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Population dynamics of the planktic foraminifer *Globigerina bulloides* from the eastern North Atlantic

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Abstract—A cumulative data set from the eastern North Atlantic was compiled and analysed to study the population dynamics of *Globigerina bulloides*. Data were generated from samples collected with a multiple opening and closing plankton net from the upper ocean (0–500 m). We analysed the total assemblage > 125 μm. The habitat of *G. bulloides* in the eastern North Atlantic is restricted mostly to the upper 60 m of the water column and depends on the availability of its food resources and, therefore, on the general hydrographic pattern. The temporal distribution of tests at different depths reveals a systematic succession that is related to the lunar cycle. We suggest that *G. bulloides* reproduces mainly within the upper 60 m of the ocean. Gametogenesis is unusual in test size classes below 125 μm but frequent in specimens larger than 150 μm. Reproduction takes place during the first week after new moon. Maturation of specimens takes place during the second half of waxing moon and during waning moon. Large numbers of mature specimens [gametogenic calcification (GAM) specimens > 250 μm] occur during the time of main reproduction. © 1997 Published by Elsevier Science Ltd

INTRODUCTION

Globigerina bulloides d'Orbigny is a non-symbiotic, spinose planktic foraminifer and is associated with temperate to sub-polar watermasses but also characteristic for upwelling environments in lower latitudes (Bé and Tolderlund, 1971; Bé and Hutson, 1977; Naidu and Malmgren, 1996a, Naidu and Malmgren, 1996b). In these regions, *G. bulloides* often dominates the foraminiferal flux to the ocean floor (Sautter and Thunell, 1989; Sautter and Sancetta, 1992) and is therefore an important source of geochemical information for palaeoceanographic reconstructions (Bard *et al.*, 1987; Kallel *et al.*, 1988; Sautter and Thunell, 1991). In contrast to most spinose species, an important part of its diet consists of algae, as indicated by the olive green to brownish coloration of its cytoplasm in freshly collected specimens and by transmission electron microscopy (TEM) investigation. Apart from some biogeographical studies, only a few accounts have been published on its lifestyle (e.g. Lee *et al.*, 1965; Spindler and Hemleben, 1980). To date, one laboratory study has been conducted with *G. bulloides*, quantifying the environmental and physiological parameters responsible for stable isotopic disequilibrium fractionation (Spero and Lea, 1996).

As passive inhabitants of their environment, planktic foraminifera are distributed by currents, turbulence, and other hydrodynamic events. Although the odds against gametes of the same species ever coming into contact in the open ocean seem great, planktic

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foraminifera have developed adaptive strategies that help maximize the probability of gamete fusion. These include (1) release of high numbers of gametes (up to hundreds of thousands per parent cell), (2) production of motile gametes that contain sufficient food reserves for prolonged locomotion, (3) synchronization of gamete release with distinct phases of the moon, and (4) establishment of a depth preference for reproduction (Spindler *et al.*, 1978, Spindler *et al.*, 1979; Almogi-Labin, 1984; Hemleben *et al.*, 1989; Bijma *et al.*, 1990, Bijma *et al.*, 1994; Erez *et al.*, 1991; Bijma and Hemleben, 1994; Marchant, 1995). The concept of lunar cyclicity (synodic cycle) in the life cycle of some spinose planktic species is generally accepted, and reports are accumulating. However, as spinose species differ significantly in their biological behaviour and in their habitat, reproductive modes have to be demonstrated for each species. Among other organisms, especially metazoans, lunar cyclicity is well known (Richmond and Jokiel, 1984) though triggering mechanisms are not well understood and still under debate.

In the following, we discuss the spatial and temporal components of the population dynamics of *G. bulloides* from the eastern North Atlantic, to provide an additional tool for palaeoceanological and palaeoclimatological interpretation of fossil faunas. It will be demonstrated that this species follows a lunar reproduction cycle. The population of *G. bulloides* mainly lives within the upper 60 m of the water column. However, its depth distribution can be modified by the availability of its diet and therefore by hydrographical conditions.

MATERIALS AND METHODS

To study the population dynamics of *G. bulloides* we compiled a data set that consists of faunal counts from depth stratified plankton samples that were collected during the R.V. *Meteor* cruise 10, legs 2 and 4 (May and August 1989), cruise 12, leg 3 (June 1990), cruise 21, legs 1, 2 and 6 (March, April and August 1992), cruise 26, leg 1 (September 1993), and during R.V. *Poseidon* cruise 200, leg 6 (June 1993) at 47°N,20°W (BIOTRANS) and 57°N,22°W (Table 1). A multiple opening and closing net (MCN) with a 0.5 m × 0.5 m mouth opening, equipped with five nets of 100 μm mesh size, was employed for vertical tows. The upper 100 m of the water column was sampled at five standard depth intervals of 20 m each (Table 2). Eighteen out of 29 days were sampled at 1–3 day intervals to cover a complete lunar cycle (Table 3).

