

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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ of ΣCO_2 is constant in the mixed layer. However, because most planktic foraminifera, if not all, change their life horizon during ontogeny and because the $\delta^{13}\text{C}$ of ΣCO_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.

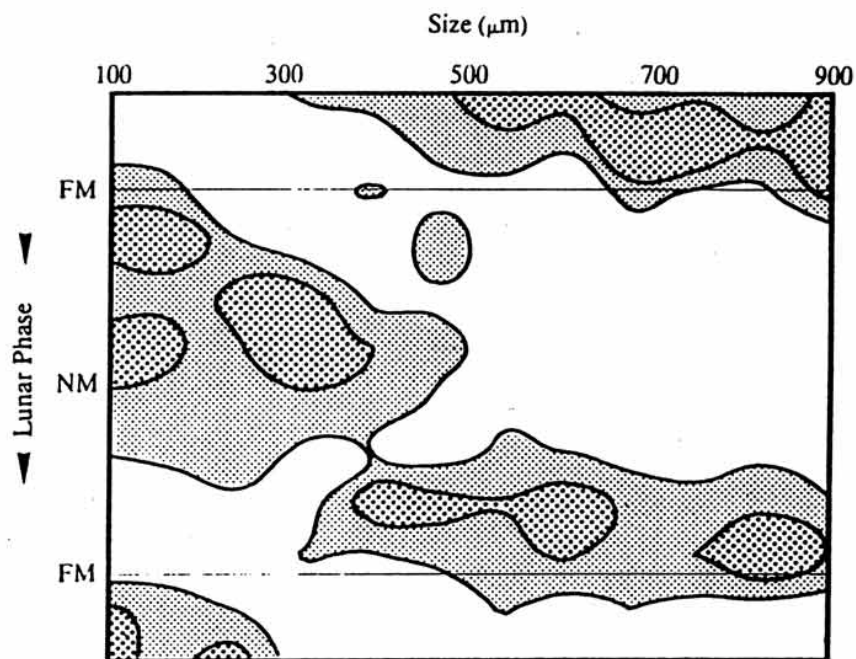


Figure 1: Lunar cycle of *G. sacculifer*. Contour plot of residual values in a size-time frame, showing that the larger size-fractions are most frequent just before full moon (FM) and that the smaller size-fractions are most frequent just after FM. Spindler *et al.* (1979).

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. Almogilabin (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*

