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Patchiness and life cycle of intertidal foraminifera: Implication for environmental and paleoenvironmental interpretation

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Abstract

This study was carried out at the mouth of a small river of the Atlantic coast of France, with the aim of investigating medium-scale patchiness and life cycles in time series samples of foraminiferal assemblages.

Sampling was carried out at three stations, irregularly between January 2000 and September 2001, and on a monthly/bimonthly basis, between September 2001 and September 2003. A monthly sampling was continued until April 2004 at two stations. Samples were also collected at ten selected sampling sites, in October 2002, with the aim of getting information about spatial distribution of foraminifera, either at the same intertidal level or at different elevations. Living assemblages were studied in each sample, and compared to total assemblages from about half of the samples. A pseudoreplication procedure was used to circumvent small-scale patchiness.

This study confirms that paralic foraminifera do not have reproducible annual life cycles and that isolated samplings of living assemblages may provide different or even contradictory results, depending if the sampling is done during the bloom or not. It also shows that, even if blooms occur at periods close together for all the species at neighboring stations, differences exist between stations located in the same environment, 10 m apart. Thus, isolated or even seasonal samplings of living foraminiferal assemblages cannot be considered as giving a valuable image of environmental conditions. Conversely, total assemblages provide integrated information about homogenized assemblages over a given period of time. This study demonstrates that exchanges of tests by transport between low marsh to high marsh is weak or absent, but small-scale post mortem transport leads to the homogenization of the assemblage.

Keywords: Foraminifera; Estuaries; Salt marshes; Life cycles; Patchiness; Preservation

1. Introduction

Seasonality in foraminiferal populations has interested researchers for many years (e.g., Myers, 1943; Walton, 1955). However, the collection and study of monthly samples over long periods is very time consuming, especially in paralic environments. It is probably why there are very few studies in which samples from the same locality have been taken monthly over a period of more than one year (Boltovskoy, 1964; Lutze, 1968; Boltovskoy and Lena, 1969a; Scott and Medioli, 1980b; Murray,

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1983; Kitazato and Matsushita, 1990; Basson and Murray, 1995; Buzas and Hayek, 2000; reviews in Murray, 2000a and Murray and Alve, 2000). These studies, carried out on living specimens (and in one case on total populations also, Scott and Medioli, 1980a), provide important data on the variability and/or cyclicity of the standing crop, both during a year and from one year to another. They show that annual ranges of variability are large in each area and that the pattern is not repeated from one year to the next. Moreover, the main species may show different patterns (Lutze, 1968; Basson and Murray, 1995). In his review, Murray (2000a) reported that, except for the Exe estuary (Murray, 1980, 1983), the data are statistically different for different whole-year datasets. He considered that the differences in monthly records could probably be attributed to patchiness in distribution patterns, which may occur both on 10-cm and 1-m sample spacing (Boltovskoy and Lena, 1969b).

After the foraminifera die, empty tests may be scattered around at a local scale by wind induced lapping, mainly in intertidal areas. Scott and Medioli (1980a) have shown that total assemblages, including living and dead individuals, integrate seasonal variations and reflect prevailing conditions.

The objectives of this study are: to provide new data on temporal changes of living foraminiferal assemblages, to compare time series data in stations close together but subject to different environmental conditions, to estimate the impact on temporal changes of spatial variability in foraminiferal assemblages subjected to the same overall conditions, to estimate the impact of transport from one station to the other, and to discuss the relationships between living and total (living and dead) assemblages.

2. Materials and methods

Foraminifera may live as deep as 30 cm in the sediment (Goldstein et al., 1995), but since the highest numbers of living foraminifera are found in the surface 0–1 cm layer (review in Alve and Murray, 2001), this study will consider only surface sediments. Recently, Tobin et al. (2005) demonstrated from three different marsh settings that the infaunal living specimens had no effect on the total population.

2.1. Sampling sites

The study area is located at the mouth of a small river (Étier de Sallertaine), in the South of the Bay of Bourgneuf (latitude about 47° N, longitude about 2° W) (Fig. 1a). About four kilometers upstream, the estuarine area is bounded by a sluice. During rainy periods, it opens when the freshwater level is higher than the tide level, allowing freshwater discharge. It remains closed during the dry later spring and summer, when it prevents the penetration of marine water upward, into agricultural areas. A small tributary joins the river near the mouth. Its

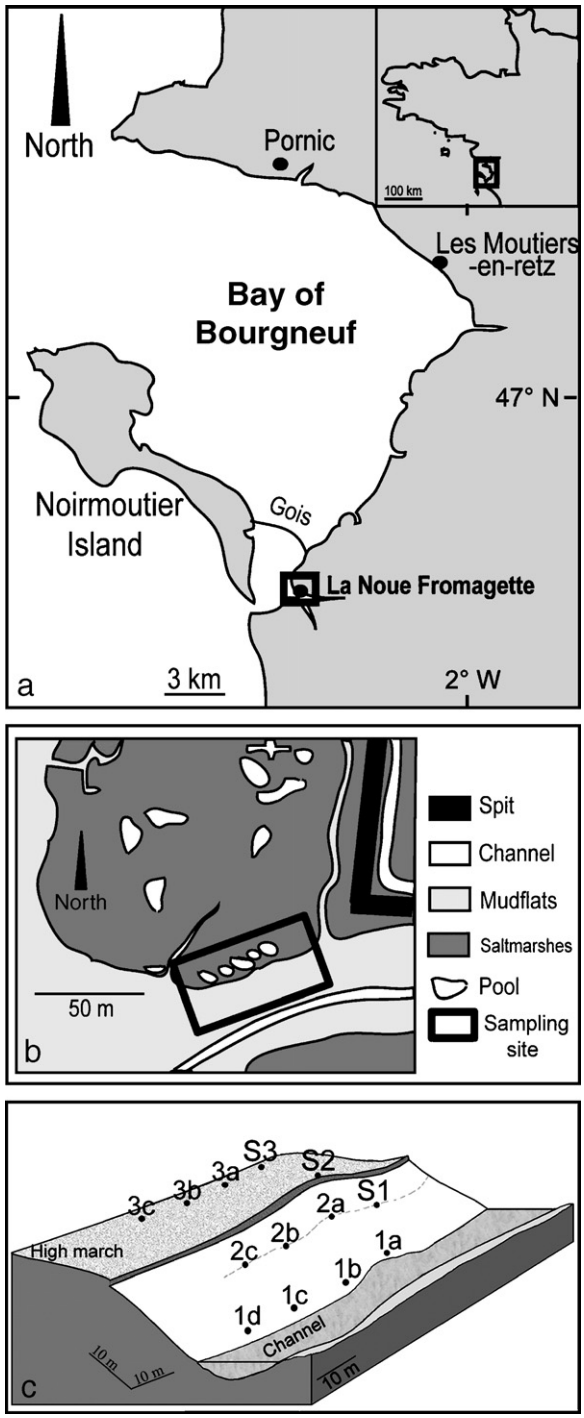

Fig. 1. Location of the study area and of the sample sites.

