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LUNAR AND SEMI-LUNAR REPRODUCTIVE CYCLES IN SOME SPINOSE PLANKTONIC FORAMINIFERS

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ABSTRACT

Reproductive cycles of spinose planktonic foraminifera appear to be related to distinct phases of the moon. Based on a time series of plankton-net tows, a synodic lunar reproductive cycle is demonstrated in *Globigerinoides sacculifer* (Brady). The reproductive cycles of *Globigerinoides ruber* (d'Orbigny) and probably *Globigerinella siphonifera* (d'Orbigny) are characterized by a semi-lunar periodicity. Samples collected during scientific cruises into the Red Sea and the northwest Atlantic Ocean and many blue water SCUBA dives in the Caribbean Sea support these observations.

Inter-species differences in lifespan result in a different empty shell output. As a consequence, the sediment does not reflect the situation in the water column. The relative abundances that are preserved in the sediment are not primarily indicative of variations in the reproduction-potential between species, but must fundamentally be interpreted as discrepancies between reproductive cycles. These results yield consequences for the interpretation of sediment analyses and implications for paleoceanography.

Reproduction is often preceded by the formation of an atypical final chamber. Time and frequency correlations demonstrate that these morphotypes are associated with the reproductive process but are not a prerequisite for gametogenesis.

INTRODUCTION

Biological rhythms are recurrences of events within biological systems at more or less regular intervals (Bünning, 1976; Aschoff, 1981). They are a general feature in all organisms, span a large range of frequencies, and may be observed in single cells, in the whole organism, or at the population level. Only four rhythms do not vary in frequency because they are synchronized with geophysical cycles, i.e., the solar (daily), lunar, tidal, and annual cycles. As a result of the influences of the lunar orbit, a variety of reproductive rhythms have evolved (Neumann, 1981). Firstly, reproductive behavior may recur every month. For example, planulation in some corals is a monthly rhythm which is coupled to the synodic lunar cycle (Richmond and Jokiel, 1984). Secondly, lunar reproductive rhythms may perform a yearly sequence. The most famous example of this type is the swarming of the palolo worm, which multiply only at the last quarter in October and November off Samoa. Thirdly, some organisms display a reproductive rhythm that pulsates on a biweekly basis. The lunar cycle induces a tidal rhythm, that is characterized by two neap and two spring tides per month. Consequently, the tidal zone harbors many examples of animals which synchronize their reproductive activities with these semi-lunar pulses. The polychaete, *Ceratocephale osawai,* performs nuptial dances at full and new moon (Korringa, 1957). Even an insect that has adopted a marine mode of life in the intertidal zone, *Clunio marinus,* exhibits a tidal periodicity in its reproductive behavior (Caspers, 1951). With respect to these biweekly rhythms, two different cycles may operate within the same organism, responding to different Zeitgebers (cues, synchronizers). This is exemplified by the flatworm *Platynereis dumerilii.* Near Naples (Italy) where tides are insignificant, a monthly rhythm of reproduction is displayed. At Brittany (France), reproduction occurs at the first and last quarter. The rhythm in the first example is induced by the lunar cycle whereas the second is entrained by tidal exposures (Korringa, 1957). Thus, organisms may be sensitive to both, tidal and lunar cycles, where local conditions determine which rhythm will dominate.

Spindler and others (1978) were the first to document that reproduction in an oceanic protozoan, the planktonic foraminifer *Hastigerina pelagica* (d'Orbigny), is coupled to the synodic lunar cycle. Almogi-Labin (1984, cited in Reiss and Hottinger, 1984) has shown that *Globigerinoides sacculifer* (Brady) reproduces with full moon in the Gulf of Elat/Aqaba. Although lunar periodicity has only been reported for these two species, field observations during routine SCUBA or plankton net collections off Barbados and Curaçao have suggested that there is also a lunar control of reproduction in other spinose planktonic foraminifera. Time series of plankton-net tows showed that both lunar and semi-lunar reproductive cycles have evolved in these protozoans (Bijma, 1986). In this paper, we document the periodicity in *G. sacculifer, Globigerinoides ruber* (d'Orbigny), and *Globigerinella siphonifera* (d'Orbigny) from the Gulf of Elat/Aqaba.

MATERIALS AND METHODS

In the Gulf of Elat/Aqaba, surface tows (0–5 m) were taken with a plankton net (202 μm mesh size), about 500 m off the H. Steinitz laboratory. A flowmeter (Tsurumi-Seiki, Kosakusho Co., Ltd., type 2197) was fixed in the center of the net, recording the relative amounts of filtered seawater. The duration of each tow was only 10 minutes to avoid clogging of the net. Tow velocity was kept as low as possible in order to prevent the interference of a pressure wave in front of the net. Samples were collected every second day during the period of October 1 through November 17, 1984.

Samples were frozen immediately and stored at −20°C. Defrosted samples were treated with NaOCl

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TABLE 1. Relative frequencies of *Globigerinoides sacculifer* in 20 size classes (width 42 μm) larger than 125 μm, total catch and the percentage aberrant phenotypes in the surface waters in the Gulf of Elat/Aqaba. Samples were collected every second day during the period 1 October–17 November 1984. Full moon is indicated by a broken line.

