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Living foraminifera and total populations in salt marsh peat cores: Kelsey Marsh (Clinton, CT) and the Great Marshes (Barnstable, MA)

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Abstract

Common species of intertidal agglutinated benthic foraminifera in salt marshes in Massachusetts and Connecticut live predominantly at the marsh surface and in the topmost sediment (0-2.5 cm), but a considerable part of the fauna lives at depths of 2.5–15 cm. Few specimens are alive at depths of 15–25 cm, with rare individuals alive between 25–50 cm in the sediments. Specimens living between the sediment surface and 25 cm deep occur in all marsh settings, whereas specimens living deeper than 25 cm are restricted to cores from the lower and middle marsh, and have an irregular distribution-with-depth. Lower and middle marsh areas are bioturbated by metazoa, suggesting that living specimens reach these depths at least in part by bioturbation. High-marsh sediments in New England consist of very dense mats of *Spartina patens* or *Distichlis spicata* roots and are not bioturbated by metazoa. In this marsh region bioturbation by plant roots and vertical fluid motion may play a role in moving the foraminifera into the sediment. The depth-distribution of living specimens varies with species: living specimens of *Trochammina inflata* consistently occur at the deepest levels. This suggests that species have differential rates of survival in the sediment, possibly because of differential adaptation to severe dysoxia to anoxia, or because of differing food preferences. There is no simple correlation between depth-in-core and faunal diversity, absolute abundance, and species composition of the assemblages. (I) is therefore possible to derive a signal of faunal changes and thus the environmental changes that may have caused them from the complex faunal signal of fossil assemblages. (I) 1998 Elsevier Science B.V. All rights reserved.

Keywords: foraminifera; salt marshs; living depth

1. Introduction

Only 6-10 benthic foraminiferal species occur in the brackish intertidal waters of coastal salt marshes, an extreme marginal environment for marine organisms (e.g., Murray, 1991). The biology of foraminifera is not well known, but studies of Recent, fully marine foraminifera have demonstrated that they live both epifaunally and infaunally, commonly down to depths of about 12–15 cm, depending upon the oxygenation of the sediment (e.g., Corliss and Emerson, 1990; Gooday, 1993; Rathburn and Corliss, 1994; Alve and Bernhard, 1995; Jorissen et al., 1995; Kitazato and Ohga, 1995). Foraminifera

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are eukaryotes and thus have been thought to be limited to environments where the dissolved oxygen content of the waters was at least about 0.1 ml/l (e.g., Phleger and Soutar, 1973). They were not expected to be alive below the top 1 cm of salt marsh sediment (e.g., Murray, 1971; Brasier, 1980), where sediment is anoxic (e.g., Teal and Kanwisher, 1961).

Recent studies, however, demonstrated that at least some foraminifera can survive severely dysoxic to periodically anoxic conditions, and may even be capable of facultative anaerobic metabolism (Moodlev and Hess, 1992; Bernhard, 1993; Alve and Bernhard, 1995). It therefore seemed possible that salt marsh foraminifera could live infaunally, and incidental infaunal occurrences of benthic foraminifera in shallow marine habitats including coastal salt marshes had been described (Buzas, 1965, 1974, 1977; Boltovskoy, 1966; Brooks, 1967; Schafer, 1971; Ellison, 1972; Frankel, 1972, 1974, 1975; Matera and Lee, 1972; Steinbeck and Bergstein, 1979; Collison, 1980; Matsushita and Kitazato, 1990). Only more recent studies, however, firmly established that salt marsh foraminifera live both epifaunally and infaunally, with living specimens occurring (rarely) down to 35 cm (Murray, 1991; Goldstein and Harben, 1993; Goldstein et al., 1995; Ozarko et al., 1997).

This observation is of major importance for the use of salt marsh foraminifera as paleo-environmental indicators and the accuracy and precision of faunal records (e.g., Ozarko et al., 1997). Marsh foraminiferal assemblages occur in zones related to the elevation of mean sea level and the tidal framework (Scott and Medioli, 1980, 1986; Scott and Leckie, 1990; Scott et al., 1990, 1996; Nelson and Kashima, 1993; Gehrels, 1994; Spencer, 1996). These zonations can then be used to infer changes in relative sea-level in coastal salt marsh sequences (e.g., Thomas and Varekamp, 1991; Gehrels, 1994; Nelson et al., 1996; Nydick et al., 1995; Guilbault et al., 1995; Scott et al., 1996). For most of the studies of living foraminiferal zonations, however, researchers sampled only the topmost 1-5 cm of the salt marsh and thus made no estimates of the relative abundance of the total population living deeper infaunally (e.g., Scott and Medioli, 1980; de Rijk, 1995). There are thus no estimates of the loss of time-resolution in core studies due to bioturbation.

In order to quantify the effect of infaunal living benthic foraminifera on the faunal record in peat cores we must establish a data base on the distribution of living foraminifera for each region. Goldstein et al. (1995) collected data on foraminifera in highly bioturbated marshes in Georgia, where marsh sediments are strongly minerogenic with organic carbon contents of 2.7-3.4% in the high marsh, 3.4-3.1% in the low marsh (Edwards and Frey, 1977). New England marshes, in contrast, have much higher concentrations of organic carbon, with typical values for the high marsh of 38-40%, for the low marsh about 20% (Thomas and Varekamp, 1991). Bioturbation by metazoan invertebrates such as crabs is considerably less in New England marshes than in the Georgia marshes, especially in the high marsh plains with Spartina patens where the sediment consists of dense, fine root-masses (McCaffrey and Thomson, 1980).

In this paper, we present data on the vertical distribution of living and dead marsh foraminifera in cores from two New England coastal salt marshes: Kelsey Marsh along the Connecticut coast (Bloom and Stuiver, 1963; Bloom, 1964; Van de Plassche et al., 1987; Thomas and Varekamp, 1991) and the Great Marshes at Barnstable, MA (Phleger and Walton, 1950; Redfield, 1972; de Rijk, 1995).

2. Study sites and methods

2.1. Kelsey Marsh (Clinton, CT; Fig. 1; Table 1)

Kelsey Marsh borders Long Island Sound to the southeast of Clinton, CT at approximately 41°16′ N 72°30′W (Bloom and Stuiver, 1963; Bloom, 1964; Van de Plassche et al., 1987; Van de Plassche, 1991; Thomas and Varekamp, 1991; Fig. 1). The marsh is divided into two lobes by a low hill, and intersected by Road CT 145.

We took cores seawards of the road in the northern (HE) and southern lobes (KMH3, 5; Fig. 1, Table 1). Indentations on the marsh surface remain from mosquito ditches dug in the 1930s. The mean tidal range is 1.5-1.7 m (NOAA tide tables), similar to that in the Wallace and Chezzetcook marshes of Nova Scotia (Scott and Medioli, 1980). Accretion rates in the high marsh (close to core HE) are about 2 mm/year. (Manoukian, 1995). The cores in the south-

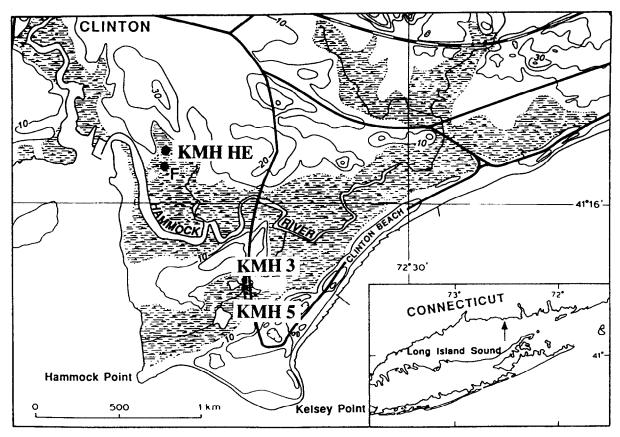


Fig. 1. Location of core sites in marshes on Kelsey Point, CT; KMH 5 is on the mudflat near a tidal creek, KMH 3 in stunted S. alterniflora, and HE in the S. patens meadow. HE was taken close to site F (Van de Plassche, 1991; Thomas and Varekamp, 1991).

