^2$,

where t is temperature in Celsius degrees, δ_s^+ is the measured $\delta^{18}O$ CO_2 obtained from the reaction of the calcite sample with concentrated phosphoric acid at 25°C, corrected for any systematic mass spectrometer affects (Craig, 1957), and δ_w^+ is the corrected $\delta^{18}O$ of CO_2 equilibrated with the water from which the carbonate was precipitated. The selection of the Horibe-Oba calcite equation is based on (1) the relatively high precision of the measurements by which it was derived ($1\sigma = \pm 0.02‰$), (2) the use of organic carbonate consisting of 100% pure calcite from the normal growth edge of naturally cultured shells (pelecypod), (3) the utilization of analyses of the water in which and during which the shell growth occurred, and (4) the incorporation of daily water temperature measurements. Details of the work of Horibe and Oba (1972), and evidence of possible errors in isotopic temperature scales due to the utilization of more than one crystal form of calcium carbonate is discussed by Kahn (1977, p. 201). The Horibe-Oba calcite-water temperature equation is parallel to the equation of Epstein *et al.* (1953) with the Horibe-Oba relationship 0.13-0.14‰ more positive between temperatures of 12.6-26.5°C. These differences are equivalent to temperature differences of 0.5-0.7°C.

Using *in situ* temperature measurements taken with the plankton collections estimates were made of the $\delta^{18}O$ calcite deposited in equilibrium with ambient seawater at each sample location using the surface water $\delta^{18}O$ value of +0.43‰ vs. PDB for 0° 11°W (Craig, Gordon, 1965, p. 38) (Table 1).

The $\delta^{13}C$ values for dissolved bicarbonate given in Table 1 are based upon the $\delta^{13}C$ measurements made by Duplessy (1972) on water samples from 00°08'N, 05°35'W (Fig. 1). Estimates of the $\delta^{13}C$ values for $CaCO_3$ in isotopic equilibrium with dissolved bicarbonate were then made using the fractionation relationship of Emrich *et al.* (1970) (Table 1).

Table 2

Preferred (a) ranges of depth, temperature and salinity for selected (b) species collected during P 6503 anchored times-series plankton station, 25-30 April, 1965 (00°01'S, 07°55'W) (from Jones, 1969).

Species	Preferred depth range (m)	Preferred temperature range (°C)	Preferred salinity range (‰)
G. aequilateralis	25-74	16.00-25.99	35.5-36.0
G. ruber (f. rosea)	0-49	25.00-28.99	35.6-36.0
G. ruber (f. alba)	25-99	14.00-28.99	35.4-35.8
G. trilobus (f. typica)	25-49 (*c*)	25.00-28.99	35.4-35.1
G. trilobus (f. sacculifera)	50-74 (*d*)	25.00-26.00	35.9-36.0
G. menardii	0-99 (*e*)	25.00-27.99	35.4-36.1
G. tumida (g)	—	—	—
N. dutertrei	25-49	24.00-26.99	35.9-36.0
O. universa	25-74	25.00-26.99	35.8-36.1
P. obliquiloculata	25-74	25.00 (*f*)	35.9-36.1
S. dehiscens (g)	—	—	—

(*a*) > 50% of the total standing crop (% SC) collected during the time-series.
(*b*) Only those species analyzed isotopically have been included in this table.
(*c*) 77% SC from 0-49 m.
(*d*) 87% SC from 0-74 m.
(*e*) Maximum per-cent SC in 25-49 m depth interval.
(*f*) 45% SC from this temperature.
(*g*) Insufficient specimens for significant calculation of preferred environmental range.

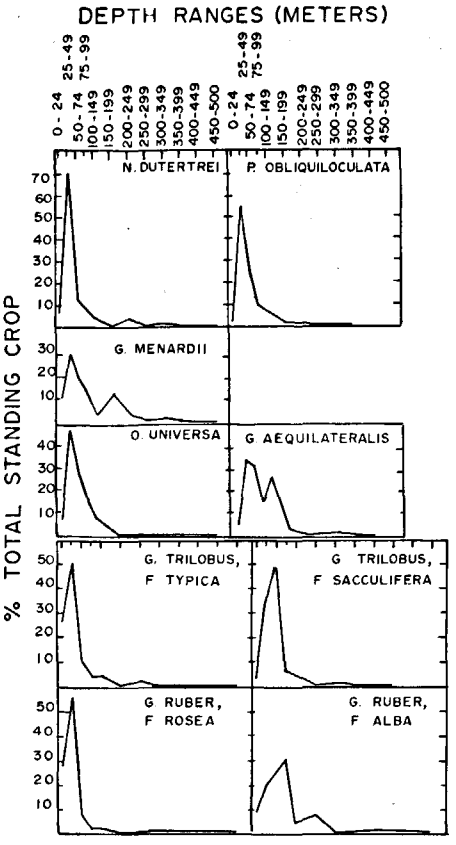


Figure 2 *Percentage of total standing crop versus depth, time-series P 6503 25-30 April, 1965, 0°01'S at 7°55'W (from Jones, 1969).*

RESULTS

Isotopic differences between species

All of the species analyzed in the present study, except perhaps *Globorotalia tumida* and *Sphaeroidinella dehiscens*, have preferred depth ranges in the upper

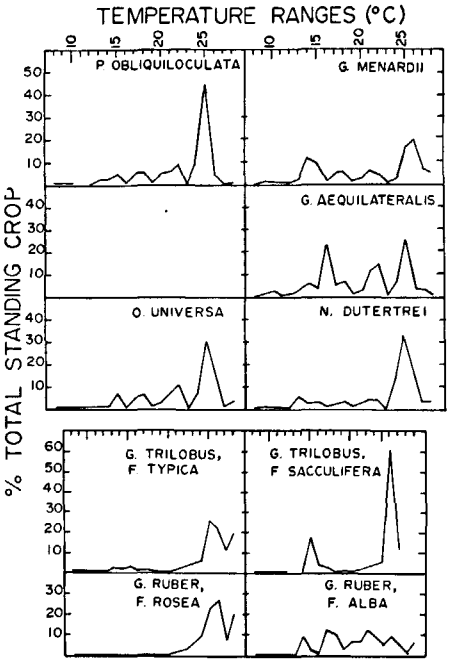


Figure 3 *Percentage of total standing crop versus temperature, time-series P 6503 25-30 April, 1965, 0°01'S at 7°55'W (from Jones, 1969).*