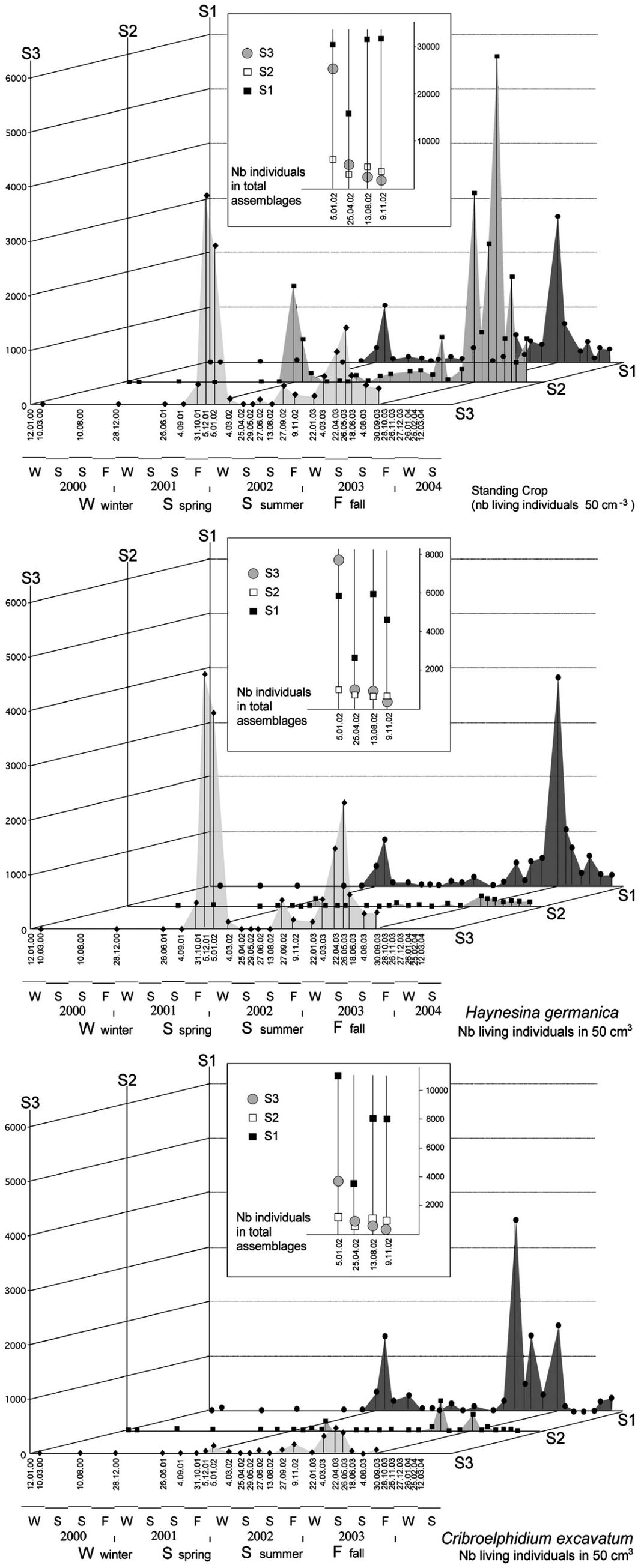

Fig. 2. Changed in the standing crops (number of living individuals in 50 cm^3 of sediment) with time at stations S1, S2 and S3. The number of specimens in the total assemblages (living+dead) is also indicated for four sampling dates.

water discharge is weak and also controlled by a sluice. Vast salt marshes stretch around the estuary.

Small boats travel through the estuary for leisure and oyster farming activities. They moor in small harbors, near the sluices. The maximum activity in the harbors is in summer and early autumn. The area was strongly affected by the Erika oil spill in January 2000 and some traces of the Prestige oil spill were noticed in May 2003.

Three sampling sites were selected for time series study (Fig. 1b and c). Station S1 in the muddy mid intertidal zone, station S2 at the seaward marsh fringe and station S3 in a small, very shallow pool, on the high marsh. Five samples were collected at the three stations between January 2000 and September 2001. Then sampling was carried out on a monthly/bimonthly basis until September 2003 and a monthly sampling was continued until April 2004 at stations S1 and S2. Living assemblages were studied in each sample and total assemblages were counted in four samples representative of each season, during 2002. Samples were also collected at ten selected sampling sites, in October 2002. They were used for studying spatial distribution, either at the same intertidal level or at different elevations. Four samples were collected close to neap low water (1a, 1b, 1c, 1d), three in the mid intertidal zone (2a, 2b, 2c), and the last three on the high marsh (3a, 3b and 3c)(Fig. 1c). Living and total assemblages were studied in each sample.

2.2. Sampling procedure

All samples were collected during spring tides, at low tide. At each station, the uppermost layer (0–1 cm) of sediment was scraped off and stored in 96% ethyl alcohol containing 1 g l^{-1} Rose Bengal stain (Walton, 1952; Murray and Bowser, 2000). One of the goals of this work was to study medium-scale patchiness (meter). It was then essential to limit the bias due to small-scale patchiness (centimeter to decimeter). To do that, we used a pseudo-replication procedure (Hurbert, 1984): sub-samples collected randomly over 1 to 2 m^2 were mixed together and homogenized. This procedure also minimizes the bias resulting from the perturbation caused by repeated samplings at the same station.

Samples were kept at least 3 days in the Rose Bengal stain. A constant volume of 50 cm^3 of sediment was washed through 500 and 63 μm sieves. The meiofauna from the 63–500 μm fraction was separated by flotation on ethylene trichlorure. When available, about 300 living (stained) foraminifera were identified, according to Loeblich and Tappan classification (1988), and counted. In case of abundant material, the sample was split, and the results were extrapolated for the whole sample of at least 300. About 300 dead individuals were also counted in selected time series samples and in all the October 2002 samples for a comparison between living and total assemblages. The density (total number of specimens in 50 cm^3 of sediment) was estimated and the absolute and relative abundances of each species were calculated (Appendices A, B, C).

3. Results

3.1. Foraminiferal species

A total of 39 taxa were identified in living assemblages and 119 in total assemblages of time series samples (Appendices 1 and 2). Species richness of living assemblages ranges between 0 and 25 in time series samples, and between 2 and 11 in October 2002 samples. In total assemblages, the richness ranges between 30 and 62 in time series samples, and between 39 and 51 in October 2002 samples. The standing crop (number of living individuals in 50 cm^3 of sediment) changes dramatically in space and time, ranging between 0 and 3818 in all the samples. The density of total assemblages (number of individuals in 50 cm^3 of sediment) ranges between 2000 and 40,000. The better-represented species, in living and total assemblages of all the samples, are *Ammonia tepida, Cribroelphidium excavatum* and *Haynesina germanica* (Appendices A and B).

3.2. Time series data: variability in standing crop and density of total assemblages

The standing crop was very low until September 2001 (Fig. 2). Blooms occurred around the same periods at the three stations: in October–December 2001, April–May 2003, and in autumn and winter 2003. High densities have been recorded at station S2 after September 2003 with a maximum in December (around 6000 living foraminifera per 50 cm^3). No bloom was recorded in 2002.

During the 2001 bloom, the dominant species had their maximum in December, except *Jadammina macrescens* (end of October). Smaller peaks could be noticed in January 2002 for *H. germanica*, at station S2 and for *C. excavatum* at station S3, showing a short-scale spatial variability in the occurrence of the bloom (Fig. 2).

Immediately after the 2001 bloom, the density of total assemblages was high at stations S1 and S3 (Fig. 2). It was lower at station S2, but reached its highest value for this station. In spring 2002 it decreased, before increasing again during summer and fall at station S1 and to a lesser extent at station S2. The trend was roughly the same for the density of the dominant species in total assemblages,

but the number of tests of *J. macrescens* and *Cribroelphidium williamsoni* decreases in fall 2002 at station S1.

The three stations clearly show different individual characteristics when considering the relative abundances of dominant species (Fig. 3). Despite some temporal variability, these characteristics remain similar during the whole time series study. In the muddy mid intertidal zone (S1), *Brizalina variabilis*, *A. tepida* and *C. excavatum* are