Table 1

Core locations

	Environment	Marsh Zone	H. man	Bioturbation Rates
Barnstable Marsh				······································
Core BAM BR	S. patens	High	Yes	Low
Core BAM 8	S. patens near creek	High/Trans.	No	Low/Med
Core BAM M	Mudflat/S. alter.	Low	No	High
Kelsey Marsh				
Core HE	S. patens	High	Yes	Low
Core KMH 3	S. alterniflora	Low	No	Low/Med
Core KMH 5	Mudflat	Low	No	High

Cores in Kelsey Marsh were collected on 24 October, 1995; cores in Barnstable (BAM BR1, BAM 8) on 17 June, 1996 and November 6, 1996 (BAM M). *H. man.*: presence of *H. manilaensis*, a low salinity indicator.

ern lobe are along transect PP1 (Van de Plassche, 1991), which extends from the marsh border fringed by *Phragmites*, to an area with stunted *Spartina alterniflora* interspersed with *Spartina patens* and *Distichlis spicata*, to a tidal creek, where mud flats are fringed by *S. alterniflora*. Several meters of marsh sediment underlie the surface (Van de Plassche, 1991). Core site KMH 3 is in the middle of the low marsh zone in stunted *S. alterniflora*; KMH 5 is on the border between *S. alterniflora* and mud flat. Core

HE in the northern lobe is in the high marsh, dominated by dense growths of *Spartina patens*. Several meters of high marsh peat underlie the marsh surface (Van de Plassche, 1991; Thomas and Varekamp, 1991).

2.2. Barnstable Marsh (Cape Cod, MA; Fig. 2, Table 1)

The Great Marshes border Barnstable Bay on the northern side of Cape Cod near Barnstable, MA at 41° 42'30"-44'30" N, 70° 22'30"-20' W (Fig. 2), and cover 5300 acres, 70% of which is mature high marsh, 10% is intertidal, and the remaining area consists of sand flats (bare at low tide) and channels (Redfield, 1972). The Great Marshes of Barnstable are much less anthropogenically influenced than Kelsey Marsh, but about half of the marsh was ditched for mosquito control in the 1930s, which resulted in over-drainage of the marsh (Redfield, 1972). A railroad track borders the southeast edge. The accretion rate for short cores (to a depth of 14 cm) varies between 1.5 and 2.0 mm/year (de Rijk, 1995). Foraminifera in the Great Marshes were first described by Phleger and Walton (1950).

Our cores were taken on a transect between Bridge and Brickyard Creeks, from the railroad tracks to Broad Sound (de Rijk, 1995; Saffert, 1996). BAM BR1 was taken in the *S. patens* meadows, and BAM 8 is located in this meadow near a small creek. Core BAM M was taken on the mud flat border between the low marsh *S. alterniflora* and Broad Sound (Fig. 2, Table 1).

2.3. Extraction of cores and surface samples

We extracted cores with lengths of 40–50 cm, 6.6 cm diameter (Nydick et al., 1995). The cores were tightly wrapped in cellophane and foil in the field. In the laboratory, the cores were immediately split and their lithology described (Fig. 3). Cores were sliced into pieces of 2.5 cm. These samples were soaked in a solution of buffered formaldehyde and rose bengal (01.% rose bengal in 20% formaldehyde buffered to pH 8–9 using sodium carbonate). Additional surface samples (thickness about 1 cm) were taken near each core site. Samples were preserved as the core samples.

2.4. Sample processing

Surface and core samples were soaked in rose bengal-formaldehyde for at least 24 h. Dense peat samples were torn into smaller fractions for thorough soaking. Samples were then wet sieved; the size fraction larger than 500 μ m was dried, weighed and stored; the fraction smaller than 63 μ m was discarded in the wet-sieving. The fraction between 500 μ m and 63 μ m was dried, weighed, and used for analysis. Samples of dried material were sprinkled in a picking tray, and all foraminifera were picked from trays until at least 100 specimens were obtained. All specimens were soaked in water for determination of live-dead status. Rose bengal is the most widely used vital stain, but results obtained with this method are not accurate, as noted by many authors (e.g., Murray, 1991). Rose bengal may stain algae and bacteria attached to the test or organic components of the test itself (Goldstein et al., 1995). We thus classified individuals as 'living' only if they showed a bright pink stain, clearly located within the chambers.

3. Results

3.1. Infaunal living population (Figs. 4 and 5)

The number of living foraminifera per cm³ varies by depth in core as well as between cores. The cores in the highest marsh areas (HE, BAM BR1) have the highest numbers of foraminifera as well as the lowest diversity. In these cores the numbers of living individuals per cm³ are highest in the samples closest to the surface (0–2.5 cm), whereas these numbers reach their maximum at 2.5–5.0 cm depth in the cores in the lower marsh areas (Fig. 4). Infaunal specimens occur to greater depths in the Great Marshes than in Kelsey Marsh (Figs. 4 and 5), but in all cores more than 90% of the total living individuals occurs above 20 cm.

At Kelsey Marsh living foraminifera occur to a depth of 30 cm, with most specimens in the epibenthic layer (0-2.5 cm). In the densely vegetated *S. patens* meadow, the living population was more dominantly epibenthic than at the other sites (Fig. 5), and the population living below 5 cm was only 5% of the total population. At KMH 3, about

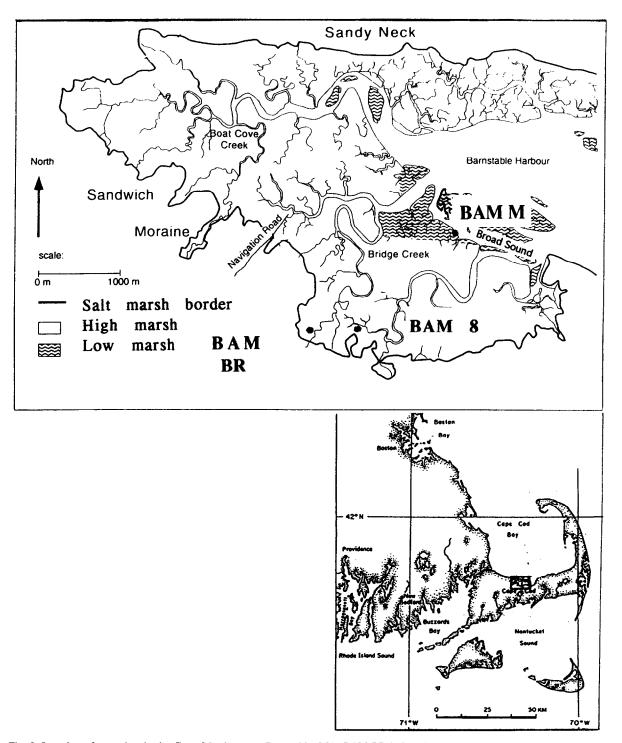
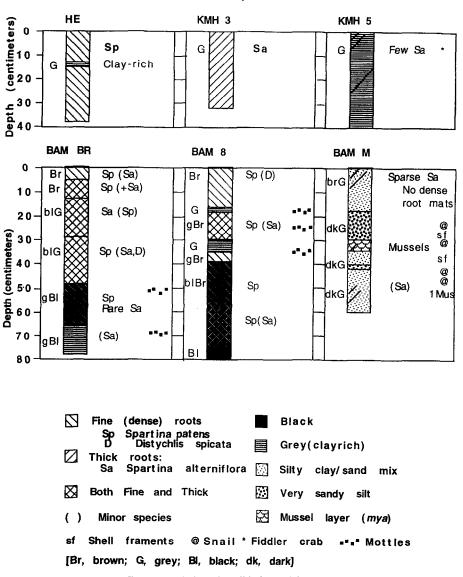


Fig. 2. Location of core sites in the Great Marshes near Barnstable, MA; BAM BR is in a *S. patens* meadow close to the edge of the marsh; BAM 8 in *S. patens* near a creek; BAM M close to the mud flats of Broad Sound (de Rijk, 1995).