Date	Size interval (μm)									
	125/167	167/208	208/250	250/292	292/333	333/375	375/417	417/458	458/500	500/542
01/10	0.38	1.92	5.00	7.69	9.23	13.08	13.46	12.69	8.46	5.38
03/10	0.47	5.61	14.02	15.89	11.21	11.68	13.08	10.28	3.74	5.61
05/10	5.88	16.34	9.15	17.65	11.11	9.15	5.88	6.54	5.23	3.92
07/10	3.70	9.26	9.26	7.41	5.56	11.11	7.4	5.56	14.81	11.11
10/10	9.18	24.49	15.31	12.24	5.10	8.16	3.06	3.06	1.02	3.06
	Full Moon									
11/10										
12/10	11.90	23.81	9.52	10.71	9.52	5.95	3.57	1.19	5.95	2.38
14/10		31.25	25.00	6.25		12.50	12.50	6.25		6.25
16/10	13.64	40.91	18.18	9.09		13.64		4.55		
18/10		11.11	22.22		22.22	33.33	11.11			
20/10	10.00	22.50	25.00	22.50	7.50	7.50		2.50		
22/10	3.26	23.91	28.26	23.91	5.98	5.98	2.72	3.80	1.09	0.54
24/10	4.67	18.00	22.67	26.67	12.67	10.67	2.67	0.67	0.67	0.67
26/10	11.79	18.70	23.58	17.07	13.01	8.54	3.25	1.63	1.63	0.41
28/10	8.03	23.55	19.67	18.56	12.47	8.31	3.88	3.05	1.66	0.83
30/10	4.26	15.74	20.00	15.32	16.60	11.49	5.53	5.11	1.70	1.70
01/11	7.94	26.84	20.63	12.99	8.80	6.78	5.63	4.62	1.88	1.44
03/11	12.86	24.05	20.24	10.00	8.10	8.33	4.29	4.52	4.29	1.19
05/11	0.56	5.85	16.43	10.58	14.76	14.21	9.19	10.31	6.96	4.46
07/11	5.00	9.83	16.72	15.17	12.24	8.97	7.59	7.24	5.86	3.10
09/11	1.06	7.92	13.98	14.51	8.44	10.55	7.65	8.71	5.54	6.60
10/11	Full Moon									
11/11	13.70	20.56	13.49	9.64	8.99	5.35	6.21	8.35	4.93	3.43
13/11	12.58	26.42	16.67	10.69	7.23	4.09	5.66	3.46	4.09	2.52
15/11	10.71	21.43	11.90	13.10	8.33	5.95	4.76	4.76	5.95	4.76
17/11	13.28	28.52	25.00	9.38	7.03	1.56	1.56	1.17	1.56	3.52

for a period of 24 hours in order to break up the organic matter and partly remove tissues. High temperature combustion (400°C) in a Bifa furnace (PA 36 B) removed most of the organic matter.

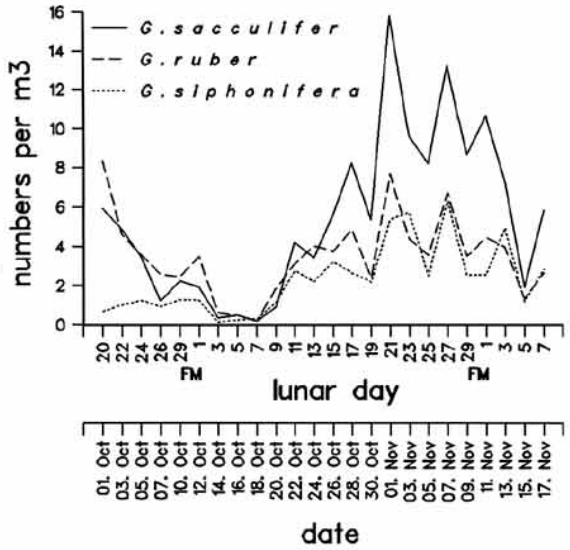

FIGURE 1. Absolute abundances per m³ of the three major species of planktonic foraminifera (*G. sacculifer, G. ruber,* and *G. siphonifera*) larger than 125 μm caught in the surface waters off the laboratory in the Gulf of Elat/Aqaba versus lunar day in the period 1 October–17 November 1984. Full moon is indicated (FM).

Size measurements were conducted with a Wild-Heerbrug binocular microscope, calibrated with a Leitz stage micrometer. In this way 20, 14 and 15 size classes were obtained for *G. sacculifer, G. ruber,* and *G. siphonifera,* respectively (size increment of 42 μm from 208 μm onwards). In order to compare consecutive tows, relative frequencies of the size classes were calculated. Because juvenile and neanic stages are omnipresent and outnumber adult individuals by at least an order of magnitude (Brummer and others, 1986, 1987), the trends in the smaller size fractions on the basis of relative frequencies are obscured. To analyze the trends of the smaller fractions, residuals were calculated. The average relative frequencies per size class for the entire period of collection represents the expected relative frequency of a certain fraction if the population structure is assumed to be constant. By subtracting this expected from the actual relative frequency, a residual is obtained that indicates when a certain size fraction is over-represented (positive sign) or under-represented (deficiency; negative sign). In other words, the residuals indicate how close a value approximates the expected value of the imaginary stable population structure. The trends are visualized by the zero iso-line. All figures are based on data shown in Tables 1 through 3.

RESULTS

About three to five days after the first full moon the absolute number of specimens of all three species

TABLE 1. Continued.

542/583	583/625	625/667	667/708	708/750	750/792	792/833	833/875	875/917	917/958	N	(%)
7.31	5.38	3.85	2.69	1.92	0.38	0.77	0.38			260	2
2.80	3.27	0.47	1.40	0.47						214	0
2.61		1.31	3.92	1.31						153	1
3.70	3.70	3.70	1.85		1.85					54	0
2.04	4.08	3.06	2.04	3.06			1.02			98	2
Full Moon											
1.19	3.57	2.38	3.57	1.19	1.19		1.19	1.19		84	6
										16	0
										22	0
										9	0
2.50										40	0
0.54										184	1
										150	0
0.41										246	0
										361	0
1.28	0.85	0.43								235	2
1.15	0.43	0.43	0.14	0.29						693	2
0.95	0.95		0.24							420	1
2.79	1.67	0.84	0.56	0.56	0.28					359	2
2.24	2.59	0.69	1.38	0.86	0.34		0.17			580	1
6.07	2.90	1.58	1.06	0.79	0.26	0.53	0.79	0.26	0.79	379	6
Full Moon											
2.57	0.86	0.86	0.43	0.43	0.21					467	1
0.94	0.94	2.20	0.31	1.26	0.31				0.62	318	3
2.38	4.17	0.60		1.9						84	4
0.39	1.95	1.17	1.56	1.17	0.39	0.78				256	3

reached a minimum (Fig. 1). Approximately nine days before full moon *G. sacculifer* and *G. ruber* reached their maximum abundances, whereas *G. siphonifera* reached its maximum abundance three days before full moon. The size distribution within each sample, however, remains about the same for all three species (Figs. 2–4). The number of specimens in the surface water reach a minimum three to seven days after full moon for all three species. Three days after full moon the surface waters are almost devoid of foraminifers larger than 125 μm, especially in October. In November the standing stock had decreased by more than 50% three days after full moon. Furthermore, the population structure changed insofar as only small to medium-sized individuals remained in the surface waters. For *G. sacculifer* and *G. ruber,* the maximum sizes caught three days after full moon were 521 μm and 313 μm respectively. The maximum sizes detected one day before or after full moon were up to 938 μm and 708 μm respectively (Figs. 2, 3). For *G. siphonifera* the same trend was observed. The maximum sizes caught around full moon were up to 646 μm. Three days after full moon in the first and the second cycle, sizes reached 354 μm (Fig. 4).