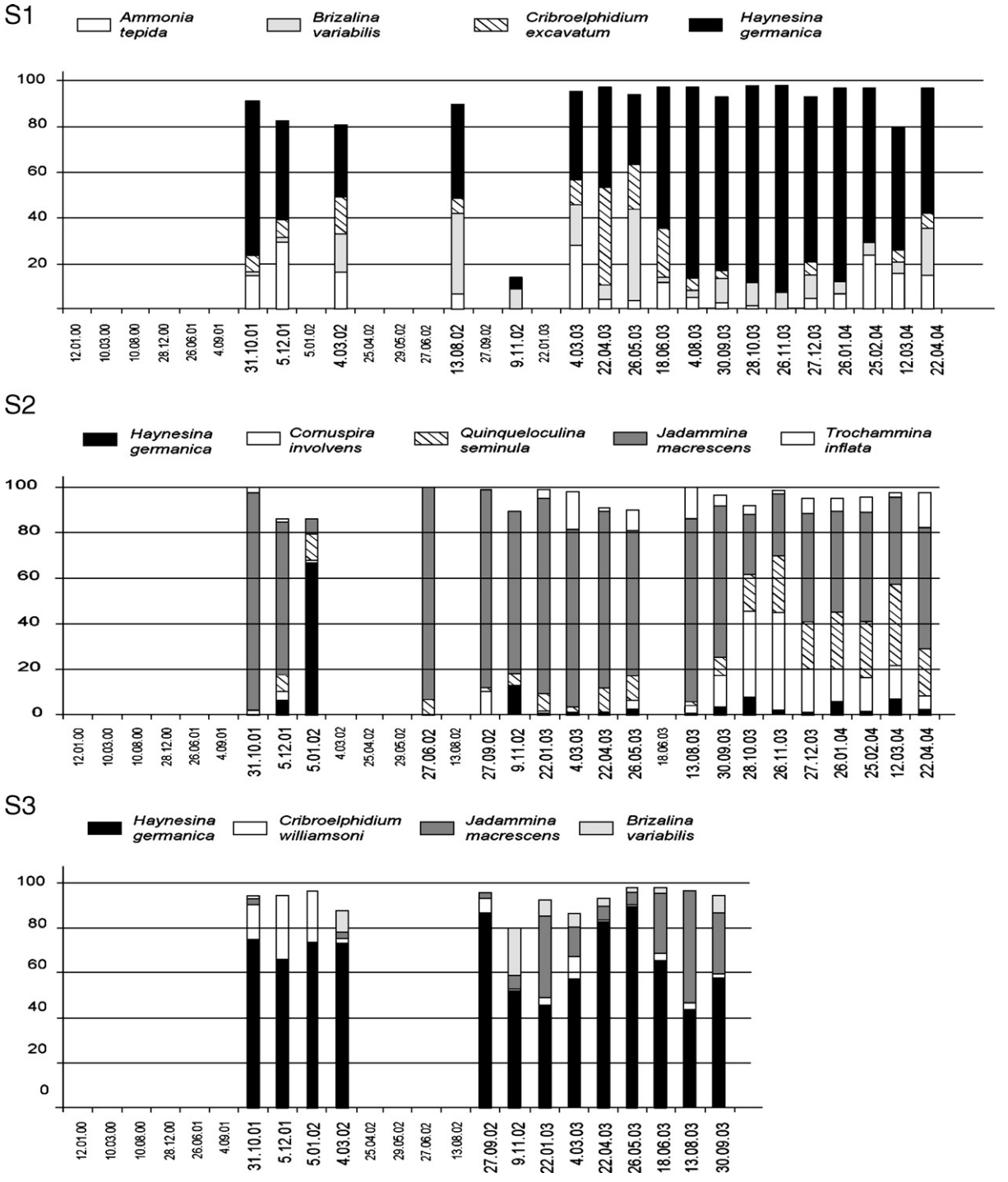

Fig. 3. Relative abundance of the dominant species in the biocenoses. Histograms are drawn only when more than 100 individuals were counted.

associated with *H. germanica* that is slightly dominant. The seaward marsh fringe (S2) is dominated by *J. macrescens*, associated with porcelaneous species after September 2003, and the pool of the high marsh (S3) is dominated by *H. germanica*.

3.3. Foraminiferal assemblages in October 2002 samples

The distribution of living assemblages shows general differences between samples from the high marsh (3a,

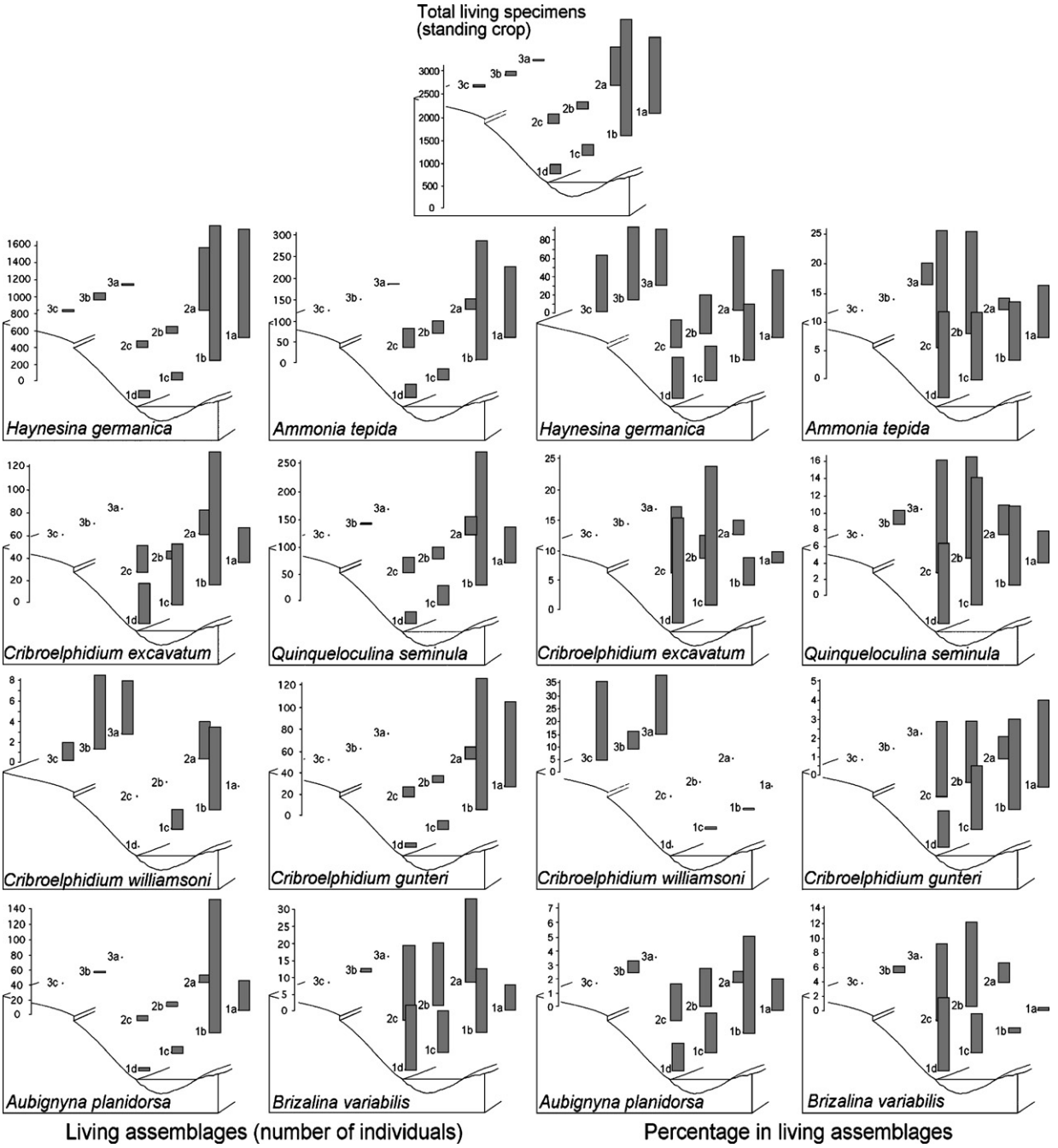

Fig. 4. Total number of living individuals in 50 cm^3 of sediment, number of living individuals and percentage of the main species at the sites sampled in October 2002.

3b, 3c), where the standing crop is very low, the mid intertidal zone (2a, 2b, 2c) and the neap low water samples (1a, 1b, 1c, 1d) (Appendix C, Figs. 4 and 5). Another noteworthy feature is the difference between the high standing crop at stations 1a and 1b, and the low standing crop at stations 1c and 1d. This difference