100 m and maximum preferred temperatures of 25-29°C (Table 2; Fig. 2 and 3). Most of the isotopic temperatures (Table 3) exceed the maximum preferred temperatures of each species including 16 samples which exceed the highest observed surface water temperature (29.62°C) in the entire equatorial Atlantic (2°19'N, 8°05'W, April 15, 1965; National Oceanographic Data Center, unpub. data). Ten $\delta^{18}O$ values are still depleted relative to the estimated minimum equilibrium $\delta^{18}O$ values for calcite $-2.39‰$ (Table 3) which results if (1) the minimum reported value for the isotopic composition of equatorial Atlantic waters ($\delta_w = +0.31‰$ vs. PDB-1; Craig, 1965) is used, and (2) it is assumed that all tests are secreted at the surface during the regions highest observed surface temperature, and (3) even the standard deviations of the measurements ($1\sigma = \pm 0.05‰$) is sub-

Table 3. *Comparison of isotopic data and environmental parameters (a)*

Sample (*b*)		Depth (m)	*In situ* temp. (MT)	$\delta^{18}O$ (OM) (*c*)	$\delta^{18}O_{eq}$ (OE)	OM-OE	Isot. temp. (IT)	IT-MT	IT-ST	Sfc. temp. (ST)	$\delta^{13}C$
7 C *aeq*	< 500	100	15.37	−2.07	0.82	−2.89	28.89	13.52	0.70	28.19	−0.14
7 C *aeq*	> 500	100	15.37	−1.66	0.82	−2.48	28.81	11.44	−1.38	28.19	−0.44
35 B *rbr*	*ros*	30	26.52	−2.69	−1.60	−1.09	32.14	5.62	3.60	28.58	—
43 B *rbr*	*ros*	45	25.17	−2.42	−1.33	−1.09	30.71	5.54	2.12	28.59	—
4 D *rbr*	< 417	260	12.63	−2.79	1.49	−4.28	32.67	20.04	3.72	28.95	1.79
4 D *rbr*	> 417	260	12.63	−2.81	1.49	−4.30	32.78	20.15	3.83	28.95	2.23
43 B *typ*	–	45	25.17	−2.43	−1.33	−1.10	30.76	5.59	2.17	28.59	—
37 C *typ*	–	45	25.07	−2.50	−1.31	−1.19	31.13	6.06	2.41	28.72	—
49 B *typ*	< 417	55	22.86	−2.37	−0.85	−1.52	30.45	7.59	2.70	27.75	1.44
49 B *typ*	> 417	55	22.86	−2.27	−0.85	−1.42	29.92	7.06	2.17	27.75	2.13
7 C *typ*	< 417	100	15.37	−1.77	0.82	−2.59	27.36	11.99	−0.83	28.19	1.59
7 C *typ*	> 500	100	15.37	−1.70	0.82	−2.52	27.01	11.64	−1.18	28.19	2.04
8 B *sac*	< 589	55	25.15	−1.78	−1.33	−0.45	27.41	2.26	−0.39	27.80	1.62
8 B *sac*	> 707	55	25.15	−1.39	−1.33	−0.06	25.47	0.32	−2.33	27.80	2.25
49 B *sac*	< 500	55	22.86	−2.25	−0.85	−1.40	29.82	6.96	2.07	27.75	1.58
49 B *sac*	> 500	55	22.86	−2.35	−0.85	−1.50	30.34	7.48	2.59	27.75	2.34
7 C *sac*	< 500	100	15.37	−1.80	0.82	−2.62	27.51	12.14	−0.68	28.19	1.76
7 C *sac*	> 707	100	15.37	−1.80	0.82	−2.62	27.51	12.14	−0.68	28.19	2.19
7 B *men*	< 841	30	26.50	−2.25	−1.60	−0.65	29.82	3.32	1.63	28.19	2.63
7 B *men*	> 841	30	26.50	−1.64	−1.60	−0.04	26.71	0.21	−1.48	28.19	2.09
49 B *men*	> 841	55	22.86	−1.75	−0.85	−0.90	27.26	4.40	−0.67	27.93	1.92
34 D *men*	N	75	18.44	−1.27	0.11	−1.38	24.88	6.44	−3.39	28.27	1.59
34 D *men*	K	75	18.44	−1.27	0.11	−1.38	24.88	6.44	−3.39	28.27	1.49
6 C *men*	> 841	105	15.74	−0.93	0.73	−1.66	23.24	7.50	−4.69	27.93	1.72
4 D *men*	< 841	260	12.63	−2.41	1.49	−3.90	30.66	18.03	1.71	28.95	1.83
4 D *men*	> 841	260	12.63	−1.71	1.49	−3.20	27.06	14.43	−1.89	28.95	1.87
6 C *tum*	< 841	105	15.74	−0.95	0.73	−1.68	23.33	7.59	−4.60	27.93	1.66
6 C *tum*	> 841	105	15.74	−0.87	0.73	−1.60	22.95	7.21	−4.98	27.93	1.48
6 D *tum*	> 707	200	13.07	−0.43	1.38	−1.81	20.89	7.82	−7.04	27.93	1.46
7 B	ADT	30	26.50	−2.23	−1.60	−0.63	29.72	3.22	1.53	28.19	3.16
7 B *dut*	JUV	30	26.50	−3.27	−1.60	−1.67	35.29	8.79	7.10	28.19	2.42
43 B *dut*	—	45	25.17	−1.72	−1.33	−0.39	27.11	1.94	−1.48	28.59	—
36 D *dut*	N	85	17.88	−1.82	0.24	−2.06	27.61	9.73	−1.27	28.88	1.87
36 D *dut*	K	85	17.88	−1.42	0.24	−1.66	25.62	7.74	−3.26	28.88	2.13
7 C *dut*	N	100	15.37	−1.34	0.82	−2.16	25.22	9.85	−2.97	28.19	2.48
7 C *dut*	K	100	15.37	−1.28	0.82	−2.10	24.93	9.56	−3.26	28.19	1.97
7 B *unv*	< 589	30	26.50	−2.89	−1.60	−1.29	33.21	6.71	5.02	28.19	2.14
7 B *unv*	> 589	30	26.50	−2.89	−1.60	−1.29	33.21	6.71	5.02	28.19	2.89
5 B *unv*	< 589	70	17.38	−1.61	0.35	−1.96	26.56	9.18	−1.10	27.66	1.98
5 B *unv*	> 589	70	17.38	−1.94	0.35	−2.29	28.22	10.84	0.56	27.66	2.51
4 D *unv*	< 500	260	12.63	−2.15	1.49	−3.64	29.30	16.67	0.35	28.95	1.88
4 D *unv*	> 500	260	12.63	−2.21	1.49	−3.70	29.61	16.98	0.66	28.95	2.12
8 B *obl*	< 417	55	25.15	−1.19	−1.33	0.14	24.49	−0.66	−3.31	27.80	0.96
8 B *obl*	> 417	55	25.15	−0.59	−1.33	0.74	21.63	−3.52	−6.17	27.80	1.01
5 B *obl*	< 417	70	17.38	−0.87	0.35	−1.22	22.95	5.57	−4.71	27.66	0.74
5 B *obl*	> 500	70	17.38	−1.40	0.35	−1.75	25.52	8.14	−2.14	27.66	1.05
7 C *obl*	< 417	100	15.37	0.01	0.82	−0.81	18.89	3.52	−9.30	28.19	1.25
7 C *obl*	> 417	100	15.37	−1.32	0.82	−2.14	25.12	9.75	−3.07	28.19	0.96
7 C *deh*	> 707	100	15.37	−1.06	0.82	−1.88	23.86	8.49	−4.33	28.19	1.86