For all three species, the same basic trends were encountered in the population structure with respect to size (Figs. 2–4). A relative increase in the number of large individuals was observed from the sixth day after full moon onwards. Soon after full moon, the number of large individuals decreased. Large individuals were entirely absent in the sample collected on the fifth day after full moon. From this day onwards, the number of large specimens steadily increased and the second disappearance of large individuals from the surface waters was observed to begin the day after the consecutive full moon. However, not all large individuals disappeared after full moon. Those remaining were apparently unable to reproduce. The drop in the number of mature individuals after full moon was less obvious in November than in October (Figs. 5–7).

Globigerinoides ruber and *G. siphonifera* show an additional increase followed by a decrease of large individuals around new moon. These peaks, however, are less outstanding than the mass reproduction around full moon. Their life histories are very similar except for the fact that the additional cycle for *G. ruber* is triggered at new moon whereas it is observed four days after new moon in the case of *G. siphonifera.* In addition, the intermediate reproduction peak in *G. siphonifera* is not as obvious as in *G. ruber.*

The highest percentages of sac-like chambers are found around full moon. For *G. ruber,* high occurrences of kummerforms are found both around full and new moon (Fig. 8). With respect to *G. siphonifera,* we did not encounter kummerform phenotypes in the surface waters.

DISCUSSION

Planktonic organisms seem to be subjected to the so called *r* selection (cf. Krebs, 1978). Among other traits, these organisms are characterized by a short life cycle where the rate of increase is the most important feature.

TABLE 2. Relative frequencies of *Globigerinoides ruber* in 14 size classes (width 42 μm) larger than 125 μm, total catch and the percentage aberrant phenotypes in the surface waters in the Gulf of Elat/Aqaba. Samples were collected every second day during the period 1 October–17 November 1984. Full moon is indicated by a broken line.

	Size interval (μm)															
Date	125/167	167/208	208/250	250/292	292/333	333/375	375/417	417/458	458/500	500/542	542/583	583/625	625/667	667/708	N	(%)
01/10	0.55	2.19	7.38	15.30	14.48	15.03	15.85	12.84	8.20	6.28	1.64	0.27			3.66	11
03/10	0.50	11.39	23.76	19.80	19.80	8.91	11.39	2.48	0.99		0.50	0.50			202	8
05/10	4.43	14.56	25.95	18.99	18.35	10.76	3.16	1.27	0.63	0.63			0.63	0.63	158	4
07/10	0.88	10.62	28.32	22.12	16.81	10.62	4.42	6.19							113	12
10/10		14.95	30.84	23.36	16.82	6.54	3.74	1.87	0.93	0.93					107	4
11/10	Full Moon															
12/10	2.61	16.99	23.53	18.95	18.95	8.50	5.23	3.92	0.65	0.65					153	23
14/10	3.70	11.11	29.63	40.74	14.81										27	0
16/10		19.05	23.81	28.57	28.57										21	5
18/10			37.50	50.00	12.50										8	0
20/10	3.70	19.75	24.69	27.16	14.81	7.41	2.47								81	6
22/10	1.47	12.50	25.74	19.85	21.32	11.76	2.94	2.94	1.47						136	13
24/10		9.09	22.73	16.48	30.68	9.66	5.11	5.68	0.57						176	6
26/10	0.61	11.59	24.39	20.12	23.78	9.76	4.27	4.27	1.22						164	14
28/10	0.47	10.33	29.58	21.60	17.37	10.33	5.63	2.35	1.88	0.47					213	19
30/10		4.72	20.75	18.87	16.04	11.32	18.87	6.60	1.89	0.94					106	25
01/11	0.29	9.44	27.73	23.01	15.04	10.32	7.67	4.42	1.77	0.29					337	21
03/11	0.52	13.61	32.46	20.42	15.71	10.99	4.19	2.09							191	9
05/11		6.45	21.94	24.52	18.06	17.42	7.74	1.94	1.94						155	22
07/11	1.36	7.48	27.89	23.13	19.05	11.90	5.78	2.38	1.02						294	9
09/11		7.19	22.22	22.88	20.92	16.99	4.58	4.58	0.65						153	17
10/11	Full Moon															
11/11	3.59	28.72	27.69	13.33	14.87	7.18	3.59	1.03							195	4
13/11	1.74	18.02	34.88	18.60	15.12	4.65	3.49	2.33	1.16						172	9
15/11	6.78	38.98	25.42	16.95	8.47	2.54	0.85								59	2
17/11	0.85	22.22	37.61	23.93	11.11	3.42		0.85							117	12

TABLE 3. Relative frequencies of *Globigerinella siphonifera* in 15 size classes (width 42 μm) larger than 83 μm, total catch and the percentage aberrant phenotypes in the surface waters in the Gulf of Elat/Aqaba. Samples were collected every second day during the period 1 October–17 November 1984. Full moon is indicated by broken line.

	Size interval (μm)														
Date	83/125	125/167	167/208	208/250	250/292	292/333	333/375	375/417	417/458	458/500	500/542	542/583	583/625	625/667	667/708	N
01/10		6.67	10.00	23.33	10.00	16.67	6.67	10.00	3.33	3.33	3.33	6.67				30
03/10		13.33	24.44	22.22	15.56	2.22	11.11	6.67	2.22		2.22					45
05/10	14.81	22.22	25.93	16.67	9.26	5.56	1.85		1.85		1.85					54
07/10		24.39	19.51	21.95	14.63	12.20	2.44		2.44		2.44					41
10/10		5.36	26.79	26.79	14.29	12.50	7.14	5.36			1.79					56
11/10	Full Moon															
12/10	9.09	18.18	23.64	18.18	7.27	5.45	7.27		7.27	1.82	1.82					55
14/10		16.67		33.33	33.33	16.67										6
16/10		27.27	27.27	27.27	18.18											11
18/10			28.57	28.57	21.43	21.43										14
20/10		4.00	12.00	34.00	24.00	6.00	10.00	4.00		4.00		2.00				50
22/10		9.09	24.79	21.49	14.88	11.57	5.79	5.79	2.48	0.83		1.65	0.83		0.83	121
24/10		1.02	11.22	29.59	18.37	15.31	5.10	5.10	5.10	5.10	2.02		1.02			97
26/10	0.71	10.64	29.79	19.15	15.60	9.22	6.38	2.13	1.42	1.42	0.71	0.71	1.42	0.71		141
28/10	1.72	17.24	26.72	28.45	8.62	9.48	2.59	1.72	0.86	0.86	1.72					116
30/10		8.33	26.04	13.54	17.71	10.42	10.42	6.25	3.13	4.17						96
01/11	2.55	21.28	28.51	20.00	11.06	5.53	2.98	3.83	0.85	1.28	0.43	1.28	0.43			235
03/11	4.80	39.60	24.80	12.80	7.60	2.40	1.60	2.40	1.20	1.60	1.20					250
05/11		2.73	10.91	27.27	23.64	14.55	8.18	3.64	2.73	4.55	0.91	0.91				110
07/11		20.65	21.74	24.64	11.59	9.42	5.43	2.17	1.45	1.09	0.72		0.36		0.72	276
09/11		2.70	22.52	28.83	14.41	9.91	8.11	5.41	1.80	1.80	1.80	1.80		0.90		111
10/11	Full Moon															
11/11	2.70	16.22	29.73	16.22	14.41	6.31	3.60	6.31	2.70			1.35	0.45			111
13/11	2.78	31.94	25.00	17.59	8.33	6.48	3.24	1.39	0.46	2.78						216
15/11		23.08	36.54	15.38	11.54	7.69	1.92		1.92		1.92					52
17/11		34.68	34.68	17.74	8.06	3.23	0.81	0.81								124