The samples were fixed in 4% hexamethyltetramine buffered formaldehyde solution (pH 8.2) and processed in our laboratory in Tübingen. Planktic foraminifera were picked, dried, and separated into size classes <100 μm, 100–125 μm, >125–150 μm, >150–200 μm, >200–250 μm, >250–315 μm and >315 μm, followed by splitting into aliquots when necessary. Tests from size fractions >125 μm were counted (Tables 2 and 3). Average numbers of tests per cubic metre were calculated by dividing the total number counted per sample by the filtered water volume (i.e. MCN mouth area × depth interval). To evaluate changes in the faunal structure with depth, the absolute number of *G. bulloides* in five size fractions was calculated for each depth interval (Table 2). For evaluating changes in the faunal structure versus time, data were sorted according to their collection time within the lunar cycle. Average test numbers were calculated for identical lunar days (Table 3). In addition, the relative frequency of test size fractions was calculated for each single lunar day. According to Bijma and Hemleben (1994), residual values were calculated by subtracting the average relative frequency of tests from the actual relative frequency.

Table 1. Temporal, spatial, and hydrographical conditions of samples analysed

MCN	Lunar day	Date	Cruise/Leg	Station	Latitude (°N)	Longitude (°W)	Depth range (m)	MLD (m)	*T* (°C)	*S*
218	15	05/05/89	M 10/2	430	47°00′	19°53′	0–20–40–60–80–100	15	13.47*	35.68*
231	19	05/09/89	M 10/2	440	46°22′	19°01′	0–20–40–60–80–100	20	13.09*	35.67*
250	21	05/11/89	M 10/2	452	46°13′	18°40′	0–20–40–60–80–100	25	13.02	34.92
261	23	05/13/89	M 10/2	460	46°14′	18°21′	0–20–40–60–80–100	25	13.14	35.41
295	28	05/18/89	M 10/2	485	46°23′	17°45′	0–20–40–60–80–100	35	13.69*	35.63*
315	2	05/21/89	M 10/2	499	46°13′	17°51′	0–14–34–54–74–94	50	13.21*	35.61*
319	7	05/26/89	M 10/2	553	58°00′	21°50′	0–20–40–60–80–100	n.d.	9.14	34.48
321	9	05/28/89	M 10/2	562	57°59′	21°53′	0–20–40–60–80–100	15	9.14*	34.98
334	11	05/30/89	M 10/2	569	57°49′	22°18′	0–20–40–60–80–100	20	10.05*	35.25*
342	13	06/01/89	M 10/2	579	57°42′	22°57′	0–20–40–60–80–100	20	9.56*	35.25*
504	6	08/20/89	M 10/4	852	47°25′	19°41′	0–20–40–60–80–100	n.d.	17.54	35.63
508	7	08/21/89	M 10/4	856	47°23′	19°41′	0–20–40–60–80–100	n.d.	17.73	35.66
510	9	08/23/89	M 10/4	868	47°22′	19°36′	0–20–40–60–80–100	n.d.	17.52	35.61
512	10	08/24/89	M 10/4	872	47°15′	19°32′	0–20–40–60–80–100	n.d.	17.87	35.61
514	11	08/25/89	M 10/4	879	47°16′	19°32′	0–20–40–60–80–100	n.d.	18.24	35.76
557	12	06/20/90	M 12/3	367	47°16′	19°32′	0–20–40–60–80–100	n.d.	15.61	35.72
559	14	06/22/90	M 12/3	374	47°16′	19°34′	0–20–40–60–80–100	n.d.	15.08	35.70
561	17	06/25/90	M 12/3	381	47°26′	18°49′	0–20–40–60–80–100	n.d.	15.55	35.66
604	10	03/27/92	M 21/1	80	47°01′	19°29′	0–20–40–60–80–100	35	13.06*	35.60*
606	11	03/28/92	M 21/1	87	47°13′	19°34′	0–20–40–60–80–100	60	11.70	35.36
624	0	04/17/92	M 21/2	129	47°09′	19°33′	0–20–40–60–80–100	n.d.	13.17	35.77
627	2	04/19/92	M 21/2	148	47°40′	19°49′	0–20–40–60–80–100	50	13.34*	35.60*
638	5	04/22/92	M 21/2	158	47°28′	19°07′	0–20–40–60–80–100	50	13.46*	35.78*
652	13	04/30/92	M 21/2	181	46°52′	18°33′	0–20–40–60–80–100	160	12.35*	35.50*
656	14	05/01/92	M 21/2	187	46°39′	18°27′	0–20–40–60–80–100	100	12.35*	35.50*
766	19	08/02/92	M 21/6	351	47°11′	19°34′	0–20–40–60–80–100	30	16.85	35.47
777	24	08/07/92	M 21/6	373	47°05′	19°41′	0–20–40–60–80–100	30	18.00*	35.89*
784	28	08/12/92	M 21/6	389	47°13′	19°35′	0–20–40–60–80–100	40	17.04	35.48
787	2	08/14/92	M 21/6	396	47°13′	19°35′	0–20–40–60–80–100	30	16.50*	35.40*
837	7	06/16/93	P 200/6	448	44°48′	19°53′	0–20–40–60–80–100	30	14.85*	35.70*
843	12	09/09/93	M 26/1	455	47°47′	19°45′	0–20–40–60–80–100	50	17.50*	35.58*

