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LABORATORY EXPERIMENTS ON THE VERTICAL MOVEMENT OF *QUINQUELOCULINA IMPRESSA* REUSS THROUGH SAND

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ABSTRACT

Foraminifera collected from the Indian River, Florida were buried in "sterile" sand to depths of 0.5, 1.0, 2.0, 3.0, and 4.0 cm. The miliolid *Quinqueloculina impressa* Reuss was the first to emerge after burial. For this species the time of emergence in minutes is related to the burial depth in centimeters by the equation $T = 434.3D^{2.0}$. Effective overburden stress, foraminiferal velocity, and time of emergence are related in a model for the vertical movement of foraminifera.

INTRODUCTION

In the past few years several researchers have found living foraminifera beneath the surface of the sediment (e.g., Richter, 1961; Buzas, 1965; 1974; 1977; Boltovskoy, 1966; Brooks, 1967; Lee and others, 1969; Akers, 1971; Schafer, 1971; Ellison, 1972; Frankel, 1972; 1975a; 1975b; Matera and Lee, 1972; Collison, 1980). Buzas (1965) and Lee and others (1969) concluded that some foraminifera are infaunal rather than epifaunal. But whether infaunal or epifaunal, foraminifera can benefit from the ability to move through the sediment: infaunal ones to feed and reproduce, and epifaunal ones to escape burial in the sediment by storms, currents, or bioturbation.

Myers (1943) stated that foraminifera could survive burial to depths of five to seven times their diameter but would not survive to reach the surface if buried much deeper. Lee and others (1969) found *Ammonia beccarii* (Linné) capable of escaping burial at depths up to 8 cm but found that *Haynesina germanica* (Ehrenberg), which they referred to as *Protelphidium tisburyensis* (Butcher), did not move to the surface after burial. They also noted that various species of *Quinqueloculina* migrated through sediment more rapidly than *A. beccarii* but did not give rates.

This study measures the rate of vertical movement for *Quinqueloculina impressa* Reuss at five burial depths under laboratory conditions.

METHODS

The experiment was conducted with foraminifera collected from a sandy area in the Indian River near Fort Pierce, Florida. At this location the living foraminiferal population is about 80–95% *Q. impressa*, 5–10% *Elphidium* spp., 5–10% *A. beccarii*, and 3–5% other species. The material was gathered from the top 6–7 cm of the sediment because earlier work in the area (Buzas, 1977) found few living foraminifera beneath this depth. The sediment was sieved in the field over a 1 mm mesh screen to eliminate macrofauna and minimize bioturbation during the experiment. The sediment was then transported to the laboratory and used to fill 6-cm-diameter, 17-cm-tall jars to a depth of 3 to 5 cm. The jars were shaken to create a level sediment surface and allowed to settle for 12–24 hours. After this period there were usually several hundred foraminifera visible on the sediment surface and on the sides of jars. Only those jars which had more than 100 visible foraminifera were used in the experiment. While designing the experiment we found it easier to

TABLE 1

Mean time of first emergence, standard deviation, standard error, and number of replicates for each burial depth.

Burial depth (cm)	Mean time of first emergence (min)	Standard deviation (min)	Standard error (min)	Number of replicates
0.5	107.7 (1 hr 47.7 min)	14.1	4.7	9
1.0	450.9 (7 hr 30.9 min)	80.3	26.8	9
2.0	1,592.6 (26 hr 32.6 min)	95.9	32.0	9
3.0	4,425.0 (73 hr 45.0 min)	587.0	146.8	16
4.0	6,566.8 (109 hr 26.8 min)	1,718.3	543.4	10

eliminate the foraminifera on the sides of the jars by isolating them from the experiment rather than picking them off the sides of the jar. We did this by inserting a 3.5-cm-diameter plastic core liner into the sediment until it was self-supporting. The core liner was filled with purified quartz sand to the desired burial depth. The quartz sand was well sorted and consisted of 0.4 to 0.6 mm subrounded grains. After some practice we were able to add the sand almost grain by grain thus insuring that the original surface was not disturbed and that the sand was uniformly deep. During preliminary trials we discovered that the white foraminiferal tests were almost impossible to see against the light quartz sand. To increase the contrast we created a dark surface on the quartz sand by adding several drops of a very fine-grained organic sediment to the core liners immediately after the sand was added. This dark layer contrasted well with the light foraminiferal tests, making it possible to see their emergence quite easily. The time of emergence of the first appearing foraminifer was recorded for each trial.