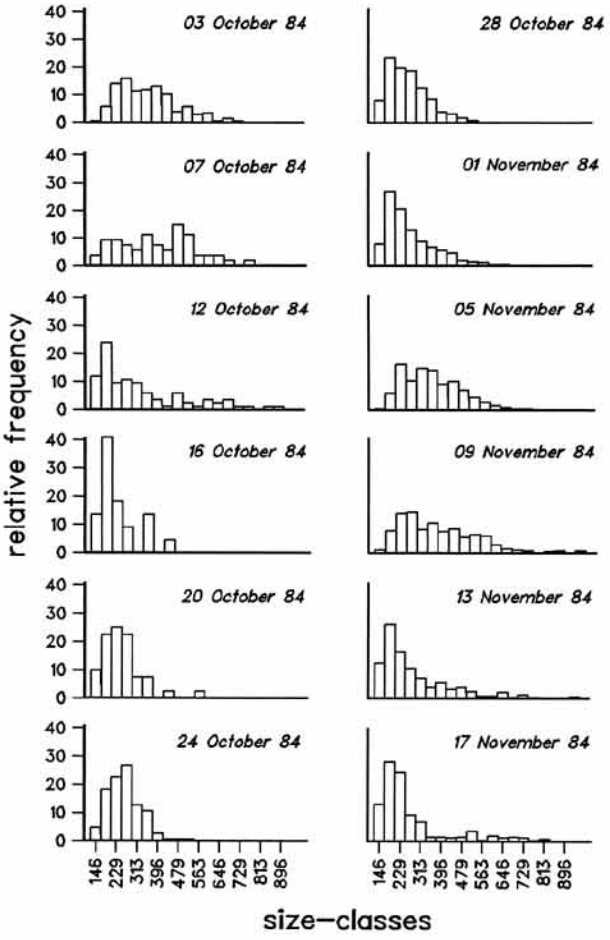

FIGURE 2. Frequency distribution of *Globigerinoides sacculifer* for every fourth day during a period including two full moon phases (11 October and 10 November). The width of each size class is 42 μm and the height is expressed in relative frequency units.

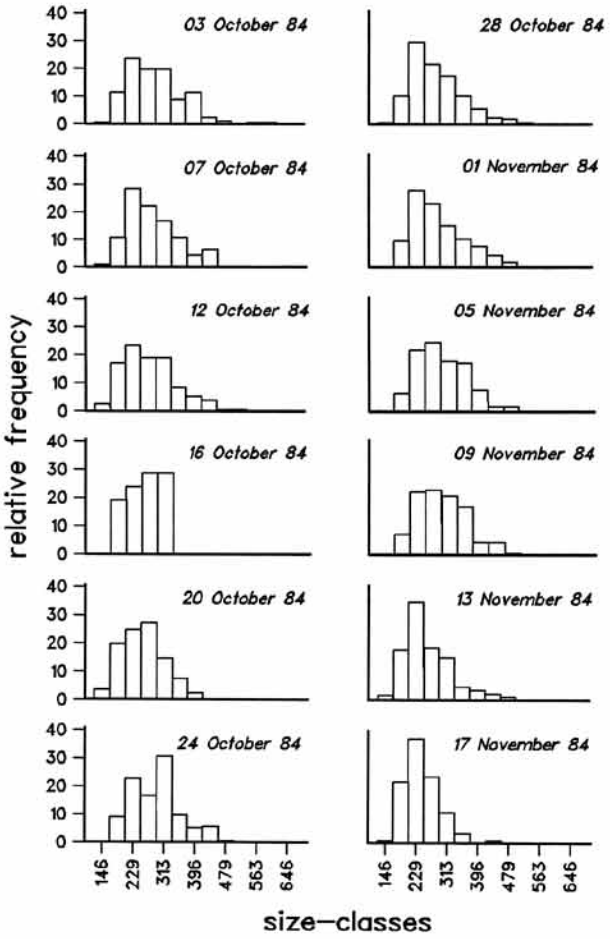

FIGURE 3. Frequency distribution of *Globigerinoides ruber* for every fourth day during a period including two full moon phases (11 October and 10 November). The width of each size class is 42 μm and the height is expressed in relative frequency units.

In order to maintain a population, planktonic foraminifera have evolved several methods to enhance the probability of gamete fusion in the open ocean.

1. Large production of gametes. During gametogenesis, the parent cytoplasm is almost completely transformed into gametes. The number of gametes that are released are in the order of 300 to 400 thousands per individual (e.g., Hemleben and Spindler, 1983).
2. It was demonstrated that planktonic foraminifers descend to a deeper habitat, probably in order to reproduce (Hemleben and others, 1979; 1988; Spindler and others, 1979; Bé, 1980; Duplessy and others, 1981; Hemleben and Spindler, 1983). Probably, gamete release takes place at a specific depth, thereby reducing the three-dimensional space (euphotic zone) to a two-dimensional plane (thermocline or halocline). Gametes are thought to concentrate at the thermocline and/or halocline, where zygote formation is postulated to occur.
3. Gamete release is synchronized. Synchronization of gamete release is effected by tying the reproductive rhythm to the lunar cycle.