(*a*) MT, *in situ* measured temperature; OM, $\delta^{18}O$ measured (foram. test); OE, *in situ* $\delta^{18}O$ equilibrium value; IT, isotopic temperature; ST, surface temperature; $\delta^{13}C$, $\delta^{13}C$ of foram. test.
(*b*) *aeq, G. aequilateralis; rbr ros, G. ruber, f. rosea; rbr, G. ruber, f. alba; typ, G. trilobus, f. typica; sac, G. trilobus, f. sacculifera; men, G. menardii; dut, N. dutertrei; unv, O. universa; obl, P. obiquiloculata; deh, S. dehiscens;* N, normalform; K, kummerform; ADT, adult; JUV, juvenile. Numbers immediately following species names are population size categories in microns delimited by the nearest standard sieve mesh.
(*c*) Most values are the means of two or more separate analyses.

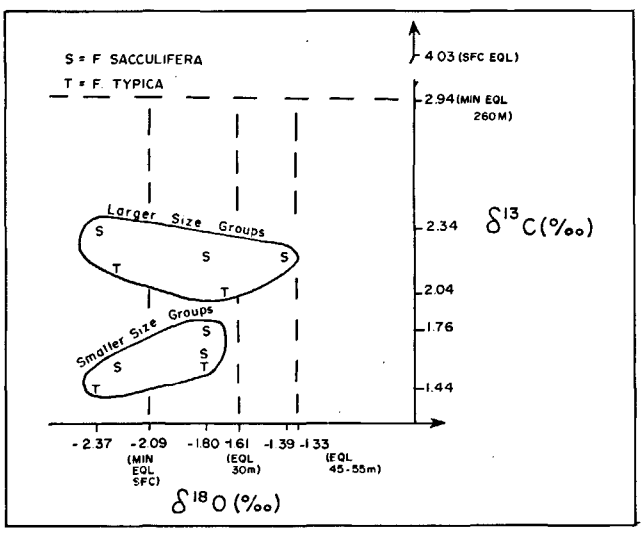
tracted. The possibility of higher δ_w values and subsurface growth would both result in greater estimated departures from isotopic equilibrium. A $\delta^{18}O$ value of $-2.09^0/_{00}$ for calcite (δ_s) precipitated in isotopic equilibrium derived from the highest surface water temperature observed during sample collection (28.99°C) and the local δ_w value ($+0.43^0/_{00}$ vs. PDB) is considered a conservative estimate upon which minimum estimates of the magnitude of departures from oxygen isotopic equilibrium are estimated. It seems reasonable to assume that most, if not all, primary test growth occurs within the preferred depth range of a particular species or phenotype. Therefore, for those taxa whose preferred depth and temperature ranges (Table 2) indicate test growth only below 0-25 m, the maximum preferred temperature is utilized for departure estimates. The local distribution of the species and phenotypes analyzed (illustrated in Figures 2 and 3) as well as the depth distribution of the samples (Table 1) is also considered. It is important to note that diurnal vertical migration is not a significant phenomenon in the region of study (J. I. Jones, pers. comm., 1968), as is most often the case in tropical regions (Boltovskoy, 1964; Berger, 1969 *a*). Also changes in depth habitat due to changes in seawater density with seasonal temperature fluctuations and specimen displacement due to upwelling or mixing of water masses are minimal in the study region (J. I. Jones, pers. comm.). The presence of juvenile populations in upper water layers (seen throughout the entire collection period) is indicative of local breeding population and indicates that the distance between the site of test growth and sample collection is minimal. Assuming an average residence time for the species of planktonic foraminifera in this study of about one week (Berger, 1971; Bé *et al.*, 1977), test growth could have occurred no more than 84 nautical miles (for those with depth habitats in the surface current) to 384 nautical miles (depth habitat in the undercurrent) upstream (Kahn, 1977 *a*, p. 62). All but one of the $\delta^{13}C$ values fall below the estimated carbonate isotopic equilibrium range (Fig. 4). Therefore, in general, the isotopic results show that there is a depletion in ^{13}C, as well as in ^{18}O in planktonic foraminiferal tests relative to equilibrium values. This impoverishment in both heavy isotopes occurs with a negative linear correlation between $\delta^{18}O$ and $\delta^{13}C$ ($r = -.412$, $p < .01$; Fig. 4).

The width of the range in isotopic temperatures (calculated only for those species collected from more than two depths), varies from 42% (for *Globigerinoides trilobus, forma typica*) to 93% (for *Neogloboquadrina dutertrei*) of that of the samples *in situ* temperature interval, possibly indicating test growth throughout various portions of the water column. This conclusion is supported by the relatively wide ranges of the calcite $\delta^{13}C$ values which even exceed those of the sampled water interval of each species. It is apparent, however, that in most cases the presence of a vital effect for both oxygen and carbon, along with the inclusion of analyses made on individuals from smaller size groups, has expanded the isotopic temperature and $\delta^{13}C$ ranges and thereby exaggerated the apparent depth interval over which growth has occurred. In fact, the ranges of the $\delta^{13}C$ values for *Globorotalia menardii* (=*G. cultrata* of authors) and *N. dutertrei* are greater than that of the calculated equilibrium $\delta^{13}C$ range in the entire upper 260 m of the water column. In addition, all of the isotopic temperature ranges (for species collected from more than two depths) exceed the magnitude of the respective preferred temperature ranges in spite of the likelihood that the lack of analyses of some species from shallower depths may have narrowed the isotopic temperature range somewhat.

The positive correlation which exists between $\delta^{18}O$ values and depth for *N. dutertrei* ($r = 0.808$, $p < .05$), *G. trilobus, G. menardii, G. tumida* also indicates test growth over at least a portion of the depth interval from which these species were analyzed. It is possible, therefore, that in some instances addition of chambers somewhat below that of the maximum preferred temperature (but probably still within the preferred temperature range) has offset all or part of a negative vital effect which would be found in specimens which grew

Figure 4

Plot of $\delta^{18}O$ versus $\delta^{13}C$ in tests of living planktonic foraminifera from the eastern equatorial Atlantic Ocean. Calcite equilibrium values, shown by vertical and horizontal lines, were calculated from the relationship of Horibe and Oba (1972) *and of Emrich* et al. (1970) *respectively (modified from Kahn, 1977 a).*
A = G. aequilateralis; *R* = G. ruber, f. alba; *Q* = G. trilobus, f. typica; *S* = G. trilobus, f. sacculifera; *M* = G. menardii; *T* = G. tumida; *D* = N. dutertrei; *U* = O. universa; *O* = P. obliquiloculata; *H* = S. dehiscens; *SFC* = *surface.*



their entire tests near the surface. Therefore in making estimates of departures from isotopic equilibrium the data from the shallowest sample was used.