RESULTS

The mean times, standard deviations, standard errors, and number of replications for each depth are listed in Table 1. In all cases the first individual to emerge was a *Q. impressa*. Examination of the data shows that the relationship between burial depths and times of emergence is not linear. A log-log plot of the data suggests a power function of the form $Y = AX^B$ (Fig. 1). A linear regression on the logarithms of the data yields the relationship $T = 434.3D^{2.0}$ where T is the time of emergence in minutes and D is the burial depth in centimeters. The regression coefficient, r^2, is 0.99.

DISCUSSION

While this experiment shows that some foraminifera can move through sediment up to 4 cm deep it does not answer the question of why they move. If they are epifaunal, the answer is simply that they could not live infaunally and must escape burial before they die. Myers (1943) thought this to be the case for *Elphidium crispum* (Linné) where burial caused by turbulence of winter storms killed up to 80% of the population. If the foraminifera are infaunal, they could move for several reasons, among them to seek food, for reproduction, or to escape a shallow anoxic layer.

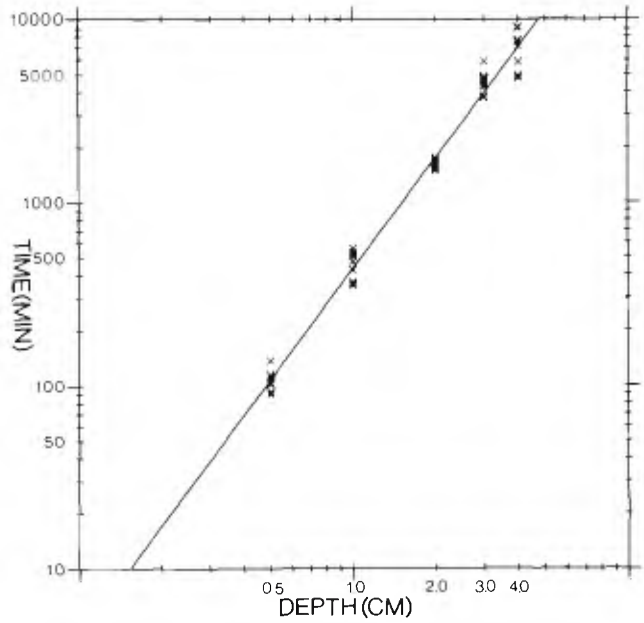

FIGURE 1

Log-log plot of burial depth versus time of first emergence. Crosses denote individual data points. The line is the regression curve $T = 434.3D^{2.0}$.

The appearance of *Q. impressa* before any of the other species agrees with the observations of Lee and others (1969) that various species of *Quinqueloculina* generally appeared before other species in small sediment cultures. On the other hand, Schafer and Young (1977) found rotalids to be the fastest crawlers. However, it must be noted that their study dealt with motion chiefly across sediment and glass plates rather than through sediment. In this experiment there are several possible reasons for their early appearance. One is simply that they are faster than any of the other species present. Other reasons are artifacts of their relative abundance, 80 to 90% of the living population. Perhaps there were so many *Q. impressa* individuals present that there were always some relatively fast individuals in the experiment. Alternatively, perhaps there was high mortality when the quartz sand was added to the sediment and the residual population consisted entirely of *Q. impressa*.