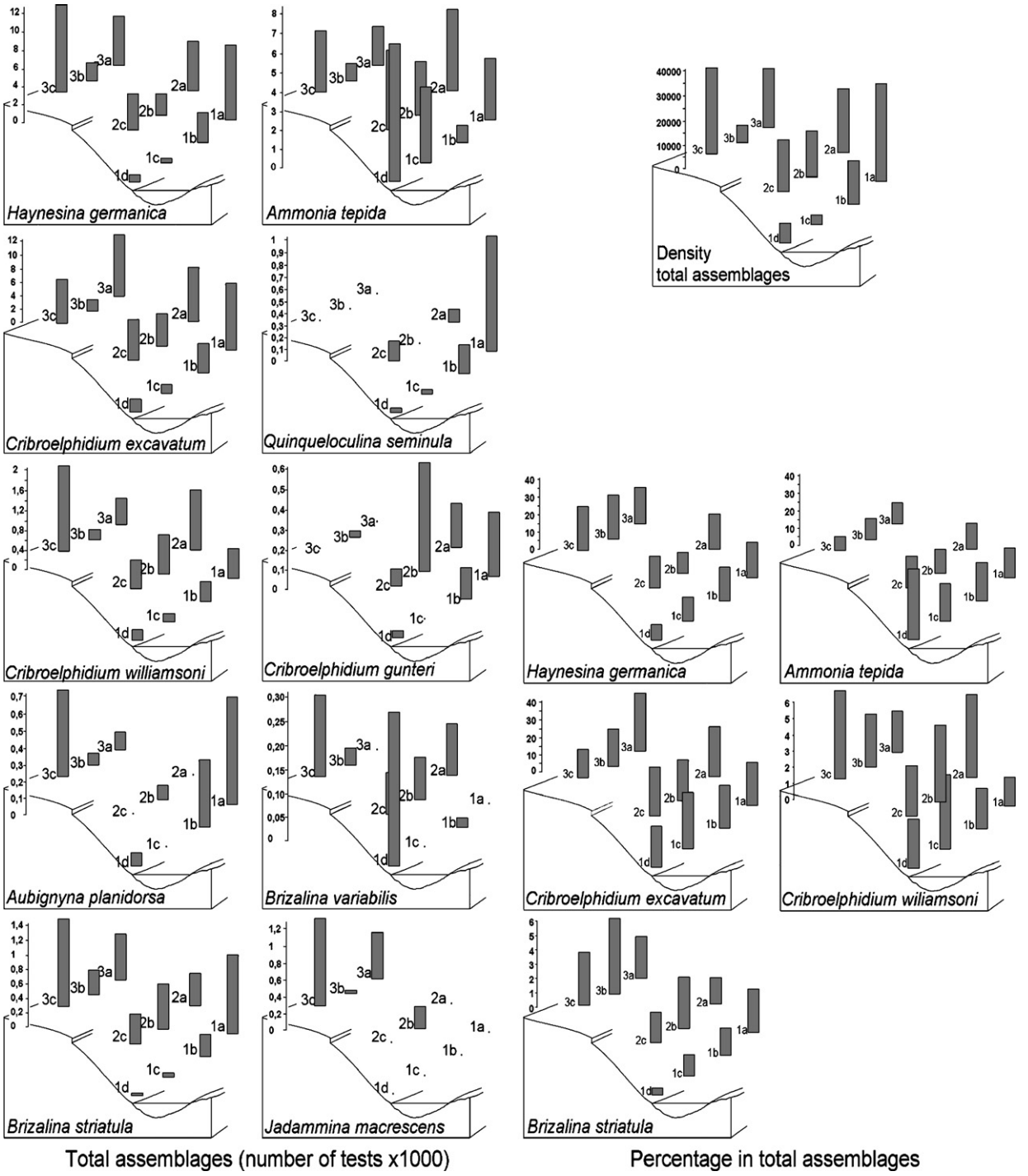

Fig. 5. Density of total assemblages, and number of individuals and percentage of species at the sites sampled in October 2002. Species selected for histograms of the number of tests are the same than species selected for living assemblages, more *Brizalina striatula* and *Jadammina macrescens*. Among these species, only those making up 5% of the assemblages were selected for histograms of the relative abundance.

shows the existence of a medium-scale patchiness. The high standing crop at stations 1a and 1b (as well as station 2a), results from the abundance of *H. germanica*. The same features are seen in total assemblages of stations 1 and 2, but they are weaker showing that total assemblages are more regularly distributed over all the stations.

H. germanica occurs at all stations, with a maximum at stations 1a, 1b and 2a. This dominant species makes up 32 to 87% of living assemblages (Fig. 4). It is somewhat less represented in total assemblages (9 to 27%) (Fig. 5). Its relative abundance is slightly higher on the high marsh than at the other stations. This feature may be observed in living as well as total assemblages.

A. tepida is rare on the high marsh where living specimens occur only at one station (3a). It is well represented in the other stations (Figs. 4 and 5).

The distribution trend of *C. excavatum* is similar to that of *A. tepida*: Well represented at the other stations, it is absent from living assemblages of the high marsh. However, it is relatively abundant in total assemblages.

Living specimens of *C. williamsoni* are rare at all stations, but they make up a notable fraction of living assemblages on the high marsh. Dead specimens are present at all stations. The time series study shows that rare living specimens may occur at the mid intertidal station.

The relative abundance of *Quinqueloculina seminula* is notable in the mid intertidal zone and at the neap low water stations. On the high marsh, it is present only at station 3b. Dead specimens are also absent from the high marsh. The distribution of *Cribroelphidium gunteri* is similar.

Living specimens of *Aubignyna planidorsa* and *B. variabilis* are very rare at all the stations. They are absent at stations 3a and 3c, on the high marsh. Dead specimens are present at all the stations, even on the high marsh.

J. macrescens is very rare in the living assemblage. Dead specimens are relatively abundant on the high marsh, and at station 2b, in the mid intertidal zone. The time series study shows that living specimens of this species may be quite abundant on the high marsh.

4. Discussion

4.1. Time series data: variability in standing crop and in density of total assemblages

The very low standing crop before September 2001 was considered as resulting from the extensive pollution of the Erika oil spill, in January 2000 (Morvan et al., 2004).

Differences recorded from one year to the other are consistent with the variability reported in the literature. Early studies on life cycles and seasonal distributions were carried out on *Elphidium crispum*. They indicated that maximum densities (reproduction period) could be observed once a year at the time of the spring phytoplankton bloom (Myers, 1942, 1943). Subsequent studies also reported seasonal cycles, with the largest living populations in autumn (Reiter, 1959) or in spring and autumn (e.g., Parker and Athearn, 1959; Scott and Medioli, 1980b; Murray, 1980; review in Alve, 1999). Many of these studies suggest that reproduction peaks, responsible for higher densities, occur once or a few times a year, but other studies pointed out that foraminiferal assemblages are not always affected by year cycles (Ellison and Nichols, 1970; Basson and Murray, 1995; Murray and Alve, 2000). Even if maximum standing crop often occurs at some particular time of the year, continuous or nearly continuous reproduction throughout the year is a commonplace (e.g. Bradshaw, 1957, 1961; Phleger and Lankford, 1957; Boltovskoy, 1964; Buzas, 1965; Brooks, 1967; Wefer, 1976; Murray, 1983; Buzas et al., 2002). Moreover, time series studies extending over more than one year show that the seasonal pattern of variability is not necessarily repeated from year to year (e.g., Lutze, 1968; Boltovskoy and Lena, 1969a; Scott and Medioli, 1980b; Basson and Murray, 1995; Murray and Alve, 2000; Murray, 2000a; Buzas and Hayek, 2000; Buzas et al., 2002). Variability affects the standing crop, the abundance of dominant species, and the species diversity (Murray, 2000a). The present study clearly shows that foraminiferal assemblages of the study area are not directly affected by seasonal cycles, but respond to more complex interannual patterns.

A sharp increase occurred in the standing crop during fall and winter 2001, at the three stations (Fig. 2). Such a phenomenon has already been reported in other paralic environments (Kitazato and Matsushita, 1990; Basson and Murray, 1995). Actually, the parameters that favor active reproduction of paralic foraminifera have not been clearly identified. Reproduction periods have often been considered as a response to increases in food supply resulting from phytoplankton blooms (e.g., Walton, 1955; Alve and Murray, 1994). However, Murray and Alve (2000) did not notice any correlation between the size of the standing crop and the chlorophyll a content of the surface sediment at either station of the Hamble Estuary. The other parameters reported to have a noticeable influence on the life cycles of intertidal benthic foraminifera are hydrodynamics (Erskian and Lipps, 1987) and temperature changes (Bradshaw, 1957, 1961; Scott and Medioli, 1980b). Temperature may act directly on the

biology of foraminifera, or, indirectly, by increasing their food supply (microflora). The blooms occurring around the same period at the three stations of the study area show that conditions favorable for reproduction are not related to the individual characteristics of the stations, but result from general environmental conditions. It is not always the case, and in the Indian River, two stations about 10 m apart, one in seagrass and the other on bare sand, exhibited a different periodicity (Buzas and Severin, 1993).

The suddenness of the bloom shows that foraminifera have the ability to prosper quickly, taking advantage of favorable environmental conditions. A quick response may be favored by the short life cycle of small paralic species that may be as short as one month (Boltovskoy and Lena, 1969a). The time lag between the bloom of *J. macrescens*, which occurs only near the marsh margin (station S2), and the bloom of other species at stations S1 and S3 indicates either that the delay before the response of the different species is different, or that changes in environmental variables is different at different stations. Even if a short time lag separates the response of the different species, it is remarkable that they all have their reproduction around the same period. This observation is consistent with observations reported from the Indian River, where the response of the different taxa shows great similarity (Buzas et al., 2002).

The rapid decrease of the standing crop after the peak values is consistent with the observations of Alve and Murray (1994) who reported that the standing crop decreased rapidly after the cessation of a benthic microfloral bloom. It is also consistent with the observations of Murray (1983) on *Haynesina depressula* (*Nonion depressulus*) in the Exe estuary, where mortality was >60% in the first month after the bloom.

The increase in the density of total assemblages, after the bloom, results obviously from the great production of living specimens during this period, and the subsequent death of these specimens. The following decrease during winter and early spring may be attributed to an important sediment input during this period, when the sluice is open: The input of a great amount of muddy fresh water leads to the burying of a fraction of the dead specimens. Higher density in summer and autumn at station S1 cannot be explained by an on-the-spot production of tests because the standing crop is low. It can hardly be explained by inward transport of empty tests because the proportion of coastal species that should have been transported landwards in the estuary did not increase. We assume that this higher density at station S1 results from a concentration of the tests due to a winnowing of the soft fine mud by the wavelets produced by the great circulation of boats in summer and early autumn.