Multiple opening and closing net (MCN) numbers are arranged chronologically. Positions around 47°N latitude and 19°W longitude are in the BIOTRANS area. Lunar day 0 is full moon; lunar day 14 is new moon. M, *Meteor* cruise; P, *Poseidon* cruise. Depth ranges describe the sampled water depth intervals. Mixed layer depths (MLD) (m) are estimated from CTD profiles (temperature, salinity, fluorescence). Sea surface temperature (*T*) and salinity (*S*) are measured by shipboard facilities, or *by CTD. n.d., no data available.

RESULTS

Large numbers of cytoplasm-bearing tests were recorded down to 300 m depth during spring (M21/1 and 2), as a result of deep water mixing. During summer (M12/3), cytoplasm-bearing tests were mainly restricted to the upper 100 m of the water column (Fig. 1). However, the distribution of cytoplasm-bearing tests is not a good indicator for the habitat of planktic foraminifers, because sinking, recently dead specimens may still contain cytoplasm. Hence, the depth of the productive layer may be overestimated from the distribution of cytoplasm-bearing tests. Because living *G. bulloides* cannot readily be distinguished from dead specimens, we have analysed the total assemblage in the following.

*Table 2. Absolute number of tests per cubic metre from different depth intervals and from different size fractions: (a) for the combined data set, and (b) during cruise M*10/2

	Size fraction (μm)					
Depth (m)	> 125–150	> 150–200	> 200–250	> 250–315	> 315	Total
(a) For the combined data set						
0–20	8.5	13.0	7.6	4.4	1.2	34.7
20–40	6.8	8.6	7.3	4.9	1.4	29.0
40–60	6.3	8.7	6.6	4.8	1.4	27.9
60–80	3.7	5.8	4.2	2.8	0.6	17.1
80–100	3.9	5.1	3.7	2.8	0.5	16.0
Average	5.9	8.3	5.9	3.9	1.0	24.9
(b) During cruise M10/2						
0–20	10.6	20.4	13.3	8.9	2.5	55.6
20–40	7.5	16.2	16.9	13.4	3.8	57.9
40–60	6.8	16.8	16.2	13.9	3.6	57.3
60–80	3.1	7.3	7.4	6.1	1.5	25.2
80–100	3.9	9.5	7.0	7.0	1.4	28.8
Average	6.4	14.0	12.2	9.8	2.5	45.0

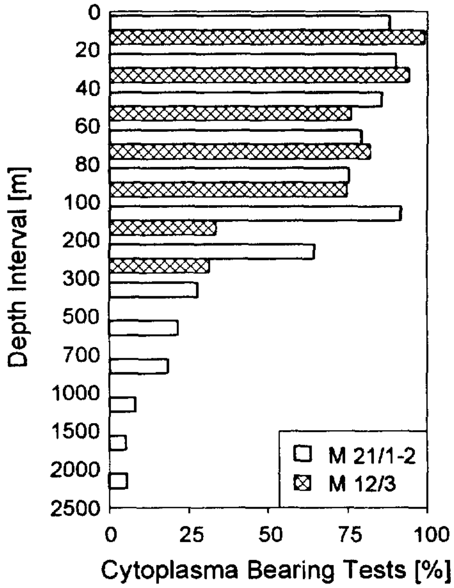

Fig. 1. Relative frequency of cytoplasm-bearing *G. bulloides* tests from depth intervals between the sea surface and 2500 m. During spring (M21/1 and -2, Table 1) large numbers of cytoplasm-bearing tests were recorded down to 300 m depth, as a result of deep mixing. During summer (M12/3) large numbers of cytoplasm-bearing tests are restricted to the upper 100 m of the water column.

