FORAMINIFERAL POPULATION DYNAMICS AND STABLE CARBON ISOTOPES

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ABSTRACT. Most planktic foraminifera live within the photic zone and exhibit a life style tied to the lunar cycle. They migrate between the reproductive depth (thermocline and/or the chlorophyll maximum) and the uppermost part of the photic zone. This ontogenetic migration pattern sets the initial $\delta^{13}C$ of the foraminiferal shell. On top of that, biological fractionation processes (vital effects) modify the signal. These processes include photosynthetic activity of the symbionts and respiration of the host/symbiont complex. *Globigerinoides sacculifer* (Brady) was chosen to model ontogenetic changes in the $\delta^{13}C$ of the shell as a function of depth migration with and without vital effects.

INTRODUCTION

Reconstructions of marine paleo-environments are frequently based on stable isotope measurements. General assumptions are that a foraminifer has a rather steady life habitat throughout ontogeny and that the $\delta^{13}C$ of $\Sigma CO_2$ is constant in the mixed layer. However, because most planktic foraminifera, if not all, change their life horizon during ontogeny and because the $\delta^{13}C$ of $\Sigma CO_2$ is not necessarily constant in the mixed layer, the isotopic composition of the foraminiferal shell is not only dependent on water-mass properties (e.g. oligotrophic vs. eutrophic) and the geographic and climatic setting (e.g. upwelling, monsoon, subarctic etc.) but to an important extent on the life history of the foraminifer. Consequently, the disequilibrium precipitation of the foraminiferal shell (so called "vital effect") reported in the literature (e.g. Berger et al., 1978) can often be explained in terms of ontogenetic migration and biological fractionation. In this paper we shall discuss the potential effect of

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some of these processes on the stable carbon isotope composition of the shell of *G. sacculifer*.

**POPULATION DYNAMICS**

Despite all the useful information on biostratigraphy, stable isotopes and biology of planktic foraminifera that has been compiled (for references see, e.g., Vincent and Berger, 1981) little knowledge exists on the population dynamics of planktic foraminifers (see Hemleben et al., 1989). Only a few papers deal with the small scale temporal and spatial events that occur in populations.

![Size (µm)](image)

**Figure 1:** Lunar cycle of *G. sacculifer*. Contour plot of residual values in a size-time frame, showing that the larger size-fractions are most frequent just before full moon (FM) and that the smaller size-fractions are most frequent just after FM. Spindler et al. (1979).

Spindler et al. (1979) were the first to document that reproduction in the planktic foraminifer *Hastigerina pelagica* (d'Orbigny) is coupled to the synodic lunar cycle. Almogi-Labin (1984) has indicated that *Globigerinoides sacculifer* (Brady) reproduces at full moon in the Gulf of Elat/Aqaba. Based on a time series of plankton-net tows, a synodic lunar reproductive cycle in *G. sacculifer* (Figure 1) has been shown by Bijma et al. (1990) and subsequently confirmed by Erez et al. (1991).
Time series samples collected in the Red Sea (METEOR Cruise 5) and the northeast Atlantic Ocean (METEOR Cruise 10) demonstrate the concept of lunar cyclicity in the life cycle of other spinose planktic species, e.g. the symbiont-free, spinose species *Globigerina*

Figure 2: Relative frequency and size fraction of *G. bulloides* in respect to full moon (1 lunar day=full moon). A: in the productive zone (0-60 m). B: in the flux zone (300-500 m).
bulloides and the symbiont bearing spineose species Orbulina universa (figs. 2-3). On the other hand, the deep living non-spinose foraminifers Globorotalia scitula, G. hirsuta, and G. truncatulinoides do not respond to the lunar cycle (Figure 4) and probably have a yearly life-cycle (Hemleben et al., 1989). Because most spineose planktic foraminifers are associated with symbiotic algae, their main habitat is the euphotic zone. For instance, the number of G. sacculifer decreases drastically with depth. On the basis of absolute abundance, 95% of the shells collected in the upper 100 m of the water column live in the upper 80 m (Figure 5A). Orbulina universa d’Orbigny shows a subsurface maximum; and even the symbiont-barren Globigerina bulloides lives almost exclusively in the euphotic zone (Figure 5B-C).