4.2. Foraminiferal assemblages in October 2002 samples

Patchy distribution of foraminiferal species is a well-known phenomenon. The first survey of patchiness, carried out at Puerto Deseado, revealed great variations both on 10-cm and 1-m sample spacing (Boltovskoy and Lena, 1969b). This small-scale patchiness of foraminiferal assemblages complicates the observations (Buzas, 1968; Buzas, 1970) and makes the use of replicate samples necessary to obtain reliable information, especially on absolute abundance data (e.g., Hayek and Buzas, 1997; Murray, 2000a; Murray and Alve, 2000). However, this type of sampling program is time consuming and rarely undertaken. In the present study, the potential bias due to small-scale patchiness of microorganisms was limited by mixing sub-samples collected over 1 to 2 m^2, using a pseudoreplication procedure (Hurbert, 1984).

Closs and Madeira (1968) reported that reproduction periods of the abundant species are diverse and may change from one station to the other. Based on the same kind of observations, Buzas et al. (2002) proposed a model wherein individual foraminifers are spatially distributed as a heterogeneous continuum, forming patches with different densities that are only meters apart. Reproduction is asynchronous causing pulsating patches that vary in space and time. One station may exhibit seasonal periodicity while a nearby station may not. In the Indian River, two stations about 10-m apart, one in seagrass and the other on bare sand, exhibited a different periodicity (Buzas and Severin, 1993). Likewise, in the Hamble Estuary, cyclicity occurred in standing crop at a station of the mid intertidal zone, whereas it was not the case at a station of the lower intertidal zone. Nevertheless, species diversity showed reasonable annual cyclicity at both stations (Murray and Alve, 2000).

The difference in standing crop between each neap low water stations (1a, 1b, 1c, 1d) affected both living and total assemblages. This difference may result either from a patchy distribution of *H. germanica*, the dominant species, or to a higher sedimentation rate at stations 1c and 1d that leads to a dilution of foraminiferal tests in a greater amount of sediment.

The absence of living and dead specimens of *Q. seminula* and *C. gunteri* on the upper marsh, whereas living and dead specimens are present at other stations, indicates that the tests are not transported from the low and mid intertidal areas to the high marsh. Conversely, the rarity of dead specimens of *J. macrescens* at the other stations whereas they are abundant at the marsh margin indicates the weakness of downward transport.

Appendix A. Counts of living specimens in 50 cm^3 of sediment at stations S1 and S2

S1

Sampling date	Jan 12 2000	Mar 10 2000	Aug 10 2000	Dec 28 2000	Jun 26 2001	Sep 4 2001	Oct 31 2001	Dec 5 2001	Jan 5 2002	Mar 4 2002	Apr 25 2002	May 29 2002	Jun 27 2002	Aug 13 2002	Sept 27 2002	Nov 9 2002	Jan 22 2003	Mar 4 2003	Apr 22 2003	May 26 2003	Jun 18 2003	Aug 4 2003	Sep 30 2003	Oct 28 2003	Nov 26 2003	Dec 27 2003	Jan 26 2004	Feb 25 2004	Mar 12 2004	Apr 22 2004
Days after beginning	0	38	191	331	511	581	638	673	704	762	814	848	877	924	969	1012	1086	1126	1175	1209	1232	1279	1336	1364	1393	1424	1454	1484	1499	1540
Species richness	6	5	9	11	1	9	11	19	15	13	14	10	9	13	7	25	5	6	6	10	7	8	12	7	5	7	7	4	9	8
Ammonia tepida		1	1		1	1	46	309	5	18	10	4	1	8		3	3	29	20	5	44	17	84	12	5	17	25	5	28	32
Asterigerinata mamilla								5		1						2													1	1
Aubignyna planidorsa			1	1		3	6	50	2	2	1		1			9				1	1	3	8							
Aubignyna sp.								7						1																
Bulimina elegans								3	2	2				1																
Bulimina elongata			1				1	2					1			1				1			8							
Bulimina marginata																1														
Bulimina patagonica																1														
Bulimina sp.														1																
Buliminella elegantissima								1	2	2		2	4	2		1	1	2		1										
Brizalina pseudoplicata		1				13		2			1		1		2	2	2		4	1										
Brizalina striatula																													46	
Brizalina variabilis	4	4	21	13		11	4	17	2	17	41		46	39	14	101	22	18	32	60	8	9	280	66	26	18	18	1	12	46
Cribroelphidium excavatum		3		1			22	87	11	17	2	2		8		5		12	225	31	87	18	100	2	1	8			12	15
Cribroelphidium gunteri			1				9	32	1	1	1			1		13		1			1	2	56				1	1	2	2
Cribroelphidium williamsoni	1							16	2	1	1					1							8				1			
Fissurina lucida			2			3		19	5			3			3	20							16	2						
Haynesina germanica	1	1	3	11		2	194	462	32	35	11	10	5	45	36	90	7	43	226	49	248	276	2064	573	343	134	305	15	124	124
Hopkinsina atlantica			1						1			2		1	1	1				1										
Hyalino nitrium																1				1										
Lobatula lobatula																1														
Neoconorbina sp.							1																							
Neoconorbina milletti																1														
Rosalina sp.										2																				
Rosalina vilardeboana											2					3														
Stainforthia fusiformis									2	3	1	2	1			3														
Stainforthia rhomboidea																1														
Cornuspira involvens				1																				2	1	1				2
Quinqueloculina elongata											4																		1	
Quinqueloculina jugosa								1						1		3							16							
Quinqueloculina seminula	2		4	1		17	5	42	1	3	1	1	1	1	17	18					6	1	40	8		2	7		3	3
Quinqueloculina steligera								1																						
Miliolinella subrotunda				4		1																								
Quinqueloculina sp.1				4			1				2	1		1																
Jadammina macrescens	1						1	1	2		2	2			1	2			8			1	8			1	1			
Paratrochammina sp.				1												2														
Textularia sp.						1																								
Tiphotrocha comprimata				2																										
Trochammina inflata	4			7				1	1																					
Total living specimens	13	10	35	46	1	52	290	1058	71	104	80	29	61	110	74	286	35	105	515	151	395	327	2696	665	376	181	358	22	229	225

(continued on next page)

Appendix A (*continued*)

S2

Sampling date																														
Jan 12 2000	Mar 10 2000	Aug 10 2000	Dec 28 2000	Jun 26 2001	Sep 4 2001	Oct 31 2001	Dec 5 2001	Jan 5 2002	Mar 4 2002	Apr 25 2002	May 29 2002	Jun 27 2002	Aug 13 2002	Sept 27 2002	Nov 9 2002	Jan 22 2003	Mar 4 2003	Apr 22 2003	May 26 2003	Jun 18 2003	Aug 13 2003	Sep 30 2003	Oct 28 2003	Nov 26 2003	Dec 27 2003	Jan 26 2004	Feb 25 2004	Mar 12 2004	Apr 22 2004		
Days after beginning	0	38	191	331	511	581	638	673	704	762	814	848	877	924	969	1012	1086	1126	1175	1209	1232	1288	1336	1364	1393	1424	1454	1484	1499	1540
Species richness	0	2	7	2	3	3	7	9	10	0	4	0	2	3	5	10	7	5	8	9	6	5	11	8	8	9	9	9	8	8
Ammonia tepida		1	2		1		2	6	1		1					3	1		2	3			3	13	13	120	8	32	1	11
Asterigerinata mamilla																														
Aubignyna planidorsa									2							2														
Aubignyna sp.																														
Bulimina elegans																														
Bulimina elongata																														
Bulimina marginata																														
Bulimina patagonica																														
Bulimina sp.																														
Buliminella elegantissima																														
Brizalina pseudoplicata																														
Brizalina striatula																			1											
Brizalina variabilis			1				2	44	9		2				1	5	1	4	5	33	1		68	57		128	12	32	5	11
Cribroelphidium excavatum			1						2							1			4	39			22		4		3	2		
Cribroelphidium gunteri																1							8							
Cribroelphidium williamsoni							3	54	6							4				7			5	3	16	24	14	14	2	5
Fissurina lucida								8	1														8							
Haynesina germanica			1	2		1	11	53	99		10			1		21	2	3	2	25	14	1	120	79	84	32	52	38	26	27
Hopkinsina atlantica																														
Hyalino nitrium																														
Lobatula lobatula																														
Neoconorbina sp.																														
Neoconorbina milletti																														
Rosalina sp.																														
Rosalina vilardeboana																														
Stainforthia fusiformis																														
Stainforthia rhomboidea																														
Cornuspira involvens								29	2						12		2			31	1	9	494	344	1072	1186	103	274	54	45
Quinqueloculina elongata																														
Quinqueloculina jugosa																														
Quinqueloculina seminula			5	1	1	1	15	55	15				8		1	5	15	3	13	82	6	2	242	142	612	1205	194	470	124	159
Quinqueloculina steligera																														
Miliolinella subrotunda																														
Quinqueloculina sp.1																										8				
Jadammina macrescens		7	4		8	1	1674	526	10		12		130	10	101	109	183	157	101	522	26	185	2330	248	710	2847	356	921	142	426
Paratrochammina sp.																														
Textularia sp.																														
Tiphotrocha comprimata																														
Trochammina inflata			3				43	15						1	1	2	9	34	2	76	6	32	167	35	37	423	46	133	6	120
Total living specimens	0	8	17	3	10	3	1750	790	147	0	25	0	138	12	116	153	213	201	130	818	54	229	3467	921	2548	5973	788	1916	360	804