As a result of the latter two strategies many gametes are consolidated in space and time to secure the survival of a species. The synchronization of gamete release from many parent cells simultaneously points toward the heterogamous nature of these spinose species of foraminifers (Spindler and others, 1979). This is an important characteristic of opportunistic species that enables them to increase the heterogeneity of the genetic pool, in order to be able to respond to drastic environmental changes.

Here, we will discuss the aspect of synchronization of gamete release. To determine the rhythm that underlies the reproductive cycles, we analyzed pulsating changes in the population structure. Several factors, however, may obscure the rhythm that controls the timing of reproduction and thus complicate this evaluation. Temporary biotic and abiotic conditions determine the size distribution (differential sensitivity of certain stages to environmental parameters; selective

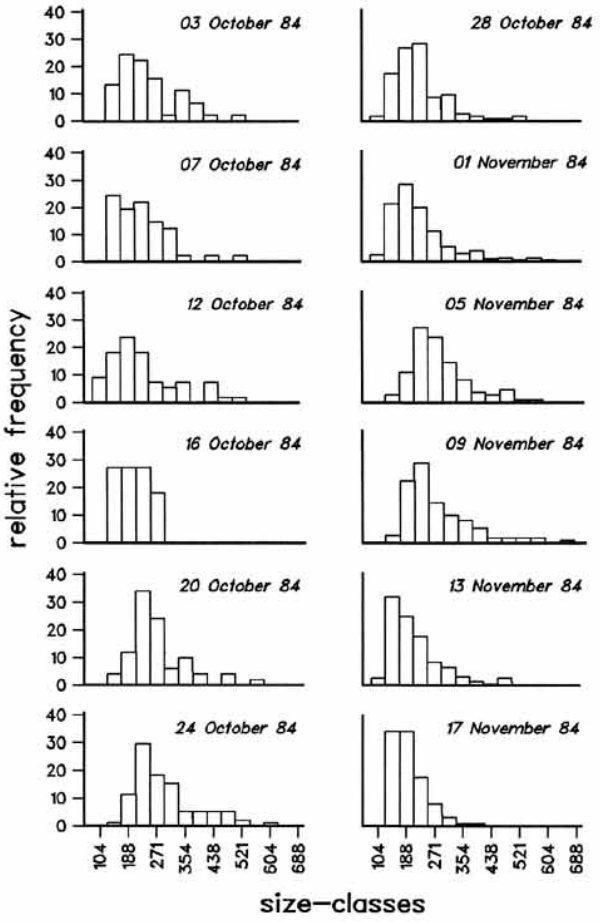

FIGURE 4. Frequency distribution of *Globigerinella siphonifera* for every fourth day during a period including two full moon phases (11 October and 10 November). The width of each size class is 42 μm and the height is expressed in relative frequency units.

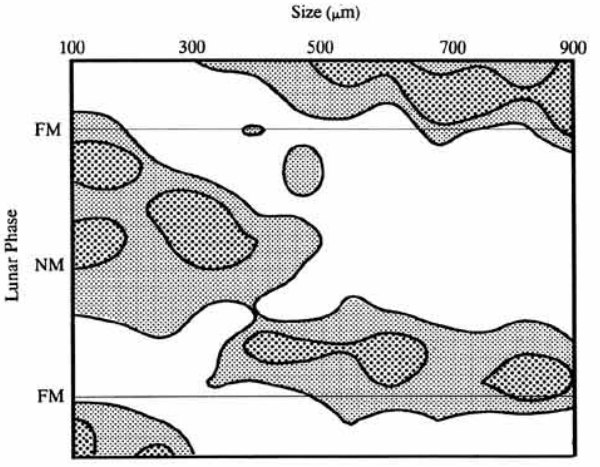

FIGURE 5. Residuals for the size classes are plotted as a function of time for *Globigerinoides sacculifer*. FM is full moon; NM is new moon. In the contour plot, the 0 and 1 iso-lines are shown: stippled = positive; coarsely stippled = maximum; blank = deficiency.

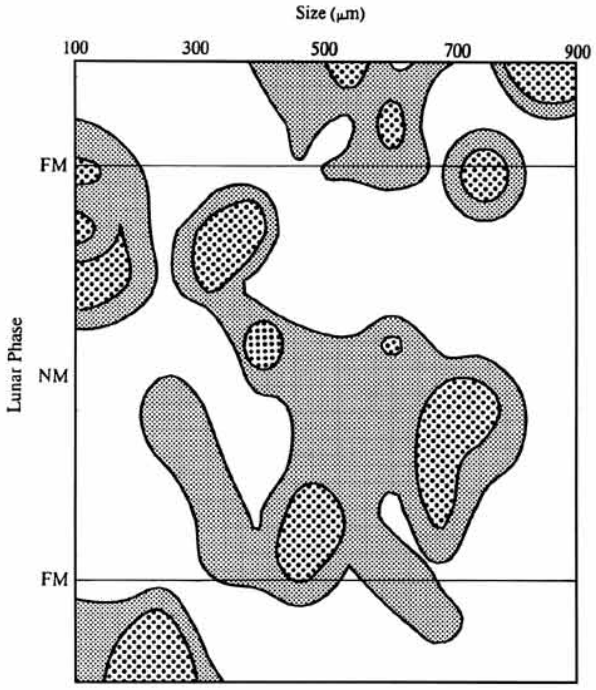

FIGURE 6. Residual for the size classes are plotted as a function of time for *Globigerinoides ruber*. For explanation see Figure 5.

predation) and the maximum sizes reached within a deme. Therefore, when samples from the same cycle but different geographic sites are combined, the reproductive rhythms may be concealed. Also, when samples from the same locality but from different periods

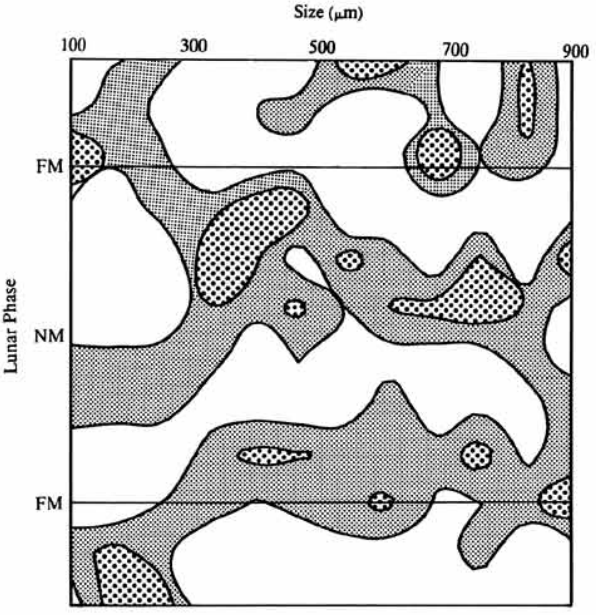

FIGURE 7. Residuals for the size classes are plotted as a function of time for *Globigerinella siphonifera*. For explanation see Figure 5.