In an attempt to explain the regression curve where the time of emergence is proportional to the square of the burial depth we developed a simple model where foraminiferal speed, and thus time of emergence, is controlled by the amount of work necessary for the organisms to move through the sediment. This model assumes that the force a foraminifer must overcome is the effective overburden stress. Nichols and others (1978) suggested that this stress might be the "critical parameter (in) determining escape from burial" for some benthic invertebrates. Clearly this is a simplification since sediment angularity, grain size distribution, and porosity can vary between sediments even though the overburden stress in each remains the same. This model would fail when a sediment has large interstitial spaces and an individual could move through them without moving the sediment grains. This model also assumes that foraminifera generate power, defined as work per unit time, at a constant rate. If they generate power at a changing rate, then the relationship between depth and time of emergence would be difficult to predict.

Work is defined as force, F, times distance, x, or where the force varies with position:

$$W = \int_{x_1}^{x_2} F\,dx \qquad (1)$$

The force a foraminifer must overcome to move through the sediment is the overburden stress of the sediment. This stress can be calculated from the equation

$$\bar{p} = (\gamma_{sat} - \gamma_{sw})x \qquad (2)$$

(Richards and others, 1974) where γ_{sw} is the bulk density of the pore water, γ_{sat} is the bulk density of the wet sediment, and x is the depth in the sediment. Because our experiment deals with burial depths of only a few centimeters and because the quartz sand used for burial was fairly well compacted during addition to the core liners we have assumed that γ_{sat} does not vary with depth. In instances where the sediment compacts under its own weight the overburden stress varies nonlinearly with depth. In our case the stress is directly proportional to the depth.

The force a foraminifer must generate to overcome the overburden stress is the opposite of the stress:

$$F = -(\gamma_{sat} - \gamma_{sw})x \qquad (3)$$

To find the work that an individual must do to move vertically through the sediment we substitute (3) in the work integral (1):

$$W = -\int_{x_1}^{x_2} (\gamma_{sat} - \gamma_{sw})x\,dx$$

$$= -\tfrac{1}{2}(\gamma_{sat} - \gamma_{sw})x^2 \Big|_{x_1}^{x_2}$$

$$= -\tfrac{1}{2}(\gamma_{sat} - \gamma_{sw})(x_2^2 - x_1^2) \qquad (4)$$

In the case where the organism is moving to the surface the final depth, x_2, is zero and

$$W = \tfrac{1}{2}(\gamma_{sat} - \gamma_{sw})x_1^2 \qquad (5)$$

Since we have assumed that the foraminifer is generating power at a constant rate, P, the amount of time it takes for the organism to move to the surface is given by:

$$T = \frac{1}{2}\frac{\gamma_{sat} - \gamma_{sw}}{P}x_1^2 \qquad (6)$$

The time is proportional to the depth squared.

We can also determine the velocity-depth relationship by examining the work and power differentials:

$$w = PT \qquad (7)$$

Since P is a constant:

$$dw = P\,dt \qquad (8)$$

From the definition of work:

$$dw = x\,dF + F\,dx \qquad (9)$$

Since F is equal in magnitude to the overburden stress and does not vary with time:

$$dF = 0 \qquad (10)$$

and

$$dw = F\,dx \qquad (11)$$

combining these we have

$$F\,dx = P\,dt \qquad (12)$$

$$\frac{dx}{dt} = \frac{P}{F} \qquad (13)$$

Since dx/dt is the definition of velocity and since the force is directly proportional to the depth (3) we have:

$$v = -\frac{P}{(\gamma_{sat} - \gamma_{sw})}\frac{1}{x} \qquad (14)$$

or the velocity is inversely proportional to depth. The negative velocity is merely the result of greater depths being indicated by larger positive numbers.

Higher velocities in the upper layers of the sediment could result in higher foraging rates and an increased ability to escape any irritating factor such as a rising reducing layer. This may be one reason for the greater abundance of foraminifera in the upper levels of the sediment.

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