The depth migration of G. sacculifer during ontogeny has recently been documented (Bijma and Hemleben, 1993). It was shown that this species does not inhabit a specific depth, but migrates up and down in the water column in response to its life cycle while growing (Figure 6). Thus, not only the absolute abundance changes with depth but also the size distribution changes with depth (Figure 6A). The small fraction (<300 μm) dominates the water column but their relative frequency decreases with depth until, between 60 and 80 m depth, the larger fractions (>300 μm) become dominant. Below 80 m depth, however, the small size fraction starts to dominate again. The cumulative plot of the relative frequency of mature (>366 μm) and immature specimens (<366 μm) versus water-depth (Figure 6A) demonstrates a bimodal pattern with a breakpoint between 60 to 80 m depth. The maximum of mature specimens coincides with the depth range 60 to 80 m. The relative number of immature specimens increases towards shallower and deeper environments. Apparently, reproduction in the central Red Sea takes place at approximately 60 to 80 m depth. Recruitment is shown by the ascent of immature specimens to the surface. High mortality rates in early ontogeny are probably responsible for the increase of immature specimens below the reproduction depth. The latter fraction is part of the shell flux to the sea floor.

A contour plot of the distribution of G. sacculifer in the productive zone demonstrates sizedependent depth preferences (Figure 6B). The plot demonstrates that the upper 20 m are the preferred habitat for immature specimens between 100 and 300 μm. The depth range between 20 and 40 m is favored by specimens from 300 to 500 μm. This is the depth where maturation takes place. Specimens between 500 and 700 μm prefer a depth range between 40 to 60 m, and specimens larger than 700 μm are found between 60 and 80 m depth, just above the reproduction depth (Figure 6B).

The depth habitat is probably dependent on the hydrological conditions and may thus differ for different water bodies. At present, we believe that the thermocline and/or the deep chlorophyll maximum determine the reproduction depth.
Figure 3: Relative frequency of *O. universa* in respect to the lunar period. A: in the productive zone (0-60 m). B: in the flux zone (300-500 m).

Figure 4: Non-spinose species do not respond to the lunar cycle. Samples were collected between 300-500 m depth. A: *G. scitula*. B: *G. hirsuta*. 
Figure 5: Mean abundance (No./m²) of planktic foraminifers in the upper 100 m of the water column. A: *Globigerinoides sacculifer* >100 μm in the Central Red Sea. B: *Globigerina bulloides* >125 μm from the North Atlantic. C: Spherical *Orbulina universa* >125 μm from the North Atlantic. The total number of specimens are bracketed.
Figure 6: A: The frequency (%) of mature (>366 μm; white) and immature (<366 μm; black) *G. sacculifer* show a characteristic break between 60 and 80 m depth. B: Contour plot of residual values in a size-depth frame, showing that larger size fractions prefer deeper depth-habitats. The cross-sections of the grid represent the data points. The centers of the nine size factions (100 μm wide) and the depth intervals are listed. The shaded area contains positive residual values, indicating a larger than average presence of a size fraction. The isolines start with 0 and are drawn at 0.05 intervals. The blank area contains negative residual values, indicating a smaller than average presence of a size fraction.

$^{813}$C OF $\Sigma$CO$_2$ AS A FUNCTION OF DEPTH

The CO$_2$-fixing enzyme of most marine algae (C$_3$-plants), RuBP-carboxylase (ribulose-1,5-bisphosphate carboxylaseoxygenase), has a higher affinity for $^{12}$CO$_2$ than for $^{13}$CO$_2$. As a result, the marine photic zone is enriched in $^{13}$C relative to equilibrium with atmospheric CO$_2$. Simultaneously, the photosynthetically fixed carbon, which is enriched in isotopically light carbon, is decomposed by bacteria resulting in lower $^{813}$C values with depth. As a result of oxygen producing photosynthesis in the surface waters and oxygen consuming bacterial decomposition in deeper waters an empirical relationship between the $^{813}$C of the total CO$_2$...
(ΣCO₂) and the apparent oxygen utilization (AOU) was established (Williams et al., 1977). Because nutrients are utilized during photosynthesis and released by bacterial decomposition, a strong negative correlation can be seen also between the δ¹³C of ΣCO₂ and nutrients. However, the correlation between δ¹³C and nutrients may be disrupted (note that the surface [PO₄] is less than the [PO₄] at 100 m depth, yet both depth have similar δ¹³C of ΣCO₂) due to the temperature dependence of the carbon isotope fractionation between atmospheric CO₂ and surface ocean ΣCO₂. The extent of the disruption depends on the relative strength of mixing within the sea and CO₂ exchange between ocean and atmosphere (Broecker and Maier-Reimer, 1992).