*Table 3. Absolute number of tests (0–60 m depth) per cubic metre, from different size fractions, arranged according to their temporal position during the lunar cycle, (a) for the combined data set and (b) during cruise M*10/2

	Size fraction (μm)					
Lunar day	> 125–150	> 150–200	> 200–250	> 250–315	> 315	Total
(a) For the combined data set						
0	24.7	20.4	6.5	1.3	0.0	52.9
2	12.2	24.0	16.5	11.5	2.6	66.8
5	13.3	8.5	4.6	1.4	0.7	28.5
6	0.9	0.5	0.2	0.0	0.0	1.6
7	4.4	6.3	3.9	2.3	0.4	17.3
9	1.5	1.1	0.6	0.2	0.0	3.4
10	5.6	5.9	3.1	0.8	0.3	15.6
11	7.5	9.4	5.1	2.4	0.3	24.6
12	10.1	9.8	3.7	1.1	0.0	24.7
13	7.8	16.6	6.5	1.9	0.3	33.2
14	5.6	5.5	3.7	2.7	0.6	18.1
15	1.3	4.8	9.9	11.9	5.5	33.3
17	7.7	9.2	6.1	4.2	0.3	27.4
19	4.1	13.3	17.1	13.5	3.8	51.8
21	0.0	0.4	5.3	7.3	2.5	15.5
23	3.7	14.1	16.0	11.3	3.9	49.0
24	1.1	0.3	0.0	0.0	0.0	1.5
28	18.6	32.0	20.1	10.7	2.3	83.7
Average	7.2	10.1	7.2	4.7	1.3	30.5
Mortality (%)		29.2	34.5	72.2	100.0	
(b) During cruise M10/2						
2	24.2	53.6	40.0	33.3	7.8	158.9
7	6.5	12.8	8.1	5.0	0.7	33.1
9	1.1	0.7	0.3	0.2	0.0	2.3
11	1.3	3.5	3.9	2.5	0.3	11.5
13	4.7	7.5	3.8	2.6	0.2	18.8
15	1.3	4.8	9.9	11.9	5.5	33.3
19	3.7	18.1	27.7	25.1	7.2	81.7
21	0.0	0.4	5.3	7.3	2.5	15.5
23	3.7	14.1	16.0	11.3	3.9	49.0
28	36.5	62.6	39.9	21.3	4.7	165.0
Average	8.3	17.8	15.5	12.1	3.3	56.9
Mortality (%)		13.0	22.1	72.8	100.0	

The difference between one size class and the next, expressed as a fraction (per cent) of the smaller size class, is equivalent to the total loss.

Bathymetric distribution

The number of *G. bulloides* tests per cubic metre decreases below 60 m depth (Fig. 2). The average number of specimens in the upper 60 m was 31 specimens m^{-3}. Between 60 and 100 m an average of 17 specimens m^{-3} was recorded.

Trends can be observed in the comparative residual values of each size class with depth. The M10/2 data show that in the upper 20 m of the water column tests from the < 200 μm

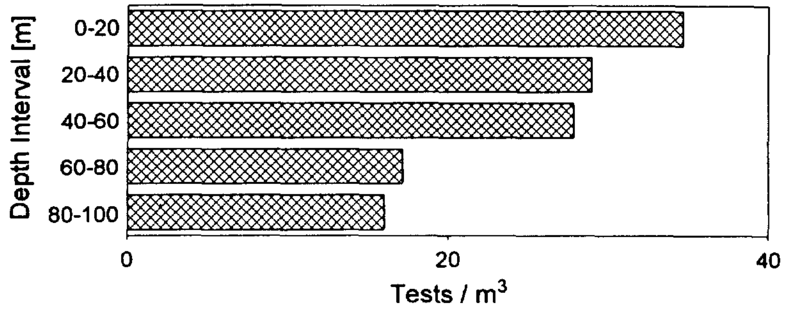

Fig. 2. Absolute number of *G. bulloides* tests per cubic metre in the upper 100 m of the water column (data from all stations, Table 1). The average number of specimens in the upper 60 m was 31 specimens m^{-3}. Between 60 and 100 m about 17 specimens m^{-3} were present.