Appendix B. Counts of living specimens in 50 cm^3 of sediment at stations S3

S3																							
Sampling date	Jan 12 2000	Mar 10 2000	Aug 10 2000	Dec 28 2000	Jun 26 2001	Sep 4 2001	Oct 31 2001	Dec 5 2001	Jan 5 2002	Mar 4 2002	Apr 25 2002	May 29 2002	Jun 27 2002	Aug 13 2002	Sept 27 2002	Nov 9 2002	Jan 22 2003	Mar 4 2003	Apr 22 2003	May 26 2003	Jun 18 2003	Aug 4 2003	Sep 30 2003
Days after beginning	0	38	191	331	511	581	638	673	704	762	814	848	877	924	969	1012	1086	1126	1175	1209	1232	1279	1336
Species richness	0	2	0	1	2	2	8	10	9	11	2	1	8	4	11	10	10	15	11	9	7	7	10
Ammonia tepida							9	101	60	4			2		2	6	4	4	2				1
Asterigerinata mamilla																							
Aubignyna planidorsa							4	43		2					4	10	1	10	4	2			
Aubignyna sp.																							
Bulimina elegans																							
Bulimina elongata																							
Bulimina marginata																							
Bulimina patagonica																							
Bulimina sp.																1							
Buliminella elegantissima																							
Brizalina pseudoplicata									4	1								2					
Brizalina striatula																							
Brizalina variabilis							6	26	32	10			8	3	1	39	11	32	28	14	13	1	22
Cribroelphidium excavatum								2	8	2			4	1	3	9		17	25	18	2		4
Cribroelphidium gunteri										3					1		1	3	3				
Cribroelphidium williamsoni							53	1093	612	2					21	1	4	50	11	16	16	10	6
Fissurina lucida								2							1			1					
Haynesina germanica					1		270	2531	2140	76			4	1	291	96	73	295	799	1258	347	155	168
Hopkinsina atlantica																							
Hyalino nitrium																							
Lobatula lobatula																							
Neoconorbina sp.																							
Neoconorbina milletti																							
Rosalina sp.																							
Rosalina vilardeboana																							
Stainforthia fusiformis																							
Stainforthia rhomboidea																							
Cornuspira involvens																		1		2			3
Quinqueloculina elongata																							
Quinqueloculina jugosa										1													
Quinqueloculina seminula							5	14	28				4		2	10	3	25	36	8	11	6	5
Quinqueloculina steligera																							
Miliolinella subrotunda																							
Quinqueloculina sp.1																							
Jadammina macrescens		5				2	9	6	16	3	1		70		9	11	60	68	57	72	142	178	80
Paratrochammina sp.																							
Textularia sp.																							
Tiphotrocha comprimata																							
Trochammina inflata													2				4	7	1			4	1
Total living specimens		5		0	1	2	356	3818	2900	104	1	0	94	5	335	183	161	516	966	1390	531	354	290

(continued on next page)

Appendix C. Relative abundance (%) of the species collected in total and living assemblages at stations sampled in October 2002

Dead											Living										
Sample number	1a	1b	1c	1d	2a	2b	2c	3a	3b	3c	Sample number	1a	1b	1c	1d	2a	2b	2c	3a	3b	3c
Total number of specimens	40000	18000	4000	8000	28000	20000	22000	27000	8000	38000	Total number of specimens	1708	2520	242	208	924	173	218	23	103	6
Species richness	46	43	40	41	54	50	51	39	41	47	Species richness	10	11	10	10	10	9	11	3	6	2
Acervulina inherens					1						*Ammonia tepida*	9	10	12	14	2	18	21	4		
Adelosina longirostra	0		0	0		0	0		0		*Aubignyna planidorsa*	2	7	3	2	1	3	3		1	
Adelosina sp.		0		0							*Brizalina pseudoplicata*				0						
Ammobaculites exiguus				0							*Brizalina striatula*		0								
Ammonia beccarii				0							*Brizalina variabilis*	0	1	5	10	3	12	11		1	
Ammonia tepida	18	22	22	38	16	15	19	14	13	9	*Bulimina elongata*							1			
Angulogerina angulosa	1	0		1	1	0	0	0	0	0	*Buliminella elegantissima*						1				
Astacolus crepidulus	0										*Cribroelphidium excavatum*	2	5	22	17	3	4	11			
Asterigerinata mamilla	1	0	1	2	1	2	1	2	0	0	*Cribroelphidium gunteri*	5	5	3	2	1	3	4			
Astrononion sp.						0					*Cribroelphidium williamsoni*		0	1		0			26	8	33
Aubignyna planidorsa	2	2		1		0		0	1	1	*Fissurina lucida*	1	1	1	1			1			
Bolivina difformis	1	0		0	0	0	1	0		1	*Haynesina germanica*	76	61	38	44	85	45	32	70	87	67
Bolivina pseudoplicata	2	0	1	1	1	1	1	1	2	3	*Stainforthia fusiformis*							0			
Brizalina pseudopunctata							0														
Brizalina spathulata						0	0				*Cornuspira involvens*	0		0		0	1				
Brizalina striatula	3	2	1	0	2	3	2	3	5	3	*Quinqueloculina jugosa*	0	0								
Brizalina variabilis	1		0	0	0	0	0		0	0	*Quinqueloculina seminula*	4	10	15	9	4	13	14		2	
Brizalina spp.		0								0											
Bulimina elegans	0	0	0	0	0		0	1	0	0	*Jadammina macrescens*					0				1	
Bulimina elongata		0					0	0			*Paratrochammina sp.*				0						
Bulimina marginata				0	0																
Buliminella elegantissima										0											
Cassidulina crassa	0		1	0	0	1	1			1											
Cribroelphidium cuvillieri	1	2	1	0		2	0		1	0											
Cribroelphidium excavatum	25	25	32	23	31	25	29	37	24	18											
Cribroelphidium gunteri	0	2	0	0	1	3	0		0	0											
Cribroelphidium magellanicum	1	2	6	1	1	3	2	5	5	2											
Cribroelphidium williamsoni	2	2	4	3	5	4	3	2	3	5											
Cribrononion gerthi	3	3	1	3	2	1	3	0	1	2											
Cribrostomoides jeffreysii				0	0	0	0	1		0											
Cyclogira sp.	0				0	1															
Dentalina sp.						0															
Deuterammina sp.					0																
Edentostomina sp.	0	0			0	0	0														
Elphidium aculeatum	0	0	1	0	0		0		0												
Elphidium macellum	1	2	2	3	0	3	1	0	0	0											
Elphidium pulvereum	0	1	2		0	1	1	0	0												
Eoeponidella pulchella	0									0											
Favulina hexagona			0		0																
Favulina melo									0												
Favulina squamosa							0		0	0											
Fissurina lucida	0	1	0	0	0	0	1	0	2	1											
Fissurina spp.						0	0	0		0											
Gavelinopsis praegeri	2	0	0	1	2	2	2	1	1	1											
Globulina gibba	0																				