Isotopic differences between phenotypes

Separate isotopic analyses were made kummerform (i. e., diameter of final chamber equal to, or less than that of the penultimate chamber; Berger, 1969 C) and normalform (i. e., diameter of final chamber greater than that of the penultimate chamber) populations of *G. menardii* and *N. dutertrei*, and of the phenotype of *G. trilobus* with a sac-like final chamber (*f. sacculifera*) and the phenotype without a sac-like final chamber (*f. typica*). In only a single comparison was there a significant difference between the phenotypes of the same sample (Table 4). Although the kummerform specimens of *N. dutertrei* from the 85 m sample recorded an isotopic temperature 2°C colder than that of the normalforms, the isotopic temperature of the kummerforms from the 100 m sample was only 0.29°C colder than the normalforms. The differences in the $\delta^{13}C$ values for these phenotypes of *N. dutertrei* from these samples were also inconsistent.

Isotopic analyses of the phenotypes of *Globigerinoides ruber* based on test wall color were unfortunately not made from specimens taken from the same sample (Table 3). Approximately equal isotopic temperatures are recorded by these phenotypes if a correction is made for the difference in the measured *in situ* temperatures found in their preferred depth range at their respective collection sites (1-1.5°C higher at station 4). Although these phenotypes have overlapping depth ranges (Table 2), *forma alba* (white) ranges into deeper depths (Fig. 2) and displays a much wider preferred temperature range (Fig. 3) than *forma rosea* (pink). The equal (or higher) isotopic temperatures of *F. alba* compared to those of *f. rosea*, therefore, indicate a slightly greater ($=0.1$-$0.2^0/_{00}$) negative departure from oxygen isotopic equilibrium (i. e., depletion in ^{18}O), although the number of analyses are too few to be conclusive. Isotopic analyses of these two phenotypes of *G. ruber* from the same plankton tow sample would be more definitive than the present comparison.

The isotopic temperature for *S. dehiscens*, a form which is considered by some authors to be an aberrant terminal stage of *G. trilobus*, is approximately 3.5°C lower than that of *G. trilobus* (*f. typica* and *f. sacculifera*) from the same sample (Table 3). It is possible that part of this difference may be due to a smaller negative departure from oxygen isotopic equilibrium in *S. dehiscens* than the $0.5^0/_{00}$ which is postulated for *G. trilobus*. If it is assumed that test growth is restricted to a single depth, the isotopic temperature yield by *S. dehiscens*, which was collected from 100 m, is indicative of test growth in oxygen isotopic equilibrium at a depth of 50 m (or a little deeper if a small vital effect is present). If, on the other hand, the outer crust is secreted at a deeper depth than the rest of the test, as suggested by Bé and Hemleben (1970), the majority of test growth must have taken place at a depth even shallower than 60 m. In any case, in the absence of any evidence of upward displacement of this population of *S. dehiscens*, crust secretion must have occurred at a depth no greater than 100 m, which is considerably shallower than the sub-500 m depths suggested by Bé and Hemleben (1970), and even less than the 140 m assumed possible by Bé and van Donk (1971). These authors, however, could be dealing with specimens with a more fully developed crust, the average depth of secretion which can be at least as shallow as 100 m (according to the results of the present study). The $\delta^{13}C$ value for *S. dehiscens* lies between that of the larger and smaller size groups of *G. trilobus*, thereby lending support to the assumed absence of upward displacement of the former species.

Isotopic differences between size groups

Significant differences in either $\delta^{18}O$ or $\delta^{13}C$ (or likely significant differences where only single comparisons were made) were found between the larger and smaller size groups from the same sample in 8 out of the 9 species

Table 4

Difference in isotopic composition between phenotypes of the same species of living planktonic foraminifera (a).

Species	Sample	Depth (m)	δ ($^0/_{00}$) normalform minus kummerform, or *f. typica* minus *f. sacculifera* (*b*)	
			$\delta^{18}O$	$\delta^{13}C$
G. menardii	34 D	75	0.01±0.03 (2)	0.10±0.12 (2)
N. dutertrei	36 D	85	−0.40±0.01 (*d*) (2)	−0.26±0.09 (2)
	7 C	100	−0.06	0.51
G. trilobus	49 B	55 (*c*)	−0.12±0.04 (2)	−0.14±0.13 (2)
	49 B	55	+0.08	−0.21
	7 C	100 (*c*)	+0.03±0.07 (2)	−0.17±0.36 (2)
	7 C	100	+0.10±0.06 (2)	−0.15±0.06 (2)

(*a*) All comparisons were made between sample aliquots in the same size class.
(*b*) Normalform vs. kummerform for *G. menardii* and *N. dutertrei*; *forma typica* vs. *forma sacculifera* for *G. trilobus*.
(*c*) "Smaller" size group. All other comparisons are between populations in the "larger" size groups. When more than one aliquot of each phenotype was analyzed (number of aliquots in parentheses) the reported value is the mean difference ± the standard error of the differences.
(*d*) Significant at the 0.01 level.

tested in this manner (Table 5). There were no significant $\delta^{18}O$ differences with test size in *G. ruber*, *G. trilobus* (*f. typica*), and *G. tumida*, indicating test growth at constant depths. Nevertheless, there are significant enrichments in ^{13}C with increasing size in *G. ruber*, and in *G. trilobus*, *f. typica* (Fig. 5). This suggests an ontogenetic decrease in the vital effect for $\delta^{13}C$ in these species. Similar ^{13}C enrichments also were present consistently in *G. trilobus* (*f. sacculifera*), *N. dutertrei*, and *O. universa*, even though the $\delta^{18}O$ results indicate growth at various depths. The large enrichment in ^{18}O with size in *N. dutertrei*, and perhaps also the smaller enrichments in *G. menardii*, appear to indicate an ontogenetic decrease in the vital effect for $\delta^{18}O$. The isotopic temperature of the larger size group of *N. dutertrei*, which was collected at 30 m, exceeds by about 4.5°C the isotopic temperature recorded by this species in this size group collected at 100 m at the same oceanographic station (Table 3). This argues against the upwelling (or vertical migration) of specimens which grew their tests at deeper depths as an alternative explanation for the observed $\delta^{18}O$ differences. In the case of *G. menardii*, the similarity in ^{18}O enrichments with increasing size for populations from both 30 m and 260 m tends to eliminate vertical relocation as a factor.