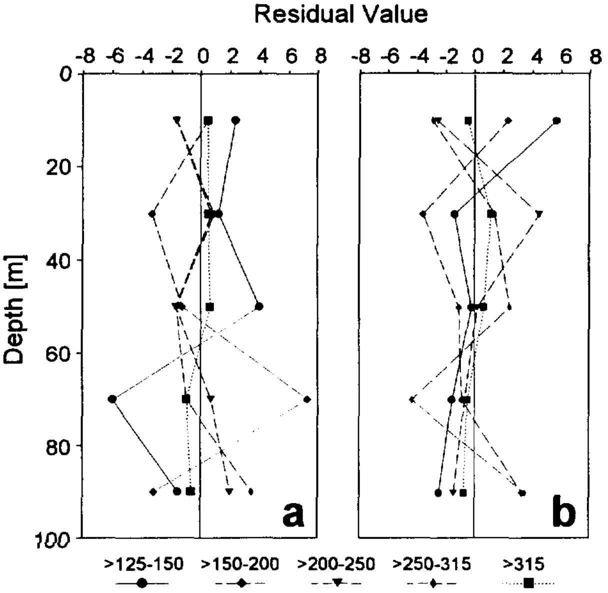

Fig. 3. Residual values of tests from different size classes and from different depth intervals. A distinct change of the test size distribution is found at 60 m depth in the BIOTRANS data (a) and in the M10/2 data (b). During M10/2 a prominent change of the test size spectrum occurred at about 20 m depth (b).

fraction dominate the fauna (Fig. 3b). Between 20 and 60 m tests >200 μm are more frequent than smaller tests, and below 60 m the distribution is rather random. Average values of the test size spectrum in the upper 60 m at the BIOTRANS site show positive residual values for very small (>125–150 μm) and very large tests (>315 μm), indicating that tests from these size classes are more frequent at this depth than on average for all depth intervals (Fig. 3a). Below 60 m, small (>125–200 μm) and large tests (>315 μm) are underrepresented, and the size distribution is dominated by medium-sized tests (>200–315 μm). As displayed by the M10/2 data and by the compiled data set, changes in the size distribution are most prominent at about 60 m depth.

Temporal distribution

The temporal distribution of tests from different depth intervals reveals a systematic succession within the lunar cycle. In the first half of the lunar cycle, between full moon (lunar day 0) and new moon (14th lunar day), large proportions of tests between > 125 μm and 200 μm diameter were found (Fig. 4). During that time, several pulses of small tests were observed. Almost no tests larger than 250 μm were present during waning moon. At new moon the test size distribution of *G. bulloides* changed abruptly, and high portions of tests > 200 μm were present. Maximum relative frequencies of tests > 200 μm were recorded twice, on the 15th and the 21st lunar day (Fig. 4). These pulses can be seen in the entire upper water column and they become very distinct when the residual values of the size classes < 250 μm and > 250 μm are plotted versus lunar day (Fig. 5). The two maxima of large tests, on the 15th and the 21st lunar day, were recorded during different sampling intervals. During a single sampling period only one maximum occurs. At the end of the waxing moon, between the 23rd and the 28th lunar day, the test size spectrum changes again, with large proportions of small tests (up to 60% of the assemblage < 150 μm). This is most distinct in the upper 60 m of the water column (Fig. 4).

Mortality and reproduction

The loss of tests as a result of growth, death, and reproduction within each size fraction is shown by a loss curve, as generated from the total number of specimens from each size fraction present in the upper 60 m of the water column (Fig. 6). The difference between one size class and the next, expressed as a fraction of the smaller size class, is equivalent to the total loss. During single sampling periods, e.g. M10/2, mortality of small specimens, between > 150 μm and 250 μm diameter, was much lower compared with the combined data (Table 3). We assume that the compiled data balance out local or temporal changes with respect to, for instance, the trophic situation, and therefore give a better representation of the average loss rate.

Tests conserve traces of gametogenesis in the ultrastructure of the shell. They develop a smooth veneer of calcite, known as gametogenic calcification (GAM). In more advanced stages of GAM calcification spine-holes become covered with calcite (Bé, 1980; Hemleben *et al.*, 1989; Hemleben *et al.*, 1991). Thus, we can determine the frequency of gametogenesis, and therefore the frequency of death owing to reproduction within each size class. With a scanning electron microscope we inspected 190 tests from sediment surface samples from the northeastern Atlantic between 1500 m and 1830 m water depth. About half of the tests between 100 μm and 125 μm and 70% of the tests between > 125 μm and 150 μm showed GAM calcification, whereas the remaining 55% and 30% of tests were accumulated in the taphocoenosis for other reasons (Fig. 6). The reproduction rate of organisms with tests > 150 μm is almost 100%.