Haynesina depressula		0			0	1				0
Haynesina germanica	21	19	14	9	21	13	19	23	27	27
Homalohedra williamsoni		1	0	0	0	0	0	0		
Hopkinsina pacifica								0		0
Hyalinonetrion sp.		0	0		1	0	0	0	0	0
Jadammina macressens				0	0	1		2	0	3
Lagena laevis	0	0	0		0		0			
Lagena semistriata					0				0	
Lagena striata	0	0	2	0	0	0	0	0	1	1
Lagena sulcata var. laevicostata	0		0						0	
Lamarckina haliotidea					0			0	1	
Lepidodeuterammina ochracea	0					0		0	1	2
Lobatula lobatula	2	3	1	3	1	2	1		0	2
Massilina secans				0			0			
Miliolinella subrotunda	0	0	1	1	0	1	0	0		
Neoconorbina nitida	1	0			0	0	0	0	0	0
Neoconorbina terquemi										
Nonion pauperatum				0		0	0		1	0
Palliolatella orbignyana	0	0	0		0	0	0		0	0
Paratrochammina cf. *P. haynesi*			0				0			
Patellina corrugata								0		1
Planorbulina mediterranensis	6	3	0	4	5	4	4	0	1	3
Polymorphina sp.	0				0					
Portatrochammina murrayi					0			0		
Pseudononion atlanticum								0		
Quinqueloculina jugosa	0	0			0					
Quinqueloculina laevigata						0				
Quinqueloculina lamarckiana			0							
Quinqueloculina lata	0		0			0	0		1	
Quinqueloculina seminula	2	1	1	0	0		1			0
Quinqueloculina stelligera	0	0	1	0		0	1		0	0
Quinqueloculina spp.		0	0		0	0	0			
Remaneica plicata								0		0
Reophax nana	0				0		0	0		
Rosalina anglica					0					
Rosalina bradyi			0			0				0
Rosalina globularis					0					
Rosalina cf. *vilardeboana*		0	0	0	0		1	0	0	0
Spiroloculina depressa		0								
Spiroloculina dilatata			0							
Stainforthia fusiformis	0	0			0	0	0	0	0	0
Svratkina tuberculata									0	
Textulara earlandi					0	0	0	0		
Textularia truncata	0	1	1	1	2	1	1	0		1
Triloculina trigonula	0	0				0	0			
Trochammina inflata				0	0	0			0	1
Vasicostella sp.				0	0					0

The distribution of *A. tepida* and *C. excavatum,* rare on the high marsh, is consistent with the distribution of these species as reported in literature (review in Murray, 1991; Debenay et al., 2000; Debenay and Gillou, 2002). The presence of relatively abundant dead specimens of these species at the high marsh stations, whereas living specimens are absent or rare suggests a post mortem transport from lower stations. However, this hypothesis is not corroborated by other species such as *Q. seminula* and *C. gunteri*, as discussed before. Other hypotheses to explain this distribution, as well as the distribution of *A. planidorsa* and *B. variabilis* that shows the same features, are 1) that dead specimens are the remains of a reproduction that took place before the period of sampling, or 2) that reproduction has taken place elsewhere on the upper marsh, near enough to allow the input of dead specimens. The presence of living specimens of these species on the high marsh, at stations S2 and S3 of the time series samplings, may corroborate both of these hypotheses. The second hypothesis suggests a small-scale transport that leads to a homogenization of the total assemblages of neighboring stations, which is consistent with the most regular distribution of total assemblages.

4.3. Relationships between living and dead foraminiferal assemblages

The use of living assemblages is sometimes considered as the only valuable approach for interpreting modern environments, while only dead assemblages are useful for paleoecological interpretations (e.g. Murray, 2000a). However, this study, in addition to previous ones, clearly point out some important limitations in the use of only living assemblages for environmental studies.

Beyond the fact that the validity of currently used staining methods is still debated, it appears that, owing to patchiness and irregular life cycles, the use of an isolated sampling of living assemblages is unlikely to give a representative image of foraminiferal populations. Alve and Murray (2001) suggest that caution should be taken in assessing the significance of diversity changes when based on occasional sampling only. Patchy heterochronous dynamics of living foraminifera makes it even questionable for the significance of time series sampling of living individuals at one or several stations for population dynamic studies at a local or regional scale. Even replication or pseudoreplication procedures do not seem to be adequate for circumventing this problem. Buzas et al. (2002) noticed that the spatio-temporal complexities of the distribution of foraminiferal assemblages "might be viewed by some as negatively reflecting upon the use of foraminifera as faunal indicators for the health and stability of a lagoon or estuary". These authors demonstrated that long-term stability is achieved through considerable short-term variability in space and time and that observations at a particular station will, in the long-term, give an assessment of a much larger area. However, the use of foraminiferal assemblages in environmental studies often necessitates quick answers that do not allow waiting for the result of long-term analyses.

The well-known study of Scott and Medioli (1980a) on living and dead assemblages concluded that "the total population integrates the small seasonal and spatial variations into a definable assemblage that reliably reflects prevailing marine conditions" (abstract, p. 814). The present study gives some more arguments towards the interest of using total assemblages. It shows that, in only one sample, the total assemblage provides information about a larger area, and longer period of time: Heterochronous patchy distribution of living assemblages, together with local dispersion of the tests may explain the presence of numerous dead specimens whereas living specimens are rare or absent at the sampling area. Total assemblages seem preferable to dead ones because they integrate living specimens, providing information about seasonal cycles at the time of sampling. Dead assemblages provide the same information, but with a delay of about one month, the time for new living specimens to die.

Limitations also exist for using total assemblages. These limitations, which have been discussed at length in previous studies result mainly from post mortem transport and destruction of tests during taphonomic processes (e.g., Murray, 1976; Alve and Murray, 1994; De Rijk and Troelstra, 1999; Murray and Alve, 1999; Goldstein and Watkins, 1999; Murray, 2000b). The present study shows that there is only limited transport in the study area. This is consistent with observations carried out in other mesotidal estuaries in the region (Goubert, 1997; Debenay et al., 2003). Goubert (1997) showed that embryonic juveniles of *C. excavatum* (size $<$ 80 μm) were very abundant in the muddy tidal transported sediments along the channel of a mesotidal estuary (400 living specimens per cm^3 of sediment), whereas the average tidal currents were not able to transport them when their diameter exceeded 100 μm. The impact of taphonomic processes is more delicate to assess, and may introduce a bias in the results. In a tropical area, for example, all the calcareous tests that grow during the dry season are dissolved by the acidic water of the rainy season (Debenay et al., 2004). Such extreme conditions are not found in temperate areas. Even if a bias exits, the question is: Is the bias greater when using total assemblages or when using living assemblages?

An important information needed for interpreting total assemblages is the sedimentation rate, which allows the evaluation of the period of time represented, depending on the thickness of the sediment layer collected. Sedimentation rates may be very high in harbors, where the superficial 1 cm of sediment scraped off for the study of epifaunal foraminifera corresponds to a few months of sedimentation and therefore, total assemblages included in this sediment obviously change with season.

Compared to other organisms used for environmental survey, foraminifera have the advantage to possess mineralized tests that are preserved in the sediment, providing integrated information on seasonal and spatial variations. This advantage must be developed by using total assemblages, with the needed care about possible information loss due to taphonomic processes, sedimentation rates, and more rarely to post mortem transport. The concomitant counts of living specimens may be of interest for improving information about species that may live at the given place.

5. Conclusion

This work carried out on temperate salt marshes confirms that paralic foraminifera do not show reproducible annual life cycles and that isolated samplings of living assemblages may provide different or even contradictory results depending if the sampling is done during the bloom or not. Neighboring samples may provide different results. Thus, isolated or even seasonal samplings of living foraminiferal assemblages cannot be considered as giving a valuable image of environmental conditions, and may lead, at least, to considerable uncertainty.

To circumvent the negative impact of such observations upon the use of foraminifera as faunal indicators for environmental studies, we recommend making the most of the preservation of the tests in the sediment: Integrated information over a given period of time may be obtained by using total assemblages. For providing valuable results, total assemblages must be used with the needed care about the negative impact of taphonomic processes and eventually post mortem transport. If the period of time represented by the collected assemblage is needed, data about the sedimentation rate are necessary. The concomitant counts of living specimens may be of interest for improving information about species that may live at the given place, but we propose to reserve the use of living assemblages alone to local investigations for studying special ecological features.

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References

Alve, E., 1999. Colonisation of new habitats by benthic foraminifera: a review. Earth Science Reviews 46, 167–185.

Alve, E., Murray, J.W., 1994. Ecology and taphonomy of benthic foraminifera in a temperate mesotidal inlet. Journal of Foraminiferal Research 24, 18–27.

Alve, E., Murray, J.W., 2001. Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England. Journal of Foraminiferal Research 31, 12–24.

Basson, P.W., Murray, J.W., 1995. Temporal variations in four species of intertidal Foraminifera, Bahrain Arabian Gulf. Micropaleontology 41, 69–76.

Boltovskoy, E., 1964. Seasonal occurrences of some living foraminifera in Puerto Deseado (Patagonia, Argentina). Journal du Conseil - Conseil Permanent International Pour l'exploration de la Mer, Copenhagen 39, 136–145.

Boltovskoy, E., Lena, H., 1969a. Seasonal occurrences, standing crop and production in benthic Foraminifera of Puerto Deseado. Contributions from the Cushman Foundation for Foraminiferal Research 20, 87–95.

Boltovskoy, E., Lena, H., 1969b. Microdistribution des foraminifères benthoniques vivants. Revue de Micropaléontologie 12, 177–185.

Bradshaw, J.S., 1957. Laboratory studies on the rate of growth of the foraminifer *Streblus beccarii* (Linné) var. *tepida* Cushman. Journal of Paleontology 31, 1138–1147.