It is often assumed (e.g. Spero and Williams, 1989) that the δ¹³C of ΣCO₂ is constant with depth in the mixed layer. This, however, is not necessarily true. In regions with a seasonal thermocline, the δ¹³C-value of ΣCO₂ is dependent on the gross assimilation rate (GAR) in the photic zone. For a station in the North Atlantic at 35°25'N, 29°30'W a subsurface δ¹³C and oxygen maximum could be correlated to a nutrient minimum (Figure 7A-B; data courtesy Ganssen and Brummer, VU, Amsterdam). Apparently, the δ¹³C of ΣCO₂ in the "mixed layer" cannot be assumed constant. As long as the rate of δ¹³C enrichment through photosynthesis is faster than the rate of mixing, a δ¹³C-gradient will develop, independent of water stratification.

PREDICTING δ¹³C OF THE FORAMINIFERAL SHELL

Already in 1978, Berger et al. demonstrated that δ¹³C is dependent on the growth stage. They correlated the changing isotopic composition with environmental and metabolic signals, which are indeed the main influencing parameters. To predict the δ¹³C of the shell of G. sacculifer at each ontogenetic stage under equilibrium conditions (i.e. no vital effects) we used several growth statistics. Foraminifers do not grow continuously, but by addition of separate chambers (accretionary growth). Consequently, the effect of newly formed chambers on the final isotope composition of the test can be calculated by using a mass balance equation:

\[ \delta^{13}C_n = \left( \frac{W_{n-1}}{W_n} \right) \delta^{13}C_{n-1} + \left( \frac{W_n - W_{n-1}}{W_n} \right) \delta^{13}C_{\text{water}} \]  

(1)

where W stands for weight and n and n-1 are the nth and the (n-1)th chamber-stage. In addition, several other relationships must be known: 1) A growth relationship was derived from Figure 8 and is based on culture experiments with G. sacculifer,
Figure 7: A: The $\delta^{13}C$ of the total dissolved CO$_2$ (•) and the oxygen concentration (+) at 35°25'N, 29°30'W as a function of depth. The polynomial for $\delta^{13}C$ is 0.000189$\cdot$depth$^2$ +0.0206$\cdot$depth+0.853. B: The silicium (•) and the phosphate concentration (+) at the same station (data courtesy of G. Ganssen and G.J.A. Brummer, Free University of Amsterdam).
Figure 8: Growth curve of *G. sacculifer*. Best fit regression line is: \( D_n = 1.27D_{n-1} + 40 \) (for specimens \( \geq 100 \mu m \)). For explanation see text. Growth below 100 \( \mu m \) was based on measurements from Brummer *et al.* 1987.

\[
D_n = 1.27 \, D_{n-1} + 48 \quad (\text{for specimens} \geq 100 \mu m)
\]  

(2)

where \( D_n \) and \( D_{n-1} \) are the diameters for the nth and the (n-1)th chamber-stage respectively. Growth below 100 \( \mu m \) was based on measurements from Brummer *et al.* 1987. 2) The size-weight function of Anderson and Faber (1984):

\[
\text{mass (\( \mu g \))} = 2.89 - 0.0238 \times \text{size} + 0.0001 \times (\text{size})^2
\]

(3)

is used for size classes \( \geq 100 \mu m \). For specimens < 100 \( \mu m \) weight we assume a linear relationship between size and weight. (e.g. a specimen of 40 \( \mu m \) weighs 40% of the weight at 100 \( \mu m \)). 3) The \( \delta^{13}C \)-depth relationship is based on the data of Figure 7A and, 4) the ontogenetic depth-migration relationships are extracted from Figure 6B:

\[
\text{depth (m)} = -0.833 \times \text{size} + 83.33 \quad \text{(for specimens} < 100 \mu m) \quad (4a)
\]

\[
\text{depth (m)} = 0.073 \times \text{size} - 4 \quad \text{(for specimens} \geq 100 \mu m) \quad (4b)
\]

Using a mass-balance equation (1), the growth relationship (2), the size-weight relationship (3) and the depth migration pattern (4a and 4b), the final \( \delta^{13}C \) may be calculated
(Table 1, Figure 9).