Where substantial depletions of ^{13}C with increasing size were recorded, they either were accompanied by conflicting results obtained from the samples collected at other depths in the water column, as in the case of *G. menardii* and *Pulleniatina obliquiloculata*, or consist only of a single comparison (*Globigerinella aequilateralis*=*G. siphonifera*) (Table 5). No species consistently showed ^{18}O depletions with increasing size, however, *P. obliquiloculata* did record ^{18}O depletions in 2 of 3 analyses. The suspected presence of upwelling at station 5, where the 70 m samples of *O. universa* and

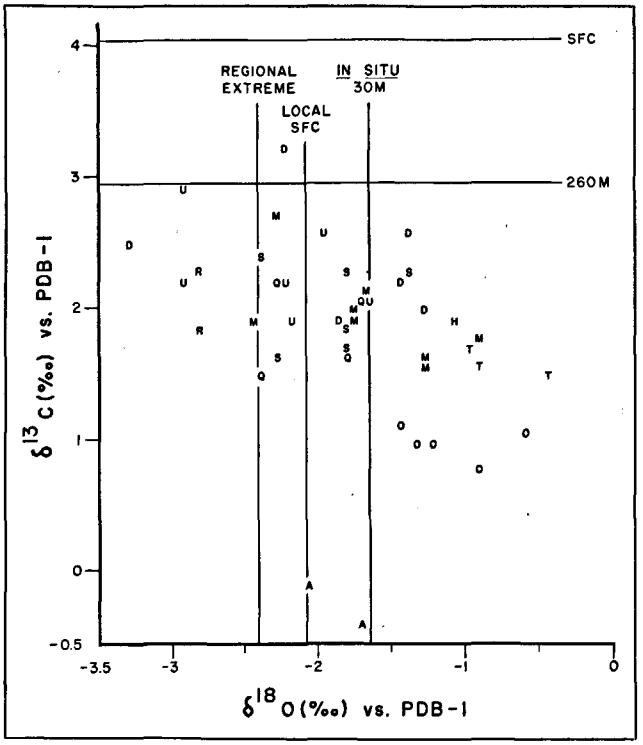


Figure 5

Oxygen and carbon isotopic compositions of larger and smaller size groups of phenotypes of Globigerinoides trilobus *collected at* 45, 55 *and* 100 *m. MIN=minimum, SFC=surface, and EQL=equilibrium value* (*Table* 1).

Table 5

Difference in isotopic composition between larger and smaller size groups of living planktonic foraminifera from the same horizontal tow.

		δ larger-smaller (‰) (*a*)		X max. dimen. (μm) (*b*)	
Species	Depth (m)	$\delta^{18}O$	$\delta^{13}C$	Larger	Smaller
G. aequilateralis	100	0.41	−0.30	665	440
G. ruber (*f. alba*)	260	−0.02±0.06	0.44±0.01 *	492	328
G. trilobus (*f. typica*)	55	0.10±0.04	0.69±0.02 *	547	359
	100	0.07±0.06	0.45±0.10 ×	572	373
G. trilobus (*f. sacculifera*)	55	0.39±0.03 *	0.63±0.11 *	920	430
	55	−0.10±0.01 ×	0.76±0.13 ×	584	385
	100	0.00±0.08	0.43±0.35	798	423
G. menardii	30	0.61±0.07 ×	−0.54±0.00 **	1 075	650
	260	0.70±0.11 ×	0.04±0.18	1 089	622
G. tumida	105	0.08	−0.18±0.11	1 052	776
N. dutertrei	30	1.04	0.74	544	366
O universa	30	0.00	0.75	613	516
	70	−0.33	0.53	730	461
	260	−0.06	0.24	603	364
P. obliquiloculata	55	0.60	0.05	481	374
	70	−0.53	0.31	568	373
	100	−1.33	−0.29	537	365

(*a*) When more than one aliquot of each size group was analyzed the reported value is the mean difference ± the standard error of the differences.
(*b*) Average standard deviation ≃ ±9%.
Significance levels: × = 0.1, * = 0.05, ** = 0.01.

P. obliquiloculata were collected, may be a factor in the inconsistency of the $\delta^{18}O$ results for these species (Table 5). Relocation does not seem to be a possible factor causing the inconsistency in the $\delta^{13}C$ results for *G. menardii* and *P. obliquiloculata.*

Summarized in Table 6 are estimates of the minimum departures from isotopic equilibrium for the various taxa and size groups examined in this study. Estimates were made using the shallowest sample(s) where possible. Definite estimates for species which may undergo upward migration (in particular *P. obliquiloculata*) could not be made.

DISCUSSION

Isotopic differences between phenotypes

Diminutive Final Chamber Growth

Berger (1969 *c*, 1970 *a*, 1970 *b*) suggests that kummerforms may represent environmentally stressed members of a species population, and indicate the termination or drastic slowing of growth. Most authors support this view (Hecht, Savin, 1970, 1972; Schott, 1970; Vilks, 1974; Malmgren, Kennett, 1976; Reiss, Halicz, 1976); however, Banerji (in Banergi *et al.*, 1971) and Olsson (1971, 1973) suggest that kummerform development is an ontogenetic feature, more or less independent of surrounding environmental conditions.

Hecht and Savin (1970, 1971, 1972) state that their oxygen isotopic data for *G. menardii*, *N. dutertrei*, and *G. ruber* supports the hypothesis that diminutive final chambers develop as a response to environmental stress. Hecht and Savin (1971) rebut the objection raised by Bé and van Donk (1971) that only the phenotypes of the shallow-dwelling species *G. ruber* shows consistent differences (a point supported by Kahn, 1977 *a*, p. 102), by offering an explanation based on an idealized growth model. In this model the zone of optimum growth (which is the zone of normalform growth) of intermediate species lies between zone of "stress" (which are the zones of kummerform growth). Hecht and Savin (1971, 1972) contend that if kummerforms of *G. menardii* and *N. dutertrei* were to be produced in stress zones both shallower and deeper than their optimum environmental depths, then the average kummerform sediment sample would be a mixture of populations which grew their tests at temperatures both higher and lower than those in the optimum zone. The average isotopic temperature of kummerform populations might then equal those of normalform ones, and would produce inconsistent results due to differences in the relative production from the 2 zones, varying with season and location.

Using the idealized growth of Hecht and Savin (1971, 1972) to explain the isotopic differences between these phenotypes from plankton samples collected from discrete depths, however, does not present such a convincing story. In order to have the isotopic temperature of kummerform populations equaling that of normalform populations of *G. menardii* collected from the optimum zone (i. e., the preferred depth range) for this species (Table 4), assuming this model, a combination of kummerforms which grew their final chambers either above or below this zone, would have had to have returned to this zone. In the case of the plankton sample of *N. dutertrei* collected below this species optimum zone at 85 m (Table 4), the proportion of kummerforms produced below the optimum zone must have exceeded significantly that of any kummerforms produced from above the optimum zone, in order to have resulted in a colder average kummerform isotopic temperature relative to that of the normalform value. In the deeper sample (100 m) of *N. dutertrei*, however, the isotopic temperature of these phenotypes are the same and, therefore, according to the model a greater proportion of kummerforms which were produced above the optimum

Table 6
Estimated minimum departures from isotope equilibrium.