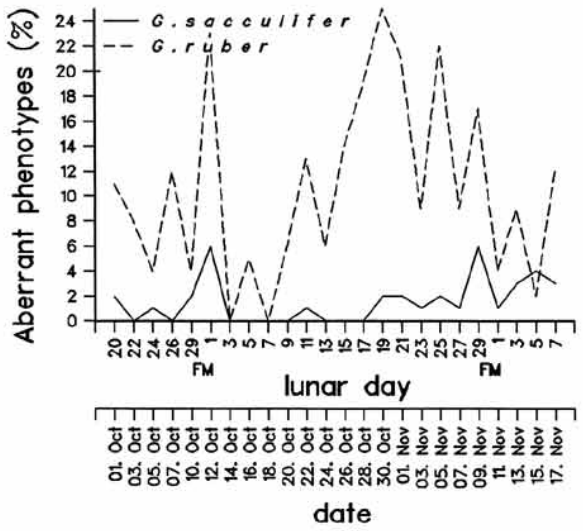

FIGURE 8. Percentage of aberrant phenotypes as a function of the lunar day for the period 1 October to 17 November. For *Globigerinides sacculifer* the sum of kummerform and sac-like chambers are considered. FM is full moon.

in the year are combined, the periodicity may be masked. For these reasons we analyzed consecutive tows from the same locality. The Gulf of Elat/Aqaba is a very stable environment (Reiss, 1977) and thus forms a perfect stage for the study of population dynamics in planktonic foraminifers. Additionally, we took samples at the same time of day, between 9 and 10 a.m., to counteract possible daily vertical migration. The resolution of the reproductive cycle may be further affected by the omnipresence of many juveniles and at least a few larger individuals throughout the lunar cycle. This demonstrates that not all individuals respond to whatever synchronizes maturation or triggers reproduction. The period of the rhythm only approximates that of the environmental cycle that it reflects. This approximation urged Halberg (1963) to introduce the prefix circa to characterize, e.g., lunar as circa lunar or semi-lunar as circa semi-lunar. With respect to semi-lunar rhythms, low resolution may additionally result from the compaction of two cycles into one lunar month, where the predecessors and the late comers mask the reproductive peaks.

The Elat/Aqaba data set shows that adult specimens disappear from the surface waters at certain phases of the moon, while shortly thereafter the surface waters are enriched in juvenile-stage individuals. Except for a general trend shown in Figure 1, minor fluctuations between consecutive collections may be explained as a result of patchiness. The observed decrease in surface water standing stock (i.e., descent to a deeper habitat, beyond our collection depth-range) together with the change towards left-skewed population distributions after a full moon (Figs. 2–4) provide evidence for the existence of a synodic lunar reproductive cycle for all three species. For both *G. ruber* and *G. siphonifera* an additional occurrence of mass reproduction is suggested around new moon. The coincidence of kummerform formation (see below) with an intermediate peak in the occurrence of larger size-classes supports the assumption of a semi-lunar reproductive cycle in this species (Figs. 6 and 8). For *G. siphonifera* no kummerform phenotypes were observed, but evidence for a semi-lunar reproductive cycle is distilled from the intermediate maximum of large adult forms around new moon, followed by a secondary peak of juveniles (Table 3; Fig. 7). There is additional evidence supporting the hypothesis of a semi-lunar reproductive cycle in *G. ruber*. Berger and Soutar (1967) suspected a semi-lunar reproductive cycle in *G. ruber* on the basis of sediment trap samples. Further evidence for a semi-lunar reproductive cycle in *G. ruber* comes from Almogi-Labin (1984, cited in Reiss and Hottinger, 1984), who observed a twofold higher density of *G. ruber* in the sediments of the Gulf of Elat/Aqaba than in the water column if compared to the abundances of *G. sacculifer*.

During many collection dives off the west coast of Barbados and Curaçao, we found a consistent correlation between full moon and the occurrence of spherical *Orbulina universa* d'Orbigny. Shortly after full moon the densities of this terminal stage of *O. universa* decreased. In between two periods of full moon spiral stages were encountered almost exclusively. We conclude on the basis of these observations that *O. universa* also has a lunar reproductive cycle. Similar observations have been made for *Hastigerina pelagica* (d'Orbigny) and confirm the results of Spindler and others (1978, 1979). This species lives just below our collection depth range until shortly before full moon. It then appears in the top surface waters to disappear again after full moon. During the *Meteor* cruise 5/5 into the Red Sea, we could confirm the reproductive cycles of the three species investigated in this paper (unpublished data). A recent expedition to the northwest Atlantic (*Meteor* cruise 10) provided evidence for the existence of a synodic lunar reproductive cycle in *Globigerina bulloides* d'Orbigny as well (unpublished data). We conclude that the lunar cycle entrains the reproductive rhythms that are observed in many spinose planktonic foraminifers.

In most discussions on the temporal control of long-term rhythms, the interpretations are dominated by two main alternatives: an endogenous timing via self-sustained oscillators with a phase-dependent control by external time cues, or a direct control by environmental factors only (Neumann, 1981). Nowadays, most evidence points towards endogenous oscillations underlying most biological rhythms. Even if a rhythm is endogenous, exogenous stimuli of a geophysical cycle will influence the oscillations (Rensing, 1973). A rhythm that originates from within the organism, persists when isolated from the respective environmental cycle. Under those artificially constant conditions, the period of the rhythm t usually deviates slightly from that of the environmental cycle T it has adapted to; i.e., it free runs with its own natural frequency. In natural conditions, however, t is corrected in each cycle so that t