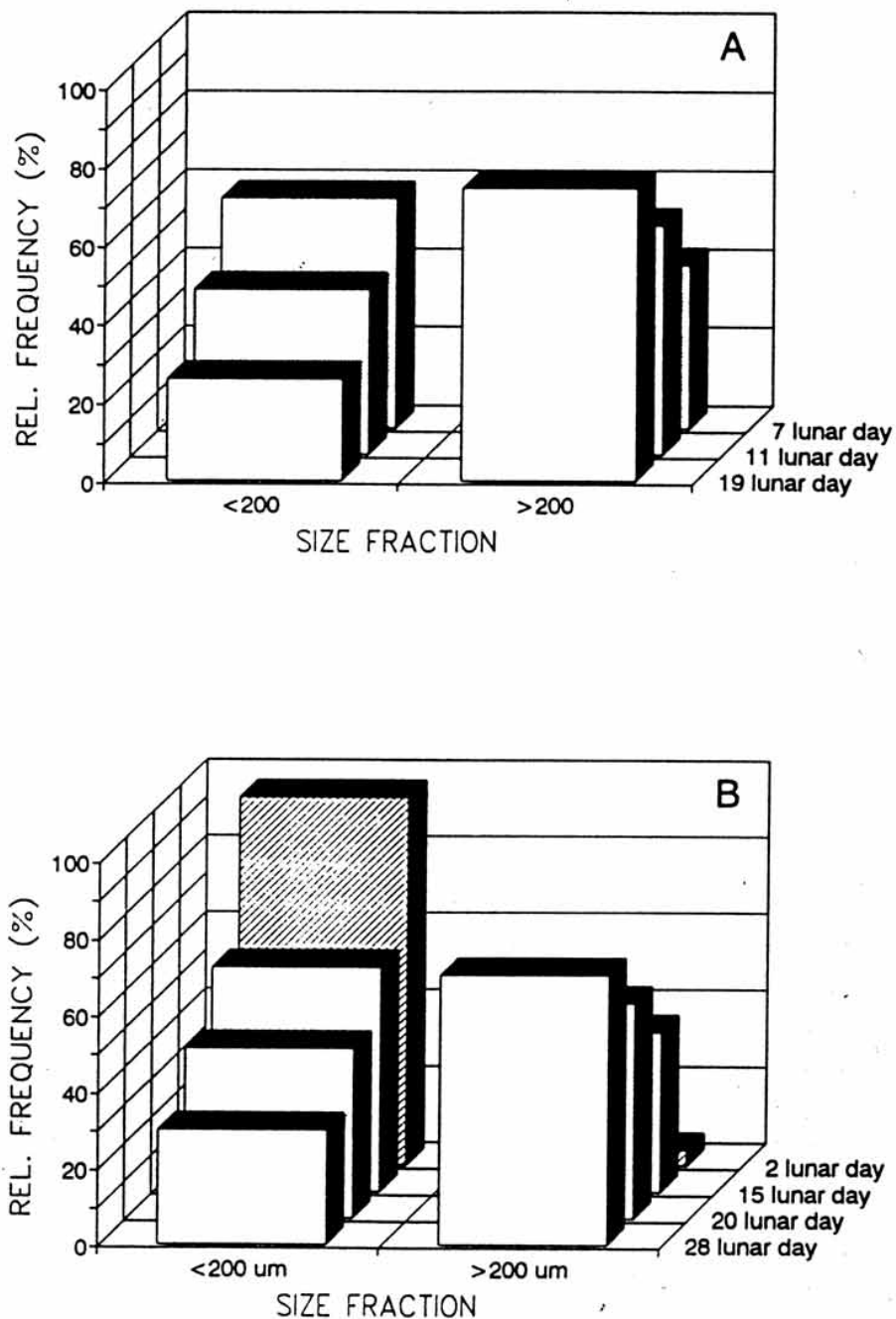


Figure 2: Relative frequency and size fraction of *G. bulloides* in respect to full moon (1. lunar day=full moon) . A: in the productive zone (0-60 m). B: in the flux zone (300-500 m).

bulloides and the symbiont bearing spinose 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 spinose 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.

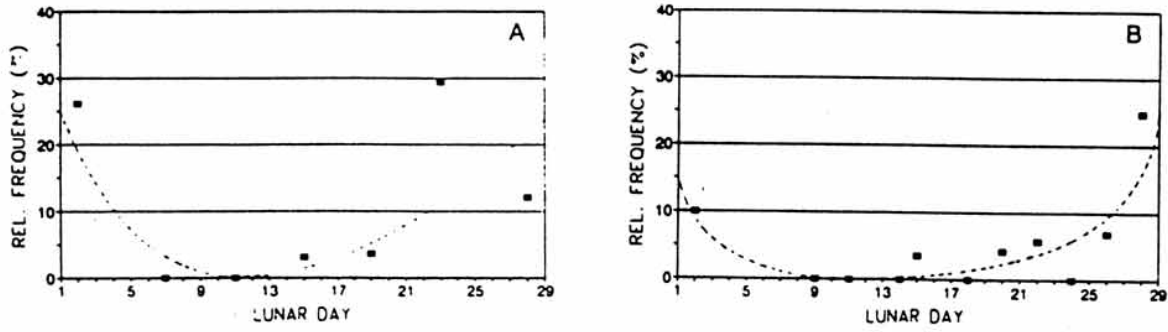


Figure 3: Relative frequency of *O. universa* in respect to the lunar period. A: in the productive zone (0-60 m). B: in the flux zone (300-500 m).