DISCUSSION

Each sample represents a transitional state of the standing stock and appears to be affected by the time of collection (e.g. lunar day and season), by the distribution of food and by the geographic position. Our samples originate from different geographic positions, from different seasons and years, and, as indicated by temperature and salinity of the surface

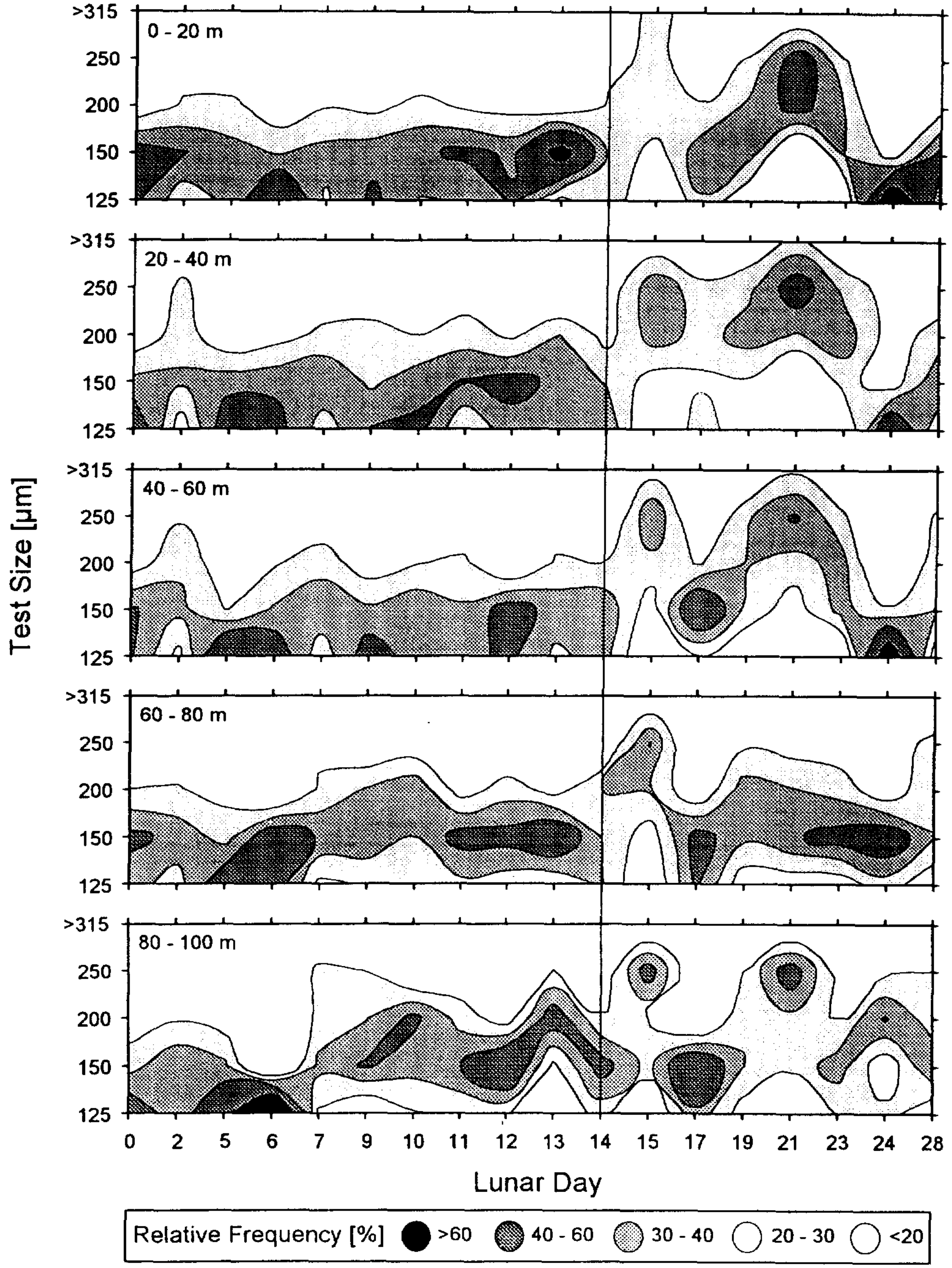

Fig. 4. Relative frequency of *G. bulloides* test size fractions from different water depth intervals, combined from various sampling periods [M10/2 and -4 (1989), M12/3 (1990), M21/1, -2 and -6 (1992), M26/1 (1993), and P200/6 (1993)]. Data are arranged according to their position in the lunar cycle. Mainly small tests (< 200 µm) occur during the first half and during the end of the lunar cycle; large numbers of large tests (> 200 µm) are found in the first week after full moon. New moon is marked by the vertical line at the 14th lunar day.