= T, in a process of entrainment to the natural cycle. This process requires and implies that a differential sensitivity exists towards a component of the environment (Zeitgeber, synchronizer), which give rise to adjustment in phase (either advance or delay) according to the phase of the cycle so perturbed (Saunders, 1977). If such a free-running rhythm persists for many periods without attenuation, the rhythm is said to belong to the class of systems of self-sustaining oscillations (innate or endogenous). Lunar periodicity continued in *H. pelagica* under laboratory conditions where it was isolated from the influence of moonlight (Spindler and others, 1979). In 85.4% of the observed cases, gametogenesis occurred within a time span of three to seven days after full moon. The influence of the earth-magnetic field, however, persists and to conclude that this species has an endogenous rhythm might be wrong. Pilot experiments showed that *H. pelagica* "counts" the light/dark cycles. If they are cultured in continuous darkness for three days, the individuals will undergo gametogenesis three days after reference individuals kept in a normal light/dark cycle or specimens in the field. Specimens kept in the light for three days will also delay their reproductive process with respect to full moon (Hemleben and Spindler, unpublished data). Consequently, changes in the earth's magnetic field may also be excluded as a Zeitgeber of the reproductive process in this species. On the other hand, biological rhythms may also be purely exogenous, triggered by the appropriate geophysical cycle (Saunders, 1977). Barnes (1975) states that synchrony in the reproductive state of a population is always the result of external forces and that the resultant rhythms are exogenous. The external agent may be a single impulse or a change in level, may be a constant influence, may vary continuously, or display periodic changes. Cultures of *G. sacculifer, G. ruber, G. siphonifera,* and *O. universa* show that a Zeitgeber, to maintain a lunar reproductive cycle in the laboratory, is absent or at least not effective. As opposed to *H. pelagica,* they do not synchronize their gamete production under laboratory conditions. Apparently, the light/dark cycle in the laboratory is not enough to support the reproductive rhythm in these species. In *G. sacculifer, G. ruber, G. siphonifera,* and *O. universa* the timing of reproduction depends primarily on the culture conditions. Reproduction in, e.g., *G. sacculifer* occurs normally between 8 to 11 days after culture begins, dependent on the size during collection but independent of the time of collection (Hemleben and others, 1987). If the temperature of the culture water is lower, life spans are shorter (e.g., Hemleben and others, 1987). If food is withheld for some time in *G. sacculifer* or if it is kept at a low feeding regime, reproduction is delayed relative to normal conditions (Bé and others, 1981). Vice versa, an increased feeding rate results in an earlier onset of gametogenesis (Hemleben and others, 1987). High light intensities, on the other hand, delay gametogenesis (Caron and others, 1982). These phenomena indicate that the species investigated in this study have an exogenous rhythm or that adverse laboratory conditions override the innate rhythm. However, *G. sacculifer, G. siphonifera,* and *O. universa* are not more susceptible to culture procedures than *H. pelagica.* Thus, we conclude that the reproductive rhythms in these species are the result of external forces. Some observations, however, suggest an innate mechanism in *H. pelagica.* In the laboratory, mature specimens that are below a critical biomass, synchronize their gamete production with the next lunar cycle (Hemleben and others, 1988). Although sexual maturity is reached, reproduction is postponed, probably in order to increase the number of gametes (e.g., Dorazio and Lehman, 1983). This also explains the presence of relatively small (due to, e.g., low prey capture) but mature specimens during and after full moon.

The dependence of the reproductive cycles on laboratory conditions may also be interpreted as an adaptation to varying circumstances that are encountered in the open ocean. A population that lives in, e.g., a eutrophic watermass may reach optimal reproductive size earlier and thus offset (advance) the reproductive cycle with respect to the moon phase. As long as the demes respond in the same fashion, synchrony of gamete release is guaranteed. Alternatively, foraminifers in these eutrophic waters may persist in their lunar cycle, but reach larger average shell lengths and hence substantially increase the biomass from which to draw gametes. Many field observations in different geographic locations under diverse environmental conditions speak in favor of the hypothesis that gametogenesis closely ensues certain phases of the lunar cycle, independent of biotic or abiotic factors. Also, the observation that large shells are encountered in regions with optimum conditions (e.g., Hecht, 1976) confirms this assumption. We conclude that the rhythms which these species display in the field reflect a response to a periodic input coming from outside the organism (exogenous rhythm).

Next we focus on the factors entraining the lunar reproductive cycle in planktonic foraminifers. The trigger for reproduction may lay in the cycle of moonlight itself or in the cycle of the earth's magnetic field resulting from the position of the moon relative to the sun and the earth. One or both of these factors might trigger a response in either the host or the symbionts or in both. The reproductive cycles of symbiont barren species (*G. bulloides* and *H. pelagica*) demonstrate that the response must come from within the foraminifer. The cytological ultrastructure of many species have been investigated over the years. So far we have not encountered an organelle that might be involved in this process, so that the trigger mechanism remains unknown.

The relative low amount of lunar illumination (3.9 nE m^{-2} sec^{-1} and less; Neumann, 1981) varies with the phases of the moon, the length of time that the moon is above the horizon, the moon's height above the horizon, and the weather. The nocturnal light climate distributed by the moon during a synodic month is relatively constant at tropical latitudes, with only slight seasonal changes in the times of moonrise and moon-

set. At higher latitudes, there exist complex seasonal changes in relation to the elevation of the moon and the sequence of times of moonrise and moonset. At higher latitudes, moonlight seems to be an unreliable environmental factor for the induction of a lunar rhythm, especially during summer (because of the low height of the full moon, long crepuscular periods, and above 55°N, a short or even no interval of total darkness about the time of new moon (Neumann, 1981). Moreover, overcasts would complicate the synchronization of reproduction. South of Spitzbergen a lunar cycle was observed in *G. bulloides* in relatively shallow sediment traps that were deployed on weekly basis (Wefer, oral communication, 1989). The existence of lunar cyclicity at these high latitudes may indicate that not the moonlight itself is responsible for the onset of gametogenesis. Here we conclude that the synchronization of the maturation process of a population is a response to a change in the strength of the earth's magnetic field rather than a response to a single impulse on the day of gametogenesis.

IMPLICATIONS FOR MICROPALEONTOLOGY

Population Dynamics

Lunar rhythmicity of reproductive cycles is reflected in plankton tows, sediment traps, and sediments. The size distribution of a species in plankton tows or sediment traps with short deployment times depends primarily on the time of collection with respect to the lunar cycle. This may give rise to an erroneous interpretation, as only fragmentary populations are collected.