Core Descriptions

Fig. 3. Description of the lithology of the cores.

5% of the total living population was below 15 cm, and no living specimens below 25 cm. At KMH 5 on the mud flat the percentage of living specimens does not decrease regularly with depth but is variable, with the deepest living specimen found at 30 cm (Fig. 4). About 95% of the total living population occurred above 20 cm.

The Barnstable cores have a higher percentage of living specimens at intermediate to deep infaunal

levels than the Kelsey marsh cores (Fig. 4). Living foraminifera were found to a depth of 50 cm, with most living epibenthic to shallow infaunal (0–5 cm). In high marsh core BAM BR1 no living specimens were present at 20 cm, but in the 25–27.5 cm sample about 4% of specimens were living; about 95% of the total living population occurred above 15 cm. At site BAM 8 the living population is relatively consistent from epibenthic to intermediate infaunal

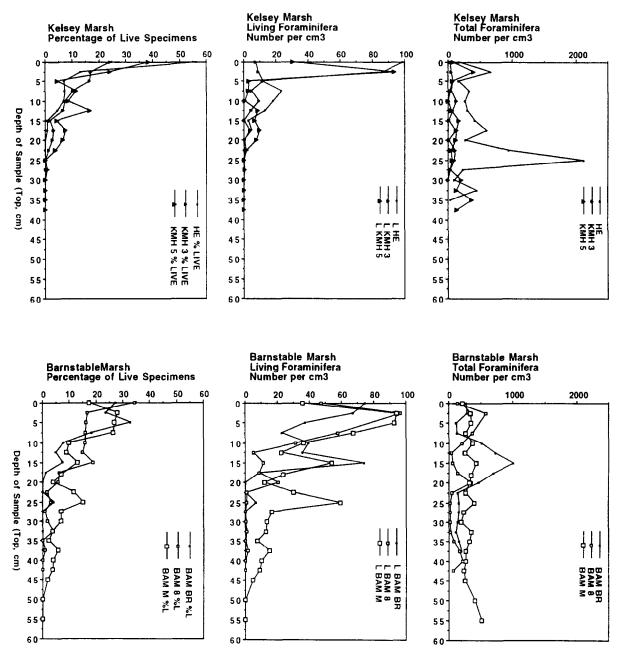


Fig. 4. Relative and absolute abundance of living and total specimens for all cores.

to a depth of 15 cm. Below 17.5 cm, the live population varies from 2-5% to a depth of 35 cm. One individual was found at 37.5-40.0 cm. The highest percent of species living at the greatest depths was at BAM M on the mud flat, yet the top 2.5 cm had the fewest living specimens, 17%, of all cores. The

living population was primarily shallow infaunal to a depth of 10 cm. In the intermediate infaunal layers the living population was variable reaching a peak in the 25-27.5 cm interval. Deep infaunally, the living population ranged from 2-7% to a depth of 50 cm.

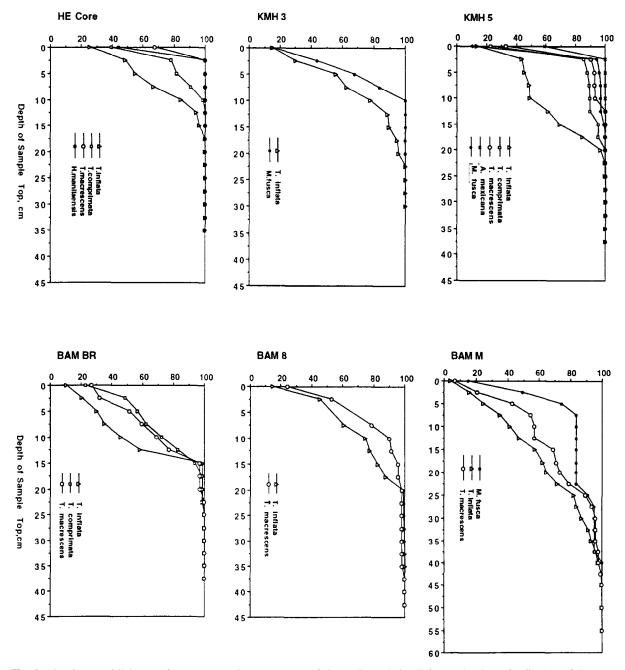


Fig. 5. Abundances of living specimens expressed as percentage of the total population living at the time of collection of the core, summed over the total depth. For each sample the number of live individuals per cubic centimeter was calculated for each species. The number of live individuals of each species (expressed in number per cm^3) was then summed over all samples in the core. Then we calculated for each sample the living specimens as a percentage of the total living specimens at the core site (total standing crop). Specimens that comprise less than 2% were not included.

3.2. Infaunal distribution of species (Figs. 6–11)

The most common species are Trochammina macrescens, Trochammina inflata, Tiphotrocha comprimata, Haplophragmoides manilaensis, Miliammina fusca, and Arenoparrella mexicana (in order of decreasing abundance) in both marshes (Table 2). All species have the most abundant living specimens per cm^3 in the upper 5 cm, with maxima at 2-5 cm in the lower marsh cores, 0-2.5 cm in the upper marsh cores. The most common species in live plus dead populations was T. macrescens, whereas the most abundant living species was commonly T. inflata. Matera and Lee (1972) found living T. inflata to be most abundant at 3-6 cm, and Ozarko et al. (1997) found the species down to 25 cm in the high marsh. In our samples T. inflata was most abundant in the epibenthic layer, while being present to deep infaunal levels. This species has the deepest living population in all cores (Table 3).

T. comprimata was more abundant in the high marsh cores especially in dense vegetation, and lives epifaunal to shallow infaunal. *Trochammina macrescens* lives to intermediate depths (Table 3); Ozarko et al. (1997) found this species down to 20 cm in the high marsh. In upper marsh zones where low salinity prevails *H. manilaensis* is epibenthic to shallow infaunal.

In the lower marsh zones, *M. fusca* is predominantly epibenthic and shallow infaunal, and occurs living in the top 5 cm. It is most abundant in the lower marsh zones (KMH 3, KMH5, BAM M). Living *A. salsum* were found only epifaunal in the low marsh areas. Calcareous specimens occurred in the low marsh to mud flat only; we found them preserved only in Core BAM M, which had a prominent mussel-layer (Figs. 3 and 11)

3.3. Dead assemblages

The total (living plus dead) number of foraminifera per cm³ is not correlated with depth below the marsh surface, but shows large fluctuations in all cores. In several cores the total number of specimens was higher in some samples within the cores than in the surface samples (e.g., core HE, 25 cm; Fig. 5). The total abundance of foraminifera, like that of living species, is highest in samples from high marsh cores. Faunal diversity, however, is greatest in the mud flat cores and decreases in the higher marsh zones. No correlation is obvious between changes in diversity and in depth of the core samples.

Similarly, the relative and absolute abundances of all species show strong fluctuations with depth-incore, and no simple increase or decrease with depth (Figs. 6–11). There is no significant positive correlation between the absolute abundance of living and dead specimens in the samples. It thus appears that the fluctuations in the total (live plus dead) assemblage can not be explained by either differential preservation (absolute abundances do not simply decrease with depth), or by enrichment of the dead assemblage by bioturbation with later living individuals. We can, therefore, try to extract a signal of primarily fluctuating abundances of species from the record, after deconvolution to take the bioturbation into consideration (e.g., Ozarko et al., 1997).