	$\delta^{18}O_{(meas)}$-$\delta^{18}O_{(eql)}$ (*a*) (‰)		Temp. error (°C) (*b*)		$\delta^{13}C_{(meas)}$-$\delta^{13}C_{(eql)}$ (*c*) (‰)	
Species	Smaller	Larger	Smaller	Larger	Smaller	Larger
G. aequilateralis	−0.57	≃0?	+2.9	≃0?	−3.18	−3.48
G. ruber (*f. rosea*)	—	−0.60 (*d*)	—	+3.2 (*d*)	—	—
G. ruber (*f. alba*)	−0.71	−0.71	+3.7	+3.7	−1.25	−0.81
G. trilobus (*f. typica*)	−0.38	−0.38	+2.0	+2.0	−1.53	−0.96
G. trilobus (*f. sacculifera*)	−0.80	−0.80	+4.1	+4.1	−1.39	−0.78
G. menardii	−0.24?	≃0	+1.3?	≃0	−1.21	−1.26
G. tumida	<0	<0	>0	>0	−1.28	−1.47
N. dutertrei	−1.33 to −1.57	−0.29 to −0.53	+7.1 to +8.3	+1.53 to +2.73	−1.43	−0.69 to −0.93
O. universa	−0.95	−0.95	+5.0	+5.0	−1.11 to −1.71	−0.73 to −0.96
P. obliquiloculata	≃0?	≃0?	≃0?	≃0?	−2.05	−2.03
S. dehiscens	—	—	—	—	—	−1.18 (*d*)

(*a*) $\delta^{18}O_{(eql)}$ values used for *aeq*, *tri* (*f. sac*), *obl*, "smaller" *men*, and 1st *dut* values derived from max. value of PTR (Table 2). $\delta^{18}O_{(eql)}$ value for *rbr* (*f. ros* & *f. alb*), *tri* (*f. typ*) = −2.09‰ (see text for derivation); 2nd value for *dut* and values for *univ* from sample station sfc. temp. "Larger" *men* value from *in situ* temp.
(*b*) Error relative to temp. calculated from $\delta^{18}O_{(eql)}$ values.
(*c*) 30 m $\delta^{13}C_{(eql)}$ of +3.85‰ (Table 1) used for *dut* "smaller", 1st *dut* "larger", and 2nd values of *univ*. All other values calculated using 100 m $\delta^{13}C_{(eql)}$ value of +3.04‰.
(*d*) Value from samples containing natural distribution of specimens from both size groups.

zone must have sunk to this level. It is also important to note that the isotopic temperature recorded by kummerform populations of *N. dutertrei* in both samples is nearly the same as that recorded by the normalforms from the 100 m sample. This would seem to indicate, at least in this case, that if kummerform phenotypes were the result of growth under environmental stress, that the stress had to be something other than temperature. However, even if the final chamber of kummerform specimens are formed at temperatures significantly different than that of the average of the earlier portion of the test, it is very likely that the mass of this diminutive chamber relative to the rest of the test is insufficient for this difference to be detected consistently by the isotopic method at its current level of precision. A more definitive experiment (now underway by the author) although far more tedious even for the largest species, would be to analyze separately the diminutive final chambers and the remaining test portions from a kummerform population which was collected from a discrete depth in the water column.

Shape of the Final Chamber in G. trilobus

Although the observed preference of the phenotype of *G. trilobus* with a sac-like final chamber (*f. sacculifera*) is for colder and deeper waters than the phenotype without a sac-like final chamber (*f. typica*) (Table 2; Fig. 2 and 3), the isotopic results (Table 3) indicate that both phenotypes secrete their tests at essentially the same temperatures, and presumably at the same depths. The depths of test secretion for both of these phenotypes, therefore, would presumably be in the zone where their depth ranges overlap (33% of the total S.C. of *f. sacculifera* occurred in the preferred depth range of *f. typica* as shown in Figure 2). Hecht and Savin (1970, 1972) obtained similar results in their oxygen isotopic analyses of these phenotypes from the core-top sediments of several regions. These authors (Hecht and Savin, 1971) suggest that these results indicate that some individuals of *f. sacculifera* may spend substantial portions of their lives at deeper depths than those at which they secrete their tests. An alternative explanation for the apparent discrepancy, which is favored by the writer, is that there is a slightly greater negative departure from isotopic equilibrium (i. e., greater depletion in both ^{18}O and ^{13}C) in *f. sacculifera* than in *f. typica* which offsets the difference in temperature and depth of test secretion.

Isotopic differences between size groups

Continued test secretion, either in isotopic equilibrium or with a constant vital effect, while sinking (or migrating downward) through the water column should result in an increase in $\delta^{18}O$ and a decrease in $\delta^{13}C$ with increasing size. Likewise, a decrease in ^{18}O and an increase in ^{13}C with test size should occur during an upward ontogenetic migration, while no differences in ^{18}O or ^{13}C should occur if a constant depth habitat is maintained. Comparisons between larger and smaller size groups of several species and phenotypes from the same horizontal tow, however, reveal that in several cases the differences in ^{18}O and ^{13}C with test size are in the same direction (Table 5). Also, in even more samples, differences in ^{18}O or ^{13}C with test size occur without any significant differences occurring in the other isotope. These observations indicate that there is an ontogenetic change in the vital effect in certain species for either $\delta^{18}O$ or $\delta^{13}C$ or both.

Depth stratification of species and phenotypes

A very important aspect of the use of oxygen and carbon isotopic ratios in paleoceanographic interpretations is the depth stratification of planktonic foraminifera. For investigations directed at determining past ocean surface water temperatures or primary productivity, a species (or phenotype) that secretes its test in isotopic equilibrium only with the uppermost water layers is ideally desired. The steeper the temperature and carbon isotope gradients, the greater the importance of the accuracy of the estimation of the depth of test secretion. Oxygen isotopic analysis of subsurface-dwelling species made in addition to analysis of surface forms can provide information about the thermal structure of the upper few hundred meters of the water column. The carbon isotopic composition of planktonic foraminiferal tests secreted in isotopic equilibrium with surface water should have more positive $^{13}C/^{12}C$ ratios than those secreted in isotopic equilibrium with deeper waters due to the preferential removal of ^{12}C from upper water layers by photosynthesis (Deuser, Hunt, 1969; Duplessy, 1972).