To a size of approximately 100 μm, the pre-adult specimens ascend to the surface water, thereby passing the δ¹³C-maximum at the depth of maximum GAR (gross assimilation rate). After passing the level of maximum GAR, the δ¹³C of the test decreases (Figure 9A). During the second part of their life cycle they slowly descend to the reproduction depth, passing the δ¹³C maximum again. During the descending phase the δ¹³C-value initially becomes lighter as long as the δ¹³C of ΣCO₂ is still lighter than the test. When they reach a size of ca. 250 μm (at approx. 15 m depth or little deeper) the δ¹³C of ΣCO₂ becomes heavier than the value of the test i.e. from there onwards, the test becomes heavier. When the δ¹³C maximum in the water column is passed, at an adult test size, the tests become lighter again.

Table 1: Equilibrium δ¹³C values (i.e. assuming no biological effect) calculated with a mass balance equation on the basis of ontogenetic migration and a changing ambient δ¹³C<sub>water</sub> with depth.

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<th>shell size (μm)</th>
<th>water depth</th>
<th>δ¹³C water</th>
<th>shell weight</th>
<th>chamber weight</th>
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Figure 9: A: The migration of *G. sacculifer* during ontogeny between the surface and approximately 70 m depth. The numbers indicate chamber formation. B: The simulated carbon isotope ratio of the shell of *G. sacculifer* under the assumptions that 1) the $\delta^{13}$C-values of $\Sigma$CO$_2$ of the mixed layer change with depth (see Figure 7A), 2) that *G. sacculifer* migrates up and down in the water column in response to ontogeny, and that 3) chambers are formed in equilibrium with the ambient water (i.e. no vital effect). Chamber numbers are indicated.
DISCUSSION

For comparison, data from Oppo and Fairbanks (1989) were used. On the small size end we added some own measurements from the Red Sea. (Figure 10). This graph demonstrates that the $\delta^{13}C$ of *G. sacculifer* increase with size but that the $\delta^{13}C$ range is much larger than the equilibrium simulation and does not show an increase at smaller sizes (Figure 9A). Apparently, the shells of real foraminifers are not secreted in equilibrium with the ambient seawater and metabolic processes may control the carbon isotope signal and even obscure the ambient value. It has been suggested that $\delta^{13}C$ disequilibrium precipitation of planktic foraminiferal calcite is controlled by both symbiotic photosynthesis (e.g. Spero and DeNiro, 1987) and foraminiferal respiration (e.g. Berger et al., 1978). The primary sources of HCO$_3^-$ for calcification are controlled by diffusion processes between the aqueous environment and the cell (Bé et al., 1981; Anderson and Faber, 1984; Spero and Williams, 1988; Spero et al., 1992). The $\Sigma CO_2$ of the seawater between the spines, which may serve as a carbonate pool for calcification, becomes enriched with $^{13}C$ due to symbiont photosynthesis. As the number of symbionts and/or irradiance levels increase (Figure 11A), the ambient environment will become progressively more enriched. Respiration counteracts

![Graph](image-url)
Figure 11: A: Chlorophyll a (square) concentration of *G. sacculifer* as a function of size: Chl. a = 0.191-8E-3*size+7.15E-5*size²-4.52E-8*size³. We assume that a symbiont (triangle) contains 2.5 pgChl a/cell (Falkowski and Dubinsky, 1981; McCloskey and Muscatine, 1984) and that 4 symbionts are sequestered at the 3-chamber stage (28 µm). The number of symbionts is plotted at the secondary y-axis. B: The gross assimilation rate of *G. sacculifer* as a function of the ontogenetic migration pattern.
the enrichment by releasing CO$_2$ derived from light organic compounds to the ambient environment (Spero et al., 1992). $^{13}$C-depleted CO$_2$ may also be released to an internal carbon pool which is used for calcification (Bijma, 1986).

The $\delta^{13}$C value of the newly formed chamber thus depends on the gross assimilation rate (GAR) and on the respiration rate. The logarithmic trend of the $\delta^{13}$C-size curve (Figure 10) could be explained by (1) a reduction of the photosynthetic activity of the symbionts caused by the change to a deeper habitat in late ontogeny or (2) by an increase of the effect of respiration with size. In order to test this assumption, we modelled the GAR of the symbionts and the respiration of the host-symbiont complex as a function of ontogeny.