Distribution of living foraminifera has been described as extremely patchy (e.g., Schafer, 1971). In order to test whether foraminiferal assemblages in core samples, which contain specimens that lived over several decades, show consistency we compared data on core HE (total, living + dead population) with data on the dead population of core E, which was collected 2 years earlier, a few meters away from core HE (Thomas, unpub. data; Fig. 12). The data on these two cores compare rather well for the more common species, suggesting that the extreme patchiness of the living populations is averaged out in the dead assemblages, representing decades per sample.

4. Discussion

Salt marsh foraminifera in New England marshes live infaunally as well as epifaunally, in agreement with what has been described in the marshes in Georgia (Goldstein and Harben, 1993; Goldstein et al., 1995), and in British Columbia (Ozarko et al., 1997). No taxa are exclusively infaunal. Living foraminifera are common to a depth of 15 cm, with most occurring in the top 5 cm. The foraminifera in Barnstable and Kelsey marshes are exclusively epifaunal (calcareous species), epifaunal through shallow infaunal, 2.5–10 cm (*M. fusca, H. manilaensis*) or epifaunal through intermediate — deep infaunal (most 15–

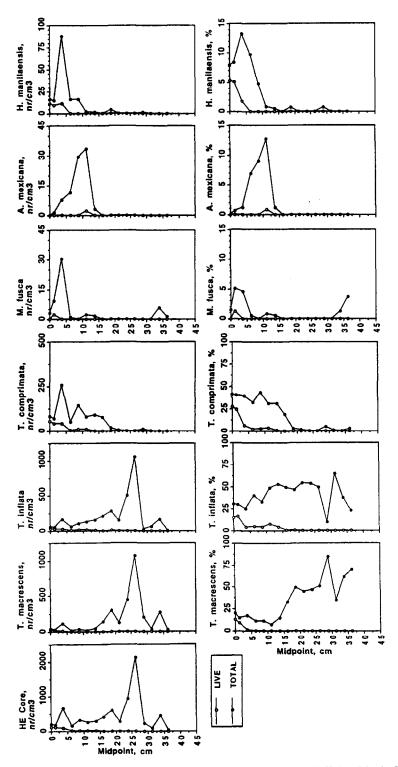


Fig. 6. Absolute and relative abundance of the most common species in core HE, high marsh, Kelsey Marsh. Specimens that comprise less than 2% were not included.

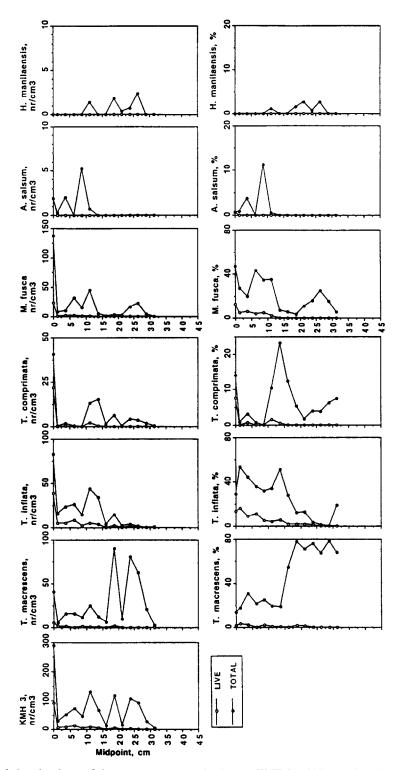


Fig. 7. Absolute and relative abundance of the most common species in core KMH 3, middle marsh, Kelsey Marsh. Specimens that comprise less than 2% were not included.

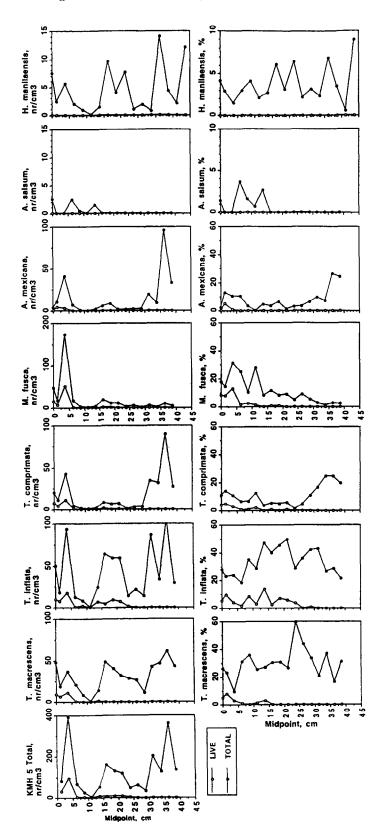


Table 2	
Species identified in New	England salt marsh cores

1	listed in order of decreasing abund mprimata, H. manilaensis, M. fusca	ance) a, and A. mexicana (except KMH3)
Species identified in few cores		
P. ipohalina	BAM BR1	No living specimens
Eggerella	BAM8, BAM M	No living specimens
A. salsum ^a	BAM M&8, KMH 3&5	Epifaunal/Shallow Infaunal
T. earlandi	КМНЗ, КМН 5, ВАМ М	No living specimens
A. inepta	KMH5	No living specimens
Calcareous species ^a	KMH5, BAM M	Epifaunal
Thecamoebians	HE, BAM BR	No living specimens

^a Some specimens identified as living at time of sampling in KMH 5.

Table 3 Classification of foraminiferal species according to infaunal depth

Depth (cm)	Name of zone	Species present							
0.0-2.5	Epifaunal	Tinf, Tmac, Tcom, Hman, Amex, Asal, calcareous species							
2.5-15.0	Shallow infaunal	Tinf, Tmac, Tcom, Hman, Amex, Mfus							
15.0-25.0	Intermediate infaunal	Tinf, Tmac, Tcom, Amex							
25.0-40.0	Deep infaunal	all rare: Tinf, Tmac, Tcom, Amex							

Abbreviations: Tinf T. inflata, Tmac T. macrescens, Tcom T. comprimata, Hman H. manilaensis, Amex A. mexicana, Asal A. salsum, and Mfus M. fusca.

25 cm, rare specimens down to 50 cm). The latter mode of live is seen in the most common species, *T. macrescens, T. comprimata, T. inflata*, and *A. mexicana*. These species are the most abundant in the large *Spartina patens* high marsh meadows which dominate the New England marshes, in contrast with the Georgia marshes which have extensive low marsh regions where *M. fusca* is most common (Goldstein et al., 1995).

In our cores from both marshes living specimens were found to greater depths in the low marsh than in the high marsh, in contrast with Ozarko et al. (1997). Their data on the high marsh agree with ours, with living specimens found to about 25 cm, and *T. inflata* living to greater depths than *Haplophragmoides wilberti* and *M. fusca*. These authors found that foraminifera live to lesser depths in the low marsh, however. We do not know what causes the discrepancy between the low marsh data; possibly the New England and British Columbia low marsh regions are different in vegetation and bioturbational processes.

The calcareous taxa were not found living infaunally. This agrees with observations that species of *Elphidium* and *Ammonia* burrow very shallow and are limited to the oxygenated sediment layers (Langer et al., 1989), and that these species move randomly in the upper 1 cm of sediment (Wetmore, 1988).

We do not know how the living agglutinated individuals reach the infaunal depths of 20 cm and more. Possible explanations are burial at the surface of the sediment and survival within; active motion through the sediment; passive motion, carried by bioturbation or moving water.

The first possibility can be excluded. At Kelsey marsh, a 25 cm deep sample was deposited at around 1865 AD (Varekamp et al., 1992), so that

Fig. 8. Absolute and relative abundance of the most common species in core KMH 5, low marsh, Kelsey Marsh. Specimens that comprise less than 2% were not included.