In general, there is fair agreement between the relative depth habitats of species and phenotypes derived from population counts from the same series of plankton tow samples, and the average isotopic temperatures of living specimens based on the combined analyses of the smaller and larger size groups (Table 7, column 3). The disagreement in the relative position of *G. ruber* (*f. alba*) and *P. obliquiloculata*, in this case is apparently due, at least in part, to interspecific differences in the magnitude of non-equilibrium oxygen isotopic fractionation. The depth rankings based on $^{18}O/^{16}O$ ratios (i. e., isotopic temperatures) and on $^{13}C/^{12}C$ ratios are affected by the proportion of samples analyzed from the larger and smaller size groups for each species (or phenotype), as well as the depth distribution and total number of samples analyzed for each form. A depth ranking based on the average isotopic temperature values or on the average $\delta^{13}C$ values of only the larger size groups would not be very different from ones based on values of both size groups combined. However, if only the smaller size group data were utilized, the change in isotopic temperature values of *G. menardii* and *N. dutertrei*, in particular, and in the $\delta^{13}C$ values of most species, would result in a significantly different depth ranking. Both the average isotopic temperature values and the average $\delta^{13}C$ values calculated from only the analyses of the smaller size groups show no relationship to the depth ranking based on the plankton tow data. There is fairly good agreement between the $\delta^{13}C$ values of the larger size groups and the depth ranking from tow data. Here interspecific differences in the magnitude of non-equilibrium carbon isotopic fractionation apparently are responsible for the disagreement of the $\delta^{13}C$ values of *P. obliquiloculata* and *G. aequilateralis* with their plankton tow depth rank. It is apparent that a better comparison of depth rankings based on isotopic

analyses and plankton tow counts could be made if the specimen size frequency distribution of the original plankton samples and the aliquots picked from them for isotopic analysis were the same.

Possible causes of non-equilibrium isotopic fractionation in planktonic foraminifera

Craig (in Revelle, Fairbridge, 1957) deduced that the carbon isotopic composition of planktonic foraminiferal tests is influenced by the utilization of metabolic CO_2. Assuming that the metabolic CO_2 has a $\delta^{13}C$ value equal to that of the organic carbon of marine organisms (about $-14^0/_{00}$), he calculated that about 30% of the carbon in these tests is derived from this source, with the remaining carbon coming from dissolved oceanic bicarbonate. Assuming a $\delta^{13}C$ value for metabolic CO_2 of about $-25^0/_{00}$, Williams *et al.* (1977). Calculated that 4-18% of the carbon in the tests of planktonic foraminifera from Indian Ocean core-top samples is derived from metabolic CO_2. Using the isotopic composition of the organic carbon of marine plankton determined by Sackett *et al.* (1965) (average $\delta^{13}C$ of samples collected from 25°C water $= -21.7^0/_{00}$) and the data of the present study, the average contribution from metabolic CO_2 to the carbon of the tests of planktonic foraminifera would be about 7% (range = 3-14%).

It also has been suggested that a portion of the oxygen in the calcite of benthic (Duplessy *et al.*, 1970) and planktonic foraminifers (Vergnaud-Grazzini, 1973, 1976) also may be derived from metabolic CO_2 as had been hypothesized previously for echinoids (Weber, Raup, 1965) and reef-building corals (Keith, Weber, 1965). Therefore, if a significant proportion of foraminiferal test carbonate is derived from metabolic CO_2 [which is depleted in both ^{13}C and ^{18}O (Weber, Woodhead, 1970)] rather than originating solely from seawater bicarbonate, both the $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios would be more negative than those of $CaCO_3$ formed in isotopic equilibrium with ambient seawater. The findings of the present study (summarized in Table 6) are consistent with this idea and support it as a possible explanation of the major cause of non-equilibrium isotopic fractionation in planktonic foraminifera. It follows then that any factor that can change the diffusion rate of metabolic CO_2 would change the proportion of metabolic CO_2 incorporated into the test, either directly by changing its concentration at the site of calcification or indirectly by altering the chance of isotopic exchange between it and the seawater bicarbonate in the body fluid (Weber, Woodhead, 1970, 1972). It is possible, therefore, that an ontogenetic decrease in the metabolic rate has caused the observed decreases in the vital effect with specimen age (i. e., size) (Table 5) by reducing the proportion of test carbonate derived from metabolic CO_2.

Another factor which could decrease the concentration of metabolic CO_2 would be its uptake by photosynthesizing zooxanthellae (Goreau, 1959; Weber, Woodhead, 1970, 1972; Weber, 1974), although Land *et al.* (1975 *a*, 1977) refute this possibility. To date zooxanthellae have been found in eleven species of planktonic foraminifera (Boltovskoy, Wright, 1976; and references). Lee *et al.* (1965) report that in *Globigerinoides ruber* zooxanthellae may occupy collectively up to almost 4/5 the volume of a chamber. The effectiveness of the zooxanthellae to fix metabolic CO_2 would be expected to decrease with increasing depth (below the uppermost water layers) as the light available for photosynthesis decreases (Weber, Woodhead, 1970; Weber *et al.*, 1976), thereby increasing the proportion of metabolic CO_2 incorporated into the test. Zooxanthellae also may influence test isotopic composition by stimulating the calcification rate (Goreau, 1959; Simkiss, 1946 *a*, 1946 *b*; Pearse, Muscatine, 1971). Land *et al.* (1975 *b*) found that in most cases the greater the calcification rate of scleractinian corals containing zooanthellae, the greater were the negative departures from isotopic equilibrium for both $\delta^{18}O$ and $\delta^{13}C$. Assuming that the calcification rate in planktonic foraminifera is greater during earlier growth stages (Berger, 1969 *b*), a similar correlation of calcification and negative departures from isotopic equilibrium would be present also in some species of planktonic foraminifera (Table 6). A reduction in the vital effect, therefore, may result from normal ontogenetic decreases in the calcification rate in planktonic foraminifera with or without zooxanthellae.

Animals are thought to reflect the isotopic composition of their food (Parker, 1964; Smith, Epstein, 1970) and

Table 7

Relationship of isotopic temperatures and $\delta^{13}C$ ratios to the depth habitat ranking from plankton tow data.