The durations of the life cycles have important implications for the reconstruction of (paleo)productivity. Using the population dynamics presented here, sediment assemblages may be converted to shell productivity in the water column to give an impression of the actual standing stock. If the ratio of, e.g., *G. sacculifer* to *G. ruber* in sediments is 1, then the productivity of *G. sacculifer* was two times higher, i.e., the standing stock was twice as large as for *G. ruber*. Hence, on the basis of relative frequencies in the sediment, the productivity of the overlying (sub)surface waters may be estimated. Similarly, comparison of the relative frequencies in the sediments and in the living plankton between a spinose reference species and non-spinose species will clarify the life span of the latter. The combination of environmental preferences and tolerance ranges of the different species (Bijma and others, 1990) together with their newly evoked reproductive cycles allow a better reconstruction of paleoceanographical settings.

Phenotypic Variation

The occurrence of atypical phenotypes have been used to reconstruct ancient ocean parameters. Phenotypic variation in planktonic foraminifera has been interpreted as a morphological response to, e.g., a climatic gradient (Mayr, 1969; Kennett, 1976). Others reported that atypical final growth stages ("kummerforms") indicate stress situations (Berger, 1969; Hecht and Savin, 1970, 1971, 1972; Hecht, 1974). Elsewhere, peculiar terminal chambers ("bullae," "sacs," "kummerforms") have been linked to reproductive processes (Bé, 1965; Bé and Hemleben, 1970; Hemleben and Spindler, 1983; Hemleben and others, 1988). Generally, the following variations in final shell morphology have been observed (Hemleben and Spindler, 1983):

1. One normal last chamber, larger than the previous one.
2. One normal last chamber equal in size with the previous one.
3. One or more (up to four) chambers smaller than the previous one (kummerform; Berger, 1970).
4. In the case of *G. sacculifer,* one polymorphous sac-like chamber, including the "fistulose" type.

The presence or absence of a sac-like chamber in *G. sacculifer* has led to the distinction of two different species (Boltovskoy, 1962): *Globigerinoides sacculifer* with a sac-like final chamber, and *G. trilobus* without this terminal feature. At present they are considered phenotypes of the same species (Bé and Hamlin, 1967). Bermudez (1961) suggested that the sac-like final chamber acts as a more efficient float mechanism than the normal chamber, causing the "sacculifer" type to live at a shallower depth than the "trilobus" form. However, Jones (1967) observed in plankton tows that "sacculifer" is found at slightly greater depth than "trilobus." In agreement with Jones (1967), R. G. Fairbanks (written communication, 1986), found that *G. sacculifer* without a sac-like final chamber is a mixed-layer dweller whereas the sac-like phenotype inhabits the chlorophyll maximum zone which coincides more or less with the thermocline where zygote formation is supposed to occur. Bé and others (1983) concluded that a sac-like chamber in *G. sacculifer* is a terminal event of shell growth and signals that gametogenesis is imminent. They conclude that it acts as a protective structure into which the multinucleated cytoplasm can expand and within which further development of the delicate stages of nuclear division can take place. Bé (1980) and Hemleben and Spindler (1983) noted that the formation of a sac-like chamber generally precedes full gamete release by about 12 to 48 hours. However, formation of a sac-like chamber is not a prerequisite for reproduction to take place; specimens of the "trilobus" type undergo gametogenesis as well. The highest percentages of sac-like chambers parallel the lunar reproductive event (Fig. 8) and are found at a density layer (R. G. Fairbanks, written communication, 1986). We therefore conclude that the formation of a sac-like chamber is correlated to the process of reproduction.

Also a diminutive or kummerform final chamber may indicate impending reproduction (Hemleben, 1982; Hemleben and others, 1988). Berger (1969) suggested that the kummerform phenotypes result from the termination or drastic slowing of growth due to environmental stress, notably lack of food. Banerji and

others (1971) considered kummerform development to be an ontogenetic feature. Criticizing Berger's definition, Olsson (1971, 1973) stated that the most important feature in the ontogenetic history of each individual is the slowing of growth in the final stages and not the relationship of the size of the ultimate and penultimate chambers. Olsson reasoned that kummerform phenotypes are adults that have reached the growth limit of the species and concluded that kummerform phenotypes are indicative of individuals that have obtained full adult size. However, there are gerontic individuals which do not possess a diminutive final chamber as well as small specimens which do have a kummerform last chamber. These observations do not support Olsson's geometric growth model.

Berger (1970, 1971) observed a high proportion of kummerforms in death assemblages relative to the standing stock. Apparently, the propensity to make an empty shell is greater in kummerform than in normal forms. Having assigned a subordinate position to predation (predators cannot be expected to distinguish between normal forms and kummerforms to any great extent), two likely sources of empty shell production remain: reproduction and environmental stress (increased mortality). Which one is more important? Hecht and Savin (1970, 1971) measured oxygen isotopes on kummerform and normal form tests of some species of foraminifers from core top samples. They report colder isotopic temperatures for kummerforms and conclude that kummerform phenotypes are produced when they leave the optimum water depth to which the species is adapted. Bé and Van Donk (1971) questioned applying the environmental stress model to all phenotypes with diminutive last chambers. If kummerform development were a result of environmental stress, one would expect this to occur in individuals at different stages of ontogeny.

For *G. ruber* the highest percentages of kummerform were recorded with full moon and two days after new moon (Fig. 8). The coincidence of reproductive activity with the occurrence of high percentages of kummerform phenotypes observed in the field suggests that this phenomenon is coupled to the event of reproduction. We conclude that kummerform chambers are terminal stages that are closely tied to the reproductive process.

CONCLUSIONS

1. The data presented here show that the reproductive rhythm of *G. sacculifer* follows the lunar cycle. Semi-lunar reproductive cycles are characteristic for *G. ruber* and possibly for *G. siphonifera.*

2. Field observations (data not presented herein) indicate that at least *O. universa* and *G. bulloides* also reproduce according to a lunar cycle.

3. The reproductive rhythms of *G. sacculifer, G. ruber, G. siphonifera,* and *O. universa* are probably exogenous. The cycle of *H. pelagica* may be endogenous.

4. Different reproductive cycles (semi-lunar versus lunar) lead to different absolute empty shell productions. Consequently, the ratio between the species in the sediment do not necessarily reflect the proportions in the standing stock of the overlying water. Life spans inferred from the reproductive cycles may be used to calculate ratios between species and thus the relative productivity of the surface waters of ancient oceans.

5. Kummerform phenotypes and sac-like chambers are linked to the process of reproduction and probably do not indicate environmental stress.

6. Knowledge of the duration of life cycles are indispensable for the interpretation of sediment trap data.

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