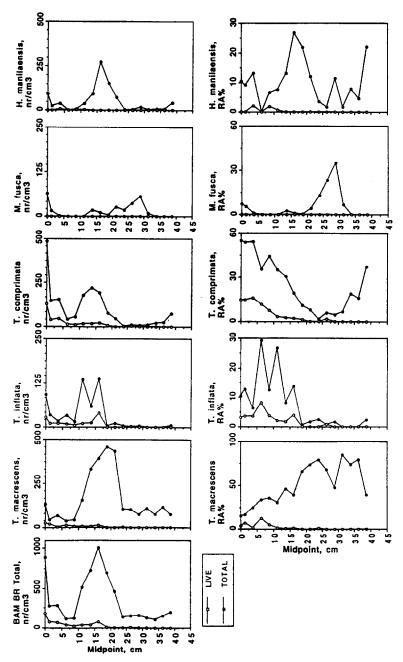


Fig. 9. Absolute and relative abundance of the most common species in core BAM BR, high marsh, Great Marshes, Barnstable. Specimens that comprise less than 2% were not included.

for a could not have survived since the accumulation and burial of that sediment.

Active burrowing by the foraminifera is possible: foraminifera have been observed to migrate in response to changes in oxygen concentrations (Alve and Bernhard, 1995; Kitazato and Ohga, 1995). This migration, however, occurs over a few cm only, and is in the direction of increased oxygen whereas oxygen concentration decreases down-core in the marshes. Many studies of foraminiferal mo-

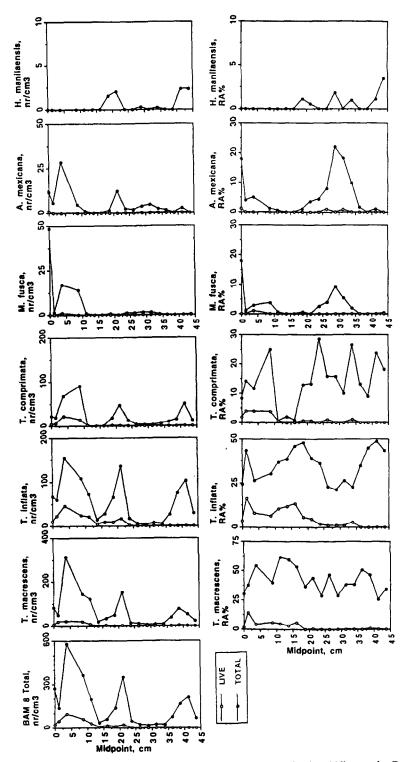
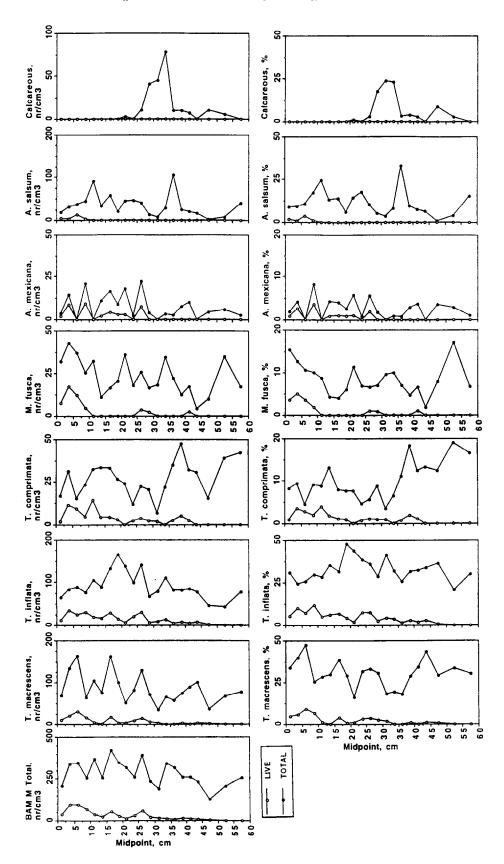


Fig. 10. Absolute and relative abundance of the most common species in core BAM 8, middle marsh, Great Marshes, Barnstable. Specimens that comprise less than 2% were not included.



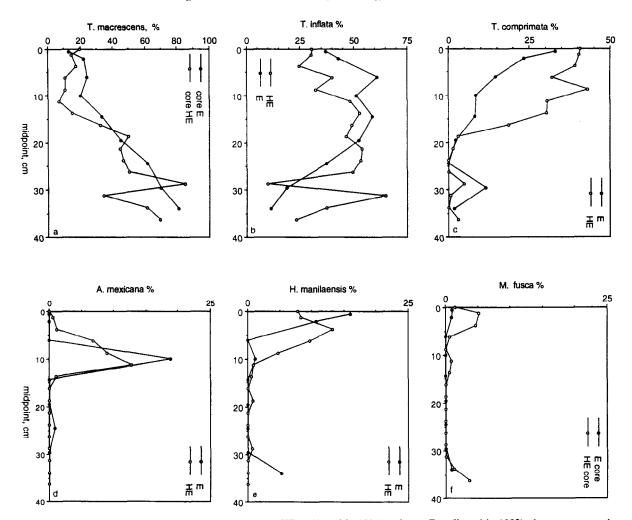


Fig. 12. Relative abundances of dead assemblages in core HE (collected in 1994) and core E (collected in 1992); the cores were taken about 1 m apart, in the high marsh meadows.

tion were set up to study escape of foraminifera after being covered with sediments (e.g., Severin and Erskian, 1981; Severin et al., 1982; Severin, 1987). Foraminifera dominantly moved upward under these conditions, although some specimens moved down; it took the *Quinqueloculina* sp. many hours to emerge from burial under 4 cm (109 h; Severin and Erskian, 1981). Measurements of more relevance to the question whether foraminifera burrow voluntarily were made by Wetmore (1988) and Kitazato (1988). Both authors observed a very wide range of speed of different species (Kitazato: specimens 0.1–11.4 mm/h; average for species 0.5–4.9 mm/h; Wetmore: average for species 0.5–7.7 mm/h). There are, however, no data available on any of the genera that we observed in the salt marshes. All laboratory test were done with foraminifera moving through loose sediment (sand, mud), very different from the extremely dense peat, consisting largely of intertwined fine roots of the marsh grasses, which forms the

Fig. 11. Absolute and relative abundance of the most common species in core BAM M, low marsh, Great Marshes, Barnstable. Specimens that comprise less than 2% were not included.

substrate through which the marsh foraminifera must move. In view of these very limited data we think it unlikely that marsh foraminifera could actively move vertically at speeds above 10 mm/h; probably they move considerably slower.

Bioturbation by animals and plant roots may certainly transport foraminifera (McCaffrey and Thomson, 1980; Collison, 1980; Long and Mason, 1983; Goldstein and Harben, 1993; Goldstein et al., 1995). The deepest and most variable percentages of living specimens occur in cores BAM M, KMH 5 and BAM 8, which are close to tidal creeks where bioturbation by metazoa (including the fiddler crab, Uca pugnans) is most intense. The least infaunal specimens occurred in the dense S. patens root mats in the high marsh areas at HE and BAM BR1 (Figs. 4 and 5). This suggests that bioturbation at least was partially responsible for the downward transport of living specimens in the lower marsh, especially because the distribution with depth of living specimens is more irregular in these cores (Fig. 4).