Bradshaw, J.S., 1961. Laboratory experiments on the ecology of foraminifera. Contributions from the Cushman Foundation for Foraminiferal Research 12, 87–106.

Brooks, A.L., 1967. Standing crop, vertical distribution, and morphometries of *Ammonia beccaril* (Linne). Limnology and Oceanography 12, 667–684.

Buzas, M.A., 1965. The distribution and abundance of foraminifera in Long Island Sound. Smithsonian Miscellaneous Collections 149, 1–89.

Buzas, M.A., 1968. On the spatial distribution of foraminifera. Contributions from the Cushman Foundation for Foraminiferal Research l9, 1–11.

Buzas, M.A., 1970. Spatial homogeneity: statistical analyses of unispecies and multispecies populations of Foraminifera. Ecology 51, 874–879.

Buzas, M.A., Severin, K.P., 1993. Foraminiferal densities and pore water chemistry in the Indian River, Florida. Smithsonian Contributions to the Marine Sciences 36, 1–38.

Buzas, M.A., Hayek, L.C., 2000. A case for long-term monitoring of the Indian River Lagoon, Florida: Foraminiferal densities, 1977–1996. Bulletin of Marine Science 67, 805–814.

Buzas, M.A., Hayek, L.C., Reed, S.A., Jett, J.A., 2002. Foraminiferal densities over five years in the Indian River Lagoon, Florida: a model of pulsating patches. Journal of Foraminiferal Research 32, 68–92.

Closs, D., Madeira, M.L., 1968. Seasonal variations of brackish Foraminifera in the Patos lagoon — Southern Brazil. Escuela Geologia Puerto Alegre, Publicação Especial 15, 1–51.

Debenay, J.-P., Gillou, J.-J., 2002. Ecological transitions indicated by foraminiferal assemblages in paralic environments. Estuaries 25, 1107–1120.

Debenay, J.-P., Gillou, J.-J., Redois, F., Geslin, E., 2000. Distribution trends of foraminiferal assemblages in paralic environments. A base for using foraminifera as bioindicators. In: Martin, R.E. (Ed.), Environmental Micropaleontology. Plenum Publishing Corporation, pp. 39–67.

Debenay, J.-P., Carbonel, P., Morzadec-Kerfourn, M-T., Cazaubon, A., Denèfle, M., Lézine, A-M., 2003. Multi-bioindicator study of a small estuary in Vendée (France). Estuarine, Coastal and Shelf Sciences 58, 843–860.

Debenay, J.-P., Guiral, D., Parra, M., 2004. Behaviour and taphonomic loss in foraminiferal assemblages of mangrove swamps of French Guiana. Marine Geology 208, 295–314.

De Rijk, S., Troelstra, S.R., 1999. The application of a foraminiferal actuofacies model to saltmarsh cores. Palaeogeography, Palaeoclimatology, Palaeoecology 149, 59–66.

Ellison, R.L., Nichols, M.M., 1970. Estuarine foraminifera from the Rappahannock River, Virginia. Contribution from the Cushman Foundation for Foraminiferal Research 21, 1–17.

Erskian, M.G., Lipps, J.H., 1987. Population dynamics of the foraminiferan *Glabratella ornatissima* (Cushman) in Northern California. Journal of Foraminiferal Research 17, 240–256.

Goldstein, S.T., Watkins, G.T., 1999. Taphonomy of salt marsh foraminifera: an example from coastal Georgia. Palaeogeography, Palaeoclimatology, Palaeoecology 149, 103–114.

Goldstein, S.T., Watkins, G.T., Kuhn, R.M., 1995. Microhabitats of salt marsh foraminifera: St. Catherines Island, Georgia, USA. Marine Micropaleontology 26, 17–29.

Goubert, E., 1997. Les *Elphidium excavatum* (Terquem), foraminifères benthiques, vivant en baie de Vilaine (Bretagne, France) d'octobre 1992 à septembre 1996: morphologie, dynamique de population en relation avec l'environnement. PhD thesis, University of Nantes, France.

Hayek, L.C., Buzas, M.A., 1997. Surveying Natural Populations. Columbia University Press, New York.

Hurbert, S.J., 1984. Pseudoreplication and the design of ecological experiments. Ecological Monographs 54, 187–211.

Kitazato, H., Matsushita, S., 1990. Seasonality in the benthic foraminiferal community and the life history of Trochammina hadai Uchio in Hamana Lake, Japan. In: Hemleben, C., et al. (Ed.), Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of agglutinated foraminifera. Kluwer Academic Publishers, pp. 695–715.

Loeblich Jr., A.R., Tappan, H., 1988. Foraminiferal genera and their classification, Van Nostrand Reinhold Company, 2volumes.

Lutze, G.E., 1968. Jahresgang der Foraminiferen-Fauna in der Bottsand Lagune (westlich Ostee). Meyniana 18, 13–30.

Morvan, J., Le Cadre, V., Jorissen, F., Debenay, J-P., 2004. Foraminifera as potential bio-indicators of the Erika oil spill in the Bay of Bourgneuf: field and experimental studies. Aquatic Living Resources 17, 317–322.

Murray, J.W., 1976. Comparative studies of living and dead benthic foraminiferal distributions. In: Hedley, R.H., Adams, C.G. (Eds.), Foraminifera. Academic Press, London, pp. 45–109.

Murray, J.W., 1980. The foraminifera of the Exe estuary, vol. 2. Devonshire Association, Exeter, pp. 89–115. special volume.

Murray, J.W., 1983. Population dynamics of benthic foraminifera: results from the Exe estuary, England. Journal of Foraminiferal Research 13, 1–12.

Murray, J.W., 1991. Ecology and Palaeoecology of Benthic Foraminifera. Longman, Harlow, UK.

Murray, J.W., 2000a. When does environmental variability becomes environmental change? The proxy record of benthic foraminifera. In: Martin, R. (Ed.), Environmental Micropaleontology. Plenum Publishing Corporation, New York, pp. 7–37.

Murray, J.W., 2000b. The enigma of the continued use of total assemblages in ecological studies of benthic foraminifera. Journal of Foraminiferal Research 30, 244–245.

Murray, J.W., Bowser, S.S., 2000. Mortality, protoplasm decay rate, and reliability of staining techniques to recognize "living" foraminifera: a review. Journal of Foraminiferal Research 30, 66–70.

Murray, J.W., Alve, E., 1999. Taphonomic experiments on marginal marine foraminiferal assemblages: how much ecological information is preserved? Palaeogeography, Palaeoclimatology, Palaeoecology 149, 183–197.

Murray, J.W., Alve, E., 2000. Major aspects of foraminiferal variability (standing crop and Biomass) on a monthly scale in an intertidal zone. Journal of Foraminiferal Research 30, 177–191.

Myers, E.H., 1942. Biological evidence as the rate at which tests of foraminifera are contributed to the sediments. Journal of Paleontology 16, 397–398.

Myers, E.H., 1943. Life activities of foraminifera in relation to marine ecology. Proceedings of the American Philosophical Society 86, 439–458.

Parker, F.L., Athearn, W.D., 1959. Ecology of marsh foraminifera in Poponesset Bay. Journal of Paleontology 33, 333–343.

Phleger, F.B., Lankford, R.R., 1957. Seasonal occurrences of living benthonic Foraminifera in some Texas bays. Contributions from the Cushman Foundation for Foraminiferal Research 8, 93–105.

Reiter, M., 1959. Seasonal variations in intertidal Foraminifera of Santa Monica Bay, California. Journal of Paleontology 33, 606–630.

Scott, D.B., Medioli, F.S., 1980a. Living vs total foraminiferal populations: their relative usefulness in paleoecology. Journal of Paleontology 54, 814–831.

Scott, D.B., Medioli, F.S., 1980b. Quantitative studies of marsh foraminiferal distributions in Nova Scotia. Implications for sea level studies. Contribution of the Cushman Foundation for Foraminiferal Research, Special Publication 17, 58.

Tobin, R., Scott, D.B., Collins, E.S., Medioli, F.S., 2005. Infaunal benthic foraminifera in some North American marshes and their influence on fossil assemblages. Journal of Foraminiferal Research 35, 130–147.

Walton, W.R., 1952. Techniques for recognition of living foraminifera. Contribution from the Cushman Foundation for Foraminiferal Research 3, 56–60.

Walton, W.R., 1955. Ecology of living benthonic Foraminifera, Todos Santos Bay, Baja California. Journal of Paleontology 29, 952–1018.

Wefer, G., 1976. Environmental effects on growth rates of benthic foraminifera (shallow water, Baltic Sea). Maritime Sediments, Special Publication 1, 39–50.