**GROSS ASSIMILATION RATE.**

The GAR is dependent on the number of symbionts and on the light intensity. During the ascending stage of the life cycle, the $\delta^{13}$C of the test increases rapidly because both, the number of symbionts and the light intensity increase. During the descending phase from early adult stage onwards, the GAR reaches a maximum after which it decreases. Below the depth of maximum GAR, the decrease of the light intensity controls the GAR. Using the sizechlorophyll a plot (Figure 11A), the PI-curve of *G. sacculifer* (Jørgensen et al., 1985) and applying the mass-balance equation, the GAR as a function of depth can be calculated:

$$\text{GAR} = \frac{I_d}{I_k} \cdot \frac{1}{\sqrt{1 + \left(\frac{I_d}{I_k}\right)^2}}$$  

(5)

where $P_{\text{max}}$ is the maximum photosynthetic rate of the symbionts, $I_k$ and $I_d$ are the saturation light intensity of the symbionts and the light intensity at depth $d$, respectively. The decrease in light intensity with depth is described by the Lambert-Beer equation:

$$I_d = I_0 \cdot e^{-(k \cdot z \cdot \text{depth})}$$  

(6)

where $I_0$ is the surface light intensity, $k$ is the extinction coefficient for clear (oligotrophic) open ocean water and $z$ is a factor that compensates for the elevation of the sun. If we assume that the maximum photosynthetic rate ($P_{\text{max}}$) equals 8.17 pMolO$_2$/h,symbiont and that the saturation light intensity ($I_k$) equals 160 $\mu$Em$^{-2}$sec$^{-1}$ (Jørgensen et al., 1985), a surface light intensity of 2000 $\mu$Em$^{-2}$sec$^{-1}$, an extinction coefficient of 0.04 (Steemann Nielsen, 1975), and $z = 1.2$, *G. sacculifer* reaches a maximum GAR of ca. 37 nMolC/h at approximately 50 m
depth (Table 2; Figure 11B). Consequently, the $\delta^{13}$C value of the test should decrease when the shell continues to calcify below approximately 50 m depth.

**RESPIRATION RATE**

The $\delta^{13}$C of oceanic plankton is dependent on their food source. Although consumers reflect the $\delta^{13}$C of their diet, they are normally slightly enriched (DeNiro and Epstein, 1978). Thus the $\delta^{13}$C value generally increases towards higher trophic levels in a process which is termed cumulative fractionation (McConnaughey and McRoy, 1979a; 1979b). Depending on the region, copepods were roughly between 2‰ and 5‰ enriched compared the POC (McConnaughey and McRoy, 1979a; Mills et al., 1983; Checkley and Entzeroth, 1985). Nonspinose, herbivorous foraminifers are therefore generally lighter than spinose, carnivorous species (cf. Figure 17 in Vincent and Berger, 1981). Unfortunately, in most reports on the isotopic composition of multiple species from the same environment, the analysis were carried out on different size fractions, making such a comparison invalid. Similarly, the change from juveniles stage in spinose species, feeding on detritus and phytoplankton, to neanic and older stages which have mostly a carnivorous diet, should be accompanied by an increase in the $\delta^{13}$C. Depending on the species, the transition from juvenile to neanic occurs roughly between 60 μm to 80 μm (Brummer et al., 1986, Hemleben et al., 1989). To our knowledge there exist no monospecific isotopic measurements from such small size fractions (pre-neanic), so that this early ontogenetic transition is not documented with isotope data.

Feeding rate also influences the $\delta^{13}$C of the test. It was shown that the rate of chamber formation and the final size of spinose planktic foraminifers increased proportionally to the feeding frequency (Bé et al., 1981; Hemleben et al., 1987; Bijma et al., 1992). In other words, at a constant temperature and equal size, the respiration rate or metabolic rate is increased at higher feeding rates, which in turn decreases the $\delta^{13}$C-value of the test. Bijma and Hemleben (unpubl. results) found that by doubling the feeding rate of *G. siphonifera*, the $\delta^{13}$C of the test decreased by approximately 1‰. In contrast, Spero and Lea (in press.) calculated that the respiratory CO$_2$ accounts for less than 3% of the shell carbon in *G. sacculifer*.