	Ave. isotopic temp. (°C)			Ave. $\delta^{13}C$ ($^0/_{00}$ vs. PDB-1)		
Plankton tow rank (*a*)	Sm (*b*)	Lg	S&L	Sm	Lg	S&L
G. ruber (*f. rosea*)	—	—	31.43	—	—	—
G. trilobus (*f. typica*)*	28.91	28.47	29.44	1.52	2.09	1.80
N. dutertrei	35.29	26.70	27.93	2.42	2.32	2.34
O. universa	29.69	30.35	30.02	2.00	2.51	2.25
*P. obliquiloculata**	22.11	24.09	23.10	0.98	1.01	1.00
G. trilobus (*f. sacculifera*)	28.25	27.77	28.01	1.65	2.26	1.96
G. aequilateralis	28.89	26.81	27.85	−0.14	−0.44	−0.29
*G. menardii**	30.24	25.67	26.81	2.23	1.78	1.89
G. ruber (*f. alba*)	32.67	32.78	32.73	1.79	2.23	2.01
S. dehiscens	—	—	23.86	—	1.86	1.86
G. tumida	23.33	21.92	22.39	1.66	1.47	1.53

(*a*) Ranked by increasing depth based on per-cent Ind. values of Jones (1969) and per-cent SC (see Fig. 2). Taxa marked with an asterisk are not significantly different in rank than the preceding taxa.
(*b*) Sm, smaller size groups; Lg, larger size groups; S&L, smaller and larger group data combined.

therefore, it is possible that the carbon isotopic composition of the CO_2 respired by different species of planktonic foraminifera may vary significantly, giving rise to significant differences in test isotopic composition. Some planktonic foraminiferal species are herbivorous, others are carnivorous and still others are omnivorous (Bé *et al.*, 1977). The principal diets of some foraminifera appear to consist of selected species of diatoms, chlorophytes (green algae) bacteria and copepods (Lee *et al.*, 1966; Bé *et al.*, 1977). Unfortunately, data are not available regarding the isotopic composition of the various species eaten by planktonic foraminifera.

Most of the above speculation on the possible causes of non-equilibrium isotopic fractionation in planktonic foraminifera has been derived from experimental evidence and working hypotheses based on the studies of corals and echinoids, as very little is known about the calcification of physiological processes in planktonic foraminifera. Much more information is needed on these processes in planktonic foraminifera before more definite statements can be made on this subject.

Implications for paleotemperature studies

The data of the present study suggests that isotopic temperatures based on most species of planktonic foraminifera are biased toward warmer values due to the vital effect. The magnitude of this bias is species dependent and also may vary with the phenotypic composition and test size distribution of a population. Although this effect readily is apparent in living populations, it is not often delineated in the fossil record due to one or more factor which most often influence paleotemperatures in the opposite direction and which in some cases are difficult and, perhaps, impossible to quantify. These factors are: collection procedure, vertical mixing, and redeposition which can affect sediment age and contemporaneity of specimens at a particular horizon; selective dissolution which alters the phenotypic composition and test size distribution of species population (Berger, 1968, 1970 *a*, 1971; Savin, Douglas, 1973); seasonal differences in test production which can alter contemporaneity and phenotypic composition or a species population (Bé, 1960; Tolderlund, Bé, 1971); width of the test growth interval, regional surface temperature profile and oceanography, specimen selection (Hecht *et al.*, 1975; Kahn, 1977 *a*) and paleotemperature scale used.

Hecht *et al.* (1975) suggest that where dissolution is suspected, species populations used for isotopic measurements should be restricted by a lower and upper size limit. The results of the present study indicate that this precedure should be employed even in the case of perfectly preserved sediments in order to avoid biases imparted by significant ontogenetic differences. Without such a procedure the largest bias would be for those species which exhibit an ontogenetic change in the vital effect but do not appreciably change their tests growth depth habitat. In some species an ontogenetic decrease in the vital effect would be partially or entirely offset by continued test growth during descent in the water column.

SUMMARY AND CONCLUSIONS

- There is a depletion in ^{13}C, as well as ^{18}O in planktonic foraminiferal tests relative to equilibrium values. Estimates of the minimum departures from isotopic equilibrium range from $-0^0/_{00}$ in *P. obliquiloculata* to $-1.57^0/_{00}$ in *N. dutertrei* for $\delta\,^{18}O$, and from $-0.69^0/_{00}$ in *N. dutertrei* to $-3.48^0/_{00}$ in *G. aequilateralis* for $\delta\,^{13}C$.
- Additional evidence of the presence of a vital effect for $\delta\,^{18}O$ is given by the fact that the magnitude of the isotopic temperature ranges for those species collected from more than two depths exceed the magnitude of the respective species preferred temperature ranges. An even greater effect is shown for $\delta\,^{13}C$ with the magnitude of the ranges of $\delta\,^{13}C$ values for *G. menardii* and *N. dutertrei* exceeding that of the calculated equilibrium $\delta\,^{13}C$ range in the entire upper 260 m of the water column.
- No significant differences in $\delta\,^{18}O$ or $\delta\,^{13}C$ were found between the following phenotypes: *a*) *G. trilobus* with and without a sac-like final chamber; *b*) *G. ruber* with and without a pink test wall; and *c*) populations of *G. menardii* and *N. dutertrei* with and without kummerform final chambers. The $\delta\,^{18}O$ results are similar to those of other authors obtained from specimens from core-top sediments of several other regions.
- The hypothesis that kummerform chambers develop as a response to environmental stress is not supported by the isotopic and distributional data of this study. It appears that even if kummerforms are the result of growth under environmental stress, the stress has to be a factor other than that of temperature.
- In general, there is fair agreement between the relative depth habitats of species and phenotypes derived from plankton tow sample population counts, and the average isotopic temperatures of living populations taken from these samples. Depth rankings based on both $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios, however, are affected by the size distribution of the populations analyzed. Depth rankings based on $^{18}O/^{16}O$ or $^{13}C/^{12}C$ ratios of smaller size groups show no relationship to the plankton tow ranking. The values of larger size groups, however, yield depth rankings which are in fairly good agreement with that of the tow ranking. This observation could be explained by the presence of a relatively large vital effect for $\delta\,^{18}O$ or $\delta\,^{13}C$ in the smaller size groups of certain taxa, which decreases with test size (i. e., age). The disagreements found in the relative position of certain species between the various isotopic rankings and the tow ranking are apparently due, at least in part, to interspecific or interphenotypic differences in the relative magnitude of departures from oxygen and carbon equilibrium.
- The data strongly suggest the presence of an ontogenetic decrease of $0.5\text{-}0.6^0/_{00}$ in the vital effect for $\delta\,^{13}C$ in *G. ruber* (*f. alba*), *G. trilobus* (both *f. typica* and *f. sacculifera*), and *O. universa*. An ontogenetic decrease in the vital effect for $\delta\,^{18}O$ is present in *N. dutertrei*, and perhaps in *G. menardii*. Some of the inconsistencies in the data, and in particular those found in *P. obliquiloculata* for both $\delta\,^{18}O$ and $\delta\,^{13}C$, suggest the presence of vertical migrations in some taxa, which could have

increased, decreased or offset any ontogenetic changes in the vital effect.

• The depletion in both ^{18}O and ^{13}C in planktonic foraminiferal tests may be explained by the utilization of metabolic CO_2, which is very depleted in both heavy isotopes. A decrease in the metabolic rate and growth rate with age (i. e., size), then may be responsible for the observed ontogenic decreases in the departures from oxygen and carbon isotopic equilibrium. The influence of zooxanthellae on the isotopic composition of species that contain them also is a likely possibility.

• Some of the biases in paleotemperatures may be prevented if species populations used for isotopic analysis are limited to a certain size range. In some cases monophenotypic populations should be used.

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