Living infaunal specimens, however, do occur at sites in the middle and upper marshes, where crabs do not or hardly bioturbate (McCaffrey and Thomson, 1980). At these sites bioturbation may occur by plant roots, especially at sites where S. alterniflora is common such as KMH3 (Howes et al., 1981; Bertness, 1992). Even at sites in the densely vegetated S. patens meadow, however, living specimens occur down to 20 cm. In addition to bioturbation by plant roots the continual vertical movement of fluid through the marsh due to the tidal cycles as well as rain fall ('tidal pumping'; McCaffrey and Thomson, 1980; Moodley and Hess, 1992; de Rijk, 1995) might be able to transport foraminifera into the substrate. Percolation rates in a Massachusetts salt marsh sediments range from 1.8-10.7 cm/h (Howes et al., 1981), i.e., much faster than what appears probable for active motion of foraminifera. The fastest rates occur below tall S. alterniflora stands along creek banks, slower rates occur in stunted S. alterniflora and S. patens stands. We do not know whether fullsize adult foraminiferal specimens (commonly 150-300 μ m) could be effectively moved with the fluids through the dense peat of the upper marsh, but the minute gametes that are produced during sexual reproduction (Kitazato and Matsushita, 1996), or the small juveniles produced during asexual reproduction (Angell, 1990; Pawlowski et al., 1995; Kitazato and Matsushita, 1996) could possibly move in this way.

Fluid flow and bioturbation by metazoa and plant roots, however, can not fully explain the varying species assemblages of living specimens with depth, because both processes would transport living specimens regardless of species into the sediment. This does not agree with our observations that different species consistently occur live at specific depths. This pattern could be explained, however, by differential species survival after transportation, in agreement with varying tolerance of very low oxygen levels by calcareous species (Alve and Bernhard, 1995), and/or varying food requirements by different species (e.g., Goldstein and Corliss, 1994; Hohenegger et al., 1989; Lee, 1990). Different species of foraminifera prefer different food sources: some species use living algae, whereas other prefer bacteria and take up dead organic matter in sediment particles. The latter clearly have better possibilities of survival within the sediments.

We do not know whether marsh foraminifera can survive true anoxia, and oxygen levels decrease with depth below the marsh surface. Carbon dioxide production and oxygen uptake in sediment below S. patens stands indicate that the top 0-2 cm of sediment only has sufficient oxygen for aerobic respiration, whereas sulfate reduction provides a limited source of oxygen that decreases with depth between 2-15 cm (Howes et al., 1984). Seasonal plant growth affects the metabolic rates within the sediment and the level of oxygen present (Howes et al., 1984; Teal and Howes, 1996). Even at depths of 20-25 cm in non-bioturbated sediment, however, conditions are not necessarily fully anoxic, because root aeration creates microhabitats with at least low levels of oxygen (Howes et al., 1981). Foraminifera might thus move actively as well as passively (carried by plant roots or by waters) in these aerated root zones, and we have no evidence that they live in fully anoxic conditions.

Our data do not show a consistent decrease in diversity and abundance (in number of specimens per cm^3) of the total (live plus dead) assemblage with depth, in contrast with the data by Goldstein et al. (1995) for Georgia marshes (Fig. 4). There is no significant positive correlation between the number of

living and dead individuals within each sample. This observation suggests that the variation in total (living plus dead) abundances of foraminifera between samples in a core can not be fully explained by differential preservation of the various species, and reflects at least in part variations within the populations over time. The signal of environmental changes, however, is affected by the infaunal living patterns of the most common species, which decreases the time resolution and necessitates deconvolution of the signal (Ozarko et al., 1997).

5. Conclusions

Agglutinated benthic foraminifera in New England salt marshes live epifaunally and infaunally, with dominant living population at depths of 0-10 cm.

Foraminifera are most abundant in the high marsh region, with a population maximum at 0-2.5 cm; in the lower marsh regions they are most abundant at 2.5-5.0 cm but do not reach the high abundances of the high marsh.

Faunal diversity of living and total assemblages tends to be greatest in the lower marsh and borders with the mud flats, and decreases with elevation in the higher marsh zones.

Intermediate to deep infaunal specimens are more common in cores from the lower marsh regions where metazoan bioturbation is more common, but occur in high marsh cores where metazoa do not burrow. Bioturbation by metazoa and plant roots, and fluid flow probably are the main factors bringing the foraminifera into the sediment.

The abundance of living specimens at depth varies by species, with consistent patterns in all cores (e.g., *M. fusca* shallow, *T. inflata* deep). The species may have differential rates of survival in the sediments, which have very low oxygen concentrations. Alternatively, species that live on dead organic material and bacteria will survive longer than species requiring living algae.

Bioturbation and root aeration create oxygenated microhabitats and we thus do not know whether marsh foraminifera tolerate true anoxia.

Comparison of total populations (living plus dead) with living populations indicate that not all changes with depth-in-core are caused by differential preservation. It is therefore possible to extract a signal of environmental change from data on the thanatocoenosis, but the record must be corrected for the effects of infaunally dwelling taxa.

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Appendix A. Systematic taxonomy

Ammoastuta inepta (Cushman and McCulloch)

- Ammobaculitus ineptus Cushman and McCulloch, 1929, p. 89, pl. 7, fig. 6
- Ammoastuta inepta (Cushman and McCulloch), Parker et al., 1953, p. 4, pl. 1, fig. 12.
- Ammoastuta inepta (Cushman and McCulloch), Scott et al., 1990 p. 729.

This species rarely occurs in our samples.

Ammonia beccarii (Linne)

Nautilus beccarii Linne, Systema Naturae, ed. 10, 1758, p. 710. Ammonia beccarii (Linne), Scott and Medioli, 1980, p. 35, pl. 5, figs. 8 and 9.

This calcareous species only occurs in low marsh environments, preferentially on or close to mud flats; it is rare or absent in most of our samples.

Ammotium salsum (Cushman and Brönnimann)

- Ammobaculites salsus Cushman and Brönnimann, 1948, p. 16, pl. 3 figs. 7–9.
- Ammotium salsum (Cushman and Brönnimann), Scott and Medioli, 1980, p. 35, pl. 1, figs. 11–13.
- This species occurs in small numbers in low marsh sample sites.

Arenoparrella mexicana (Kornfeld)

- Trochammina inflata (Montague) var. mexicana Kornfeld, 1931, p. 86, pl. 13, fig. 5.
- Arenoparrella mexicana (Kornfield), Scott and Medioli, 1980, p. 35, pl. 1 figs. 8–11.

This species occurs in small numbers in low marsh sample sites, and especially close to tidal creeks.

Eggerella advena (Cushman)

Verneuillina advena Cushman, 1921, p. 141. Eggerella advena (Cushman), Scott et al., 1990, p. 385, pl. 2, figs. 1, 2.

Elphidium excavatum (Terquem)

Polystomella excavata Terquem, 1876, p. 429.

Cribrononion excavatum (Terquem), Scott and Medioli, 1980, p. 35-36, pl. 5, figs. 5, 6.

Haplophragmoides manilaensis Anderson

- Haplophragmoides manilaensis Anderson, 1953, p. 22, pl. 4, figs. 8a, b.
- Haplophragmoides bonplandi (Todd and Brönnimann), Scott and Medioli, 1980, p. 40, pl. 2, figs. 4, 5.
- Haplophragmoides manilaensis (Anderson) Thomas and Varekamp, 1991, p. 155.

This species occurs primarily in the high marsh near the terrestrial edge of the marsh, where it is very common, both in Clinton Marsh and in Barnstable Marsh.

Miliammina fusca (Brady)

Quinqueloculina fusca Brady, in Brady and Robertson, 1870, p. 47, pl. 11, figs. 2, 3.

- Miliammina fusca (Brady), Phleger and Walton, 1950, p. 280, pl. 1, figs. 19a, b.
- Miliammina fusca (Brady) Scott and Medioli, 1980, p. 40-41, pl. 2, figs. 1-3.

This species is one of the most common species, found in Clinton and Barnstable marsh, but is somewhat more abundant in middle to low marsh sites than at high marsh sites.

Polysaccammina ipohalina Scott

Polysaccammina ipohalina Scott, 1976, p. 318, pl. 2, figs. 1-4, text figures 4a-c.