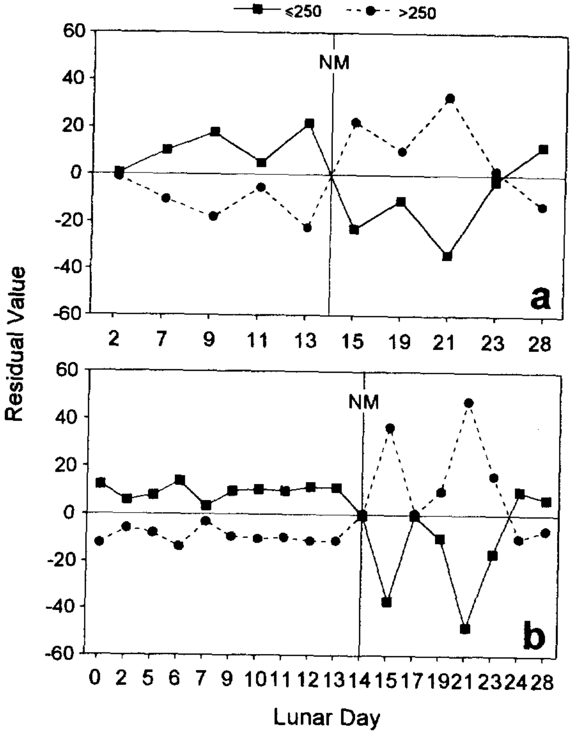

Fig. 5. Residual values, displaying the difference between the average relative frequency and the actual relative frequency of test size classes > 125–250 μm and > 250 μm, from the M10/2 data (a), and from the combined data set (b). During the first half of the lunar cycle large proportions of small tests are recorded from the upper 60 m of the water column. At new moon (NM, 14th lunar day) residual values change, and more than average large tests are found. At the end of the waxing moon residual values change again and large proportions of small tests are recorded.

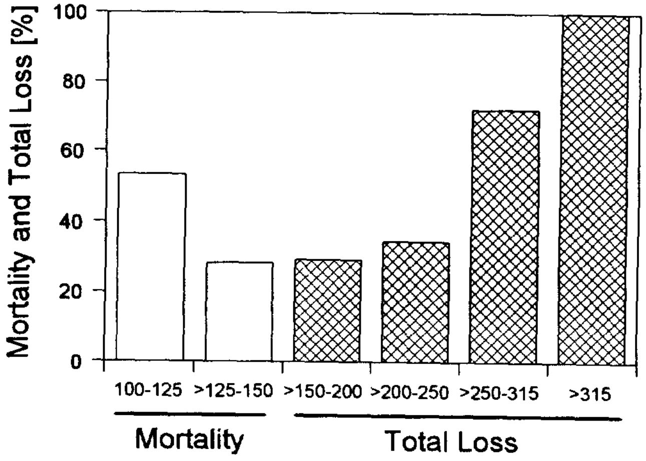

Fig. 6. Mortality (white) and total relative loss (cross-hatched) of specimens as a function of test size. All tests > 150 μm show traces of gametogenesis, whereas only 70% and about 45% of the assemblage between > 125–150 μm and 100–125 μm is suspected to have reproduced. Total loss < 150 μm was not calculated.

water (Table 1), from different water masses. If reproduction in *G. bulloides*, or in any other planktic foraminiferal species, is initialized by lunar influence, then temporal changes in the specific population structure (test size spectra) should be similar at equal geographic longitudes, although local biotic and abiotic parameters may mask the signal. In terms of hydrography, the BIOTRANS area is a very unstable region of the eastern North Atlantic, and, in particular, samples may originate from the North Atlantic Current (NAC), from the North Atlantic Transitional Water (NATW) (Ottens, 1991), or from eddies, which are frequent in this part of the ocean (Beckmann *et al.*, 1987). Therefore, the spatial and temporal clustering of all samples does not represent the dynamics of a single population.

From the average depth distribution of tests we suggest that the main living fauna of *G. bulloides* dwells in water depth above 60 m. Although growth and reproduction are suggested to take place only in the upper 60 m (Fig. 2), the selection of the habitat strongly depends on physico-chemical and biological parameters (adequate food resources) of a watermass rather than depth alone (Ortiz *et al.*, 1995). In times of deep mixing of the surface ocean, particularly during storms in spring, the living fauna can be distributed over the upper 200 m of the water column (Schiebel *et al.*, 1995).