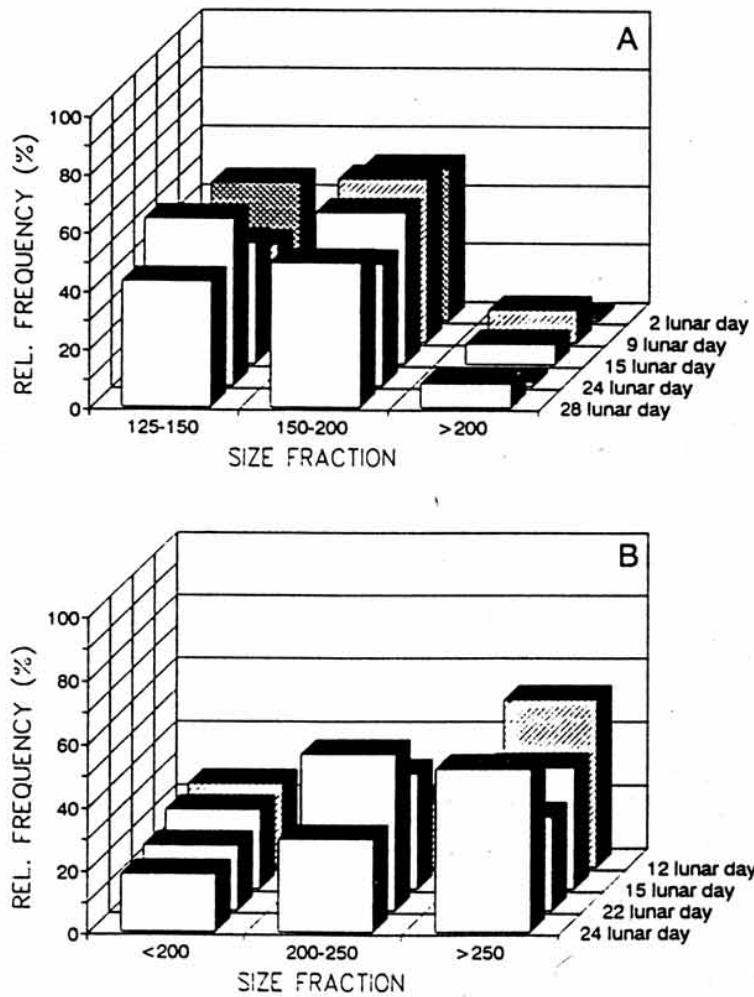


Figure 4: Non-spinose species do not respond to the lunar cycle. Samples were collected between 300-500 m depth. A: *G. scitula*. B: *G. hirsuta*.

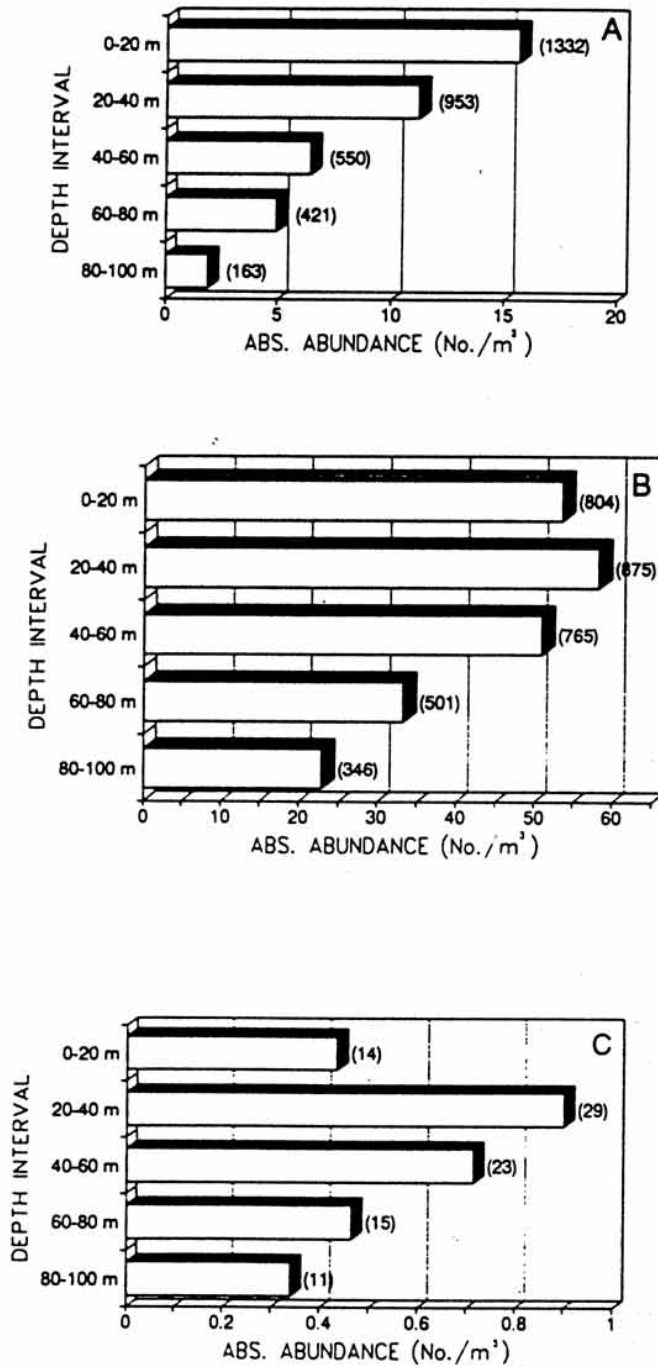


Figure 5: Mean abundance (No./m³) of planktic foraminifers in the upper 100 m of the water column. A: *Globigerinoides sacculifer* >100 µm in the Central Red Sea. B: *Globigerina bulloides* >125 µm from the North Atlantic. C: Spherical *Orbulina universa* >125 µm from the North Atlantic. The total number of specimens are bracketed.