Polysaccammina ipohalina Scott, Scott and Medioli, 1980, p. 43, pl. 2, figs. 8–11.

This species is rare and often fragmented; it is believed to be tolerant of exposure to fresh water (Scott, 1976).

Protelphidium orbiculare (Brady)

Nonionia orbicularis Brady, 1881, p. 415, pl. 21, fig. 5.

Protelphidium orbiculare (Brady), Scott and Medioli, 1980, p. 43, pl. 5, fig. 7.

Quinqueloculina sp.

In a few samples rare, small specimens were seen that show typically quinqueloculine chamber arrangement, and a thin, translucent carbonate test. They could not be ascribed to a known species, possibly because the tests were partially dissolved.

Textularia earlandi Parker

Textularia earlandi Parker, 1952, p. 458 (footnote). Textularia earlandi Parker, Scott et al., 1990, p. 732. Only a few individuals of this species were observed.

Tiphotrocha comprimata (Cushman and Brönnimann)

Trochammina comprimata Cushman and Brönnimann, 1948, p. 41., pl. 8, figs. 1–3.

Tiphotrocha comprimata (Cushman and Brönnimann) Scott and Medioli, 1980, p. 44, pl. 5, figs. 1–3.

This species occurs in moderate abundances in high and middle marsh faunas in Clinton and Barnstable Marsh, mostly with *T. macrescens* and *T. inflata*; its abundance was highest at sites with dense vegetation (e.g., Site HE).

Trochammina inflata (Montagu)

Nautilus inflatus Montagu, 1808, p. 81, pl. 18, fig. 3.

- Trochammina inflata (Montagu), Phleger and Walton, 1950, p. 280, pl. 2, figs. 1-3.
- Trochammina inflata (Montagu) Scott and Medioli, 1980, p. 44, pl. 3, figs. 12–14; pl. 4, figs. 1–3.

This is one of the most common species, occurring in almost all samples from Clinton and Barnstable marsh. It is most abundant in the middle marsh area, but is also common in high marsh and on the mud flats. It is absent or rare in samples from the terrestrial border of the marsh where *H. manilaensis* is common.

Trochammina macrescens Brady

Trochammina inflata (Montagu) var. macrescens Brady, in Brady and Robertson, 1870, p. 290, pl. 11, figs. 5a-c.

- Trochammina macrescens Brady, Phleger and Walton, 1950, p. 281, pl. 2, figs. 6–9.
- Trochammina macrescens Brady, Scott and Medioli, 1980, p. 44-45, pl. 1 figs. 8-11.

This species was one of the most common foraminiferal species in Clinton and Barnstable marsh, usually co-occurring with *T. inflata* and *T. macrescens*. It is most abundant in the high and middle marsh areas, but is also common on the mud flats.

Appendix B. Counts and weights (Tables B1-B8)

Abbreviations of species names for all Appendix tables:

A. inepta:	Ammoastuta inepta
A. bec.:	Ammonia beccarii
A. sal.:	Ammotium salsum
A. mex.:	Arenoparrella mexicana
Calc.:	various calcareous species
Egg.:	Eggerella advena
E. exc.:	Elphidium excavatum
H. man.:	Haplophragmoides manilaensis
M. fus.:	Miliammina fusca
P. ipo.:	Polysaccammina ipohalina
P. orb.:	Protelphidium orbiculare
Quel.:	Quinqueloculina spp.
T. earl.:	Textularia earlandi
T. com.:	Tiphotrocha comprimata
T. inf.:	Trochammina inflata
T. mac.:	Trochammina macrescens
Thecam .:	thecamoebians.

Table B1 Numbers of living and dead foraminifera Core HE

Core site	Depth (cm)	Status	M. fusca	T. inflata	T. compr.	T. macr.	H. man.	A. mex.	Total	Percentage	Species	Thecam
HE-s	0.00	live		32	56	27	11		126	60.9	4	
		dead	3	31	28	14	5		81	39.1	5	
		total	3	63	84	41	16		207	100.0	5	
HE-I	0-2.5	live	2	26	38	14	8		88	56.8	5	
		dead	6	21	25	9	5	1	67	43.2	6	
		total	8	47	63	23	13	1	155	100.0	6	1
HE-2	2.5-5.0	live		7	11	2	3		23	13.2	4	
		dead	8	36	57	28	20	2	151	86.8	6	
		total	8	43	68	30	23	2	174	100.0	6	1
HE-3	5.0-7.5	live		8	4				12	6.9	2	
		dead	1	62	52	19	17	12	163	93.1	6	
		total	1	70	56	19	17	12	175	100.0	6	1
HE-4	7.5-10	live		7	5				12	7.2		
	110 10	dead		47	67	18	8	15	155	92.8	2 5	
		total		54	72	18	8	15	167	100.0	5	
HE-5 10-12	10-12.5	live		9	4			1	14	11.9	3	
		dead	1	48	32	8	1	14	104	88.1	6	
		total	1	57	36	8	1	15	118	100.0	6	
HE-6	12.5-15	live		7	1				8	4.4	2	
		dead	1	89	54	27	1	2	174	95.6	6	
		total	1	96	55	27	1	2	182	100.0	6	
HE-7	15-17.5	live	-	1					1	0.6	1	
		dead		81	31	54			166	99.4	3	
		total		82	31	54			167	100.0	3	
HE-8	17.5-20	live		1					1	0.8	1	
	1110 20	dead		61	4	66	1		132	99.2	4	
		total		62	4	66	1		133	100.0	4	
HE-9	20-22.5	total		111	3	92			206	100.0	3	
HE-10	22.5-25	total		90		79			169	100.0	2	
HE-11	25-27.5	total		64		65			129	100.0	2	
HE-12	27.5-30	total		14	7	123	1		145	100.0	4	
HE-13	30-32.5	total		98	1	52			151	100.0	3	
HE-14	32.5-35.0	total	2	58	-	95			155	100.0	3	
HE-15	35.0-37.5	total	5	32	4	96			137	100.0	4	

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Table B2 Numbers of living and dead foraminifera for Core 3KMH

Core site	Depth (cm)	Status	M. fus.	A. sal.	T. inf.	T. com.	T. mac.	H. man.	T. earl.	Total	Percentage	Species
3KMH-3	0.0	live	13	1	21	12	3			50	31.0	5
		dead	54		24	10	19			107	68.2	4
		total	67	1	45	22	22			157	100.0	5
3KMHC-1	0-2.5	live	5		18		4			27	24.1	3
		dead	25	1	42	1	16			85	75.9	5
		total	30	1	60	1	20			112	100.0	5
3KMHC-2	2.5 - 5.0	live	6		12	1	3			22	16.8	4
		dead	18	5	46	3	37			109	83.2	5
		total	24	5	58	4	40			131	100.0	5
3KMHC-3	5.0-7.5	live	4		16					20	14.0	2
		dead	56		35	1	31			123	86.0	7
		total	60		51	1	31			143	100.0	7
3KMHC-4	7.5-10	live	5		8		4			17	10.1	3
		dead	49	19	45		38			151	89.9	4
		total	54	19	53		42			168	100.0	4
3KMHC-5	10-12.5	live	2		7	3	1			13	7.1	4
		dead	60	1	55	16	35	2	1	170	92.9	4
		total	62	1	62	19	36	2	1	183	100.0	5
3KMHC-6	12.5-15	live			9	1	1			11	6.5	3
		dead	12		77	38	31			158	93.5	4
		total	12		86	39	32			169	100.0	4
3KMHC-7	15-17.5	live			2					2	1.6	1
		dead	7		34	16	70			127	98.4	4
		total	7		36	16	70			129	100.0	4
3KMHC-8	17.5-20	live			2		2			4	3.1	2
		dead	4		14	7	98	2		125	96.9	5
		total	4		16	7	100	2		129	100.0	5
3KMHC-9	20-22.5	live			2		1			3	2.6	2
		dead	13		13	2	81	3		112	97.4	5
		total	13		15	2	82	3		115	100.0	5
3KMHC-10	22.5-25	live			2					2	1.3	1
		dead	24		3	6	114	1		148	98.7	5
		total	24		5	6	114	1		150	100.0	5
3KMHC-11	25-27.5	dead	39		2	6	104	4		155	100.0	5
3KMHC-12	27.5-30	dead	17			7	87			111	100.0	3
3KMHC-13	30-32.5	dead	3		10	4	36			53	100.0	4