Respiration rate is further dependent on temperature and biomass. We assume a constant temperature, but with increasing biomass, respiration of the foraminifer increases according to the formula of Fenchel and Finlay (1983):

\[
\text{respiration (ngC/hr)} = 10^{0.75} \times \text{LOG(volume)} - 4.99
\]  

(7)
Table 2: The gross assimilation rate and the respiration rate (both in nMolC/hr, foram) are calculated in dependence of number of symbionts, depth migration and size. The difference between these two is expressed as the vital effect (%). The vital effect is maximally 1 %.

<table>
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<th>chamber (#)</th>
<th>size (µm)</th>
<th>depth (m)</th>
<th>Li (pE/m²,s)</th>
<th>Chl. a (ng)</th>
<th>symb. (#)</th>
<th>GAR (nMolC/hr)</th>
<th>volume (µm³)</th>
<th>Resp. GAR (nMolC/hr)</th>
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The volume increases with increasing size (Figure 12A). As a rule of thumb, respiration of the symbionts is usually considered to dissipate some 10% of the gross primary production achieved at saturation (e.g. Barnes and Hughes, 1982). In late ontogeny, the total respiration reaches the same order of magnitude as the photosynthesis of the symbionts (table 2). As the total respiration increases, the internal carbon pool and the ambient environment receive more $^{12}$C and the $\delta^{13}$C-value of the test decreases.
THE OVERALL VITAL EFFECT

The effect of photosynthesis raises and the effect of respiration lowers the $\delta^{13}$C-size curve (Figure 6B). The biochemical pathways that deliver the carbon may be different as well. For instance, if carbon from the internal carbon pool (depleted by respiration) is the dominant source for calcification, the effect of respiration is important. If, on the other hand, epitactic growth is the predominant process, symbiotic photosynthesis may be the most important process because carbon from the ambient environment (enriched by photosynthesis) will be used. We assume that both processes affect the carbon isotope value of the shell to an equal extent, i.e. in relation to their absolute carbon turnover rates. Consequently, we can estimate the vital effect by subtracting the absolute carbon release by respiration from the absolute carbon fixation by the symbionts. The relative vital effect at each ontogenetic stage can now be calculated by setting the maximum absolute change in carbon equal to 100 % vital effect (Figure 13A). Apparently, the vital effect is negligible in early ontogeny. Afterwards it tends to increase the $\delta^{13}$C-value of the shell. It reaches a maximum between the 18th and 19th-chamber stage. At the end of the life cycle the effect of the vital processes is to reduce the $\delta^{13}$C of the shell. In the present simulation experiment we allow a vital effect for the carbon isotopes that is two times as strong as that for oxygen isotopes (ca. 0.5‰ e.g. Hemleben et al., 1989). An increase between 1 and 2‰, in the carbon isotope composition due to light intensity alone was reported by Spero (1988) and Spero and Deniro (1987) respectively. A decrease of about 1‰, was found at higher feeding frequency in G. siphonifera (Bijma et al., unpub. results). In other words, a vital effect of about 1‰, is very realistic for carbon isotopes. The resulting change of the $\delta^{13}$C of the shell with ontogeny can be calculated (Figure 13B). Thus the vital effect tends to amplify the shape of the equilibrium signal that results from the migratory pattern (cf. Figure 13B with Figure 9B). Depending on local conditions, the shapes of the curve may of course vary, just as the amplitude.

Several arguments, indicate that photosynthesis of the symbionts may not be such an important controlling mechanism for carbon fractionation as we assume here: 1) G. siphonifera cultured in continuous darkness show the same trend as specimens cultured under light, although the slope may be slightly less inclined (Bijma and Hemleben, unpublished results). 2) Spinose non-symbiotic species such as e.g. G. bulloides also show the same general pattern of figure 10. 3) Chamber formation (calcification) in G. sacculifer predominantly occurs between 6 p.m. and 12 p.m. (Bijma, 1986).

If only host-symbiont respiration is considered the shape of the curve becomes even further away from reality. We therefore conclude that more information on the mechanisms that control foraminiferal $\delta^{13}$C is needed before the carbon isotope black box can really be opened.
Figure 13 A: The difference between the GAR and the total respiration expressed as percent vital effect. B: The $\delta^{13}$C as a function of ontogeny if vital effect is included. The maximum effect of the vital processes on the $\delta^{13}$C of the shell is assumed to be 1 %o (circle: original signal; asterisk: fract. (G); triangle: fract. (R); square: fract. (G-R)).
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