According to our vertical plankton tow data, at least two different zones can be distinguished in the water column: a productive zone, where growth and reproduction take place (0–60 m), and a flux zone (below 60 m depth), which contains postgametogenic and dead specimens (empty tests or tests filled with various amounts of cytoplasm remnants) that sink to the ocean floor. A third zone (0–20 m) was recognized in the data set from M10/2 (Fig. 3b): if the size distribution is a reliable indicator for reproduction, it follows that during the M10/2 sampling period, reproduction in *G. bulloides* occurred mainly in the upper 20 m of the ocean. During that time, the lower boundary of the mixed layer depth (Table 1: average MLD = 25 m) coincides with the position of the chlorophyll maximum (CM), ranging from 20 m to 30 m depth (Meyerhöfer and Stienen, 1990). Comparing the depth distribution of *G. bulloides* (Fig. 2) with the position of the MLD and the CM, we suggest that the depth habitat of *G. bulloides* is related to the general hydrography and to the availability of food, rather than to the physical stratification of the water column itself. The CM is thought to be the main feeding level for juvenile planktic foraminifera. The reproduction depth is thus not biologically fixed but determined by the highly variable hydrography and the distribution of food sources.

Because of the mesh size of our collecting gear, equivalent data are not available for specimens below 100 μm, and may not be quantitative for specimens below 125 μm. Therefore, as juvenile and most neanic specimens are not included in our samples, we cannot determine the exact timing of reproduction of *G. bulloides*. Nevertheless, we can estimate the time of reproduction by ontogenetic data (Sverdlove and Bé, 1985). The diameter of the proloculus of *G. bulloides* is 20 μm on average. Young specimens grow fast, thus a test size of 125 μm can be reached in less than 10 days after reproduction (Hemleben *et al.*, 1989; Spero and Lea, 1996). Growth rates are affected by many factors, such as temperature and quality and abundance of food. Resulting pulses of small tests (> 125 μm) were recorded between the second half of the waxing moon and the new moon of the next lunar cycle (Fig. 7). These small specimens are thought to result from the reproduction of large *G. bulloides*, mainly during the first half of the waxing moon.

Marchant (1995) suggested from a sediment trap investigation off Chile that *G. bulloides* reproduces twice a month. Sediment traps with sampling intervals of 8–9 days were moored between 2173 m and 3520 m depth. As a result of differential sinking velocity (Takahashi

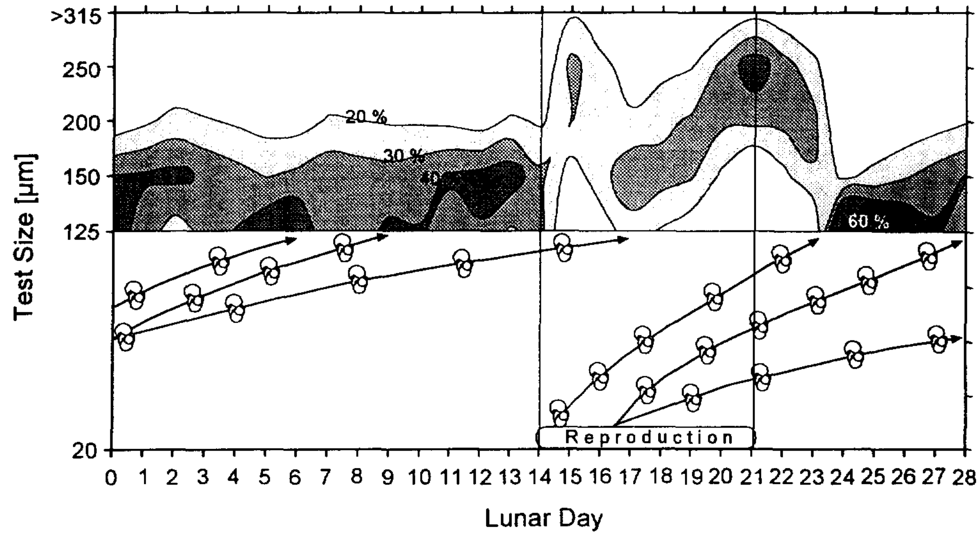

Fig. 7. Average relative test size distribution of *G. bulloides* > 125 µm (0–60 m, linear time scale by interpolation of data) and suspected schematic test size distribution between 20 µm and 125 µm test size. Some possible growth curves of specimens are indicated by arrows. Reproduction is placed at times when large proportions of large specimens (GAM specimens) are recorded, which is during the first week of the waxing moon.

and Bé, 1984), tests of different sizes reach the sediment traps within different time spans. Therefore, the assemblage reported by Marchant (1995) may not reflect the primary dynamics of living *G. bulloides* but a pattern that is masked by differential sinking velocities.

We have shown that *G. bulloides* reproduces once per lunar cycle, during the first week after new moon, and mainly within the upper 60 m of the ocean. During the second half of waxing moon and during waning moon specimens mature, and during the first week of the waxing moon large numbers of terminal test stages (GAM individuals) lead to a new start of the ontogenetic life cycle (Fig. 7).

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