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Table B3 Numbers of living and dead foraminifera for Core 5KMH

Core site	Depth (cm)	Status	M. fus.	A. sal.	T. inf.	T. com.	Т. тас.	H. man.	A. mex.	Calc.	A. inep.	T. earl.	Total	Percentage	Species
5KMH-s	0.00	live	12		8	6	7			1			34	23.6	5
		dead	26	2	32	10	31	6	3				110	76.4	7
		total	38	2	40	16	38	6	3	1			144	100.0	8
5KMH-1	0-2.5	live	11		13	7	11		7	3			52	38.2	6
		dead	20		18	12	21	4	8	1			84	61.8	7
		total	31		31	19	32	4	15	4			136	100.0	7
5KMH-2	2.5 - 5.0	live	18		6	4	4		1				33	23.9	5
		dead	43		27	11	9	2	13				105	76.1	6
		total	61		33	15	13	2	14				138	100.0	6
5KMH-3	5.0-7.5	live	2		2	1	1						6	4.4	4
		dead	34	5	23	8	41	4	14				129	95.6	7
		total	36	5	25	9	42	4	14				135	100.0	7
5KMH-4	7.5-10	live	3		10	1							14	11.4	3
		dead	13	2	33	7	44	5	4		1		109	88.6	8
		total	16	2	43	8	44	5	4		1		123	100.0	8
5KMH-5	10-12.5	live	2		4	3	2			1			12	8.2	5
		dead	41	1	38	15	35	3				1	134	91.8	7
		total	43	1	42	18	37	3		1		1	146	100.0	8
SKMH-6	12.5-15	live			15		3						18	16.4	2
		dead	9	3	37	4	27	3	5		3	1	92	83.6	8
		total	9	3	52	4	30	3	5		3	1	110	100.0	8
5KMH-7	15-17.5	live	1		4	1							6	4.1	3
		dead	17		55	7	45	9	5			4	142	95.9	7
		total	18		59	8	45	9	5			4	148	100.0	7
5KMH-8	17.5-20	live	1		11								12	7.5	2
		dead	13		61	8	49	5	10		1		147	92.5	7
		total	14		72	8	49	5	10		i		159	100.0	7
5KMH-9	2022.5	live			8	1		-					9	6.5	2
5140111 /	20 22.0	dead	13		61	7	37	9	2			1	130	93.5	7
		total	13		69	8	37	9	2			î	139	100.0	7
5KMH-10	22.5-25	live	10		5	Ū	57		-			•	5	3.6	i
511111110	22.0 20	dead	7		35	2	83	3	4				134	96.4	6
		total	7		40	2	83	3	4				139	100.0	6
5KMH-11	25-27.5	live	,		-10	-	05	5					0	0.0	0
514411-11	25-21.5	dead	12		46	6	56	4	4				128	100.0	6
		total	12		46	6	56	4	4				128	100.0	6
5KMH-12	27 5-30	live	12		1	0	50	-	-				128	0.8	1
514011-12	27.5~50	dead	7		54	14	44	3	8				130	99.2	6
		total	7		55	14	44	3	8				130	100.0	6
5KMH-13	30-32.5	dead	4		62	24	30	10	14		1		145	100.0	7
5KMH-14	32.5-35	dead	4 2		38	35	53	5	10		*		143	100.0	6
5KMH-14	35-37.5	dead	5		51	44	39	1	47				178	100.0	6
5KMH-15	33–37.5 37.5–40	dead	3		24	22	39	10	27				121	100.0	6
5151911-10	51.5-40	ucau	J		24	44	35	10	<i>∠1</i>				121	100.0	0

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Table B4	
Numbers of living and dead foraminifera for Core BAM BR	

Core site	Depth cm	Status	M. fus.	T. inf.	T. com.	T. mac.	H. man.	A. max.	P. ipo.	Total	Percentage	Species	Thecam
BAM BRI	0-2.5	live		4	16	8		2		30	27.3	4	
S. patens		dead	6	10	43	10	10	1		80	72.7	6	
		total	6	14	59	18	10	3		110	100.0	6	1
	2.5 - 5.0	live		5	23	2	3	1		34	23.6	5	
		dead	1	4	55	34	16			110	76.4	5	
		total	1	9	78	36	19	1		144	100.0	6	
	5.0-7.5	live		9	13	14				36	32.7	3	
		dead		23	26	23		1	1	74	67.3	5	
		total		32	39	37		1	1	110	100.0	5	
	7.5-10	live		4	8	5	2			19	18.3	4	
		dead		9	38	32	2 5		1	85	81.7	5	
		total		13	46	37	7		1	104	100.0	5	
	10-12.5	live		3	5	2	1			11	7.7	4	
		dead		35	45	42	10			132	92.3	4	
		total		38	50	44	11			143	100.0	4	
	12.5-15	live		2	3	1				6	4.9	3	
		dead	3	8	34	35	16			116	95.1	5	
		total	3	10	37	56	16			122	100.0	5	
	15-17.5	live		8	4	3				15	7.4	3	
		dead	2	20	35	77	55			189	92.6	5	
		total	2	28	39	80	55			204	100.0	5	
	17.5-20	live			2					2	1.2	1	
		dead	1	1	16	108	36			162	98.8	5	
		total	1	1	18	108	36			164	100.0	5	
	20-22.5	dead	5	2	9	85	14			115	100.0	5	
	22.5-25	dead	15	3	2	92	4			116	100.0	5	
	25-27.5	live		1	2	2	·			5	4.2	3	
		dead	28	-	5	79	2			114	95.8	4	
		total	28	1	7	81	2			119	100.0	5	
	27.5-30	dead	40	2	5	54	13			114	100.0	5	
	30-32.5	dead	8	-	8	100	2			118	100.0	4	
	32.5-35	dead	~		19	75	8			102	100.0	3	
	35-37.5	dead			171	85	5			107	100.0	3	
	37.5-40	dead		3	47	49	28			127	100.0	4	

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Table B5
Numbers of living and dead foraminifera for Core BAM 8C

Core site	Depth (cm)	Status	M. fus.	A. sal.	T. inf.	Т. сот.	T. mac.	H. man.	A. mex.	Egg.	Total	Percentage	Specie
BAM 8C	0–2.5	live			16	4	14				34	34.3	3
S. patens		dead	1		27	10	23		4		65	65.7	5
near creek		total	1		43	14	37		4		99	100.0	5
	2.5 - 5.0	live	1		8	4	4				17	16.7	4
		dead	2		19	8	51		5		85	83.3	5
		total	3		27	12	55		5		102	100.0	5
	5.0-7.5	live											
		dead											
		total											
	7.5-10	live			10	6	9				25	16.0	3
		dead	6		37	33	53		2		131	84.0	5
		total	6		47	39	62		2		156	100.0	5
	10-12.5	live			18	1	8				27	15.8	3
		dead	1		45		97		1		144	84.2	4
		total	1		63	1	105		1		171	100.0	5
	12.5-15	live	•		12	-	3				15	14.9	2
	12.5 15	dead			27	2	57				86	85.1	2 3
		total			39	2	60				101	100.0	3
	15-17.5	live			14	-	6				20	18.7	2
	15 17.5	dead			35	1	51				87	81.3	3
		total			49	1	57				107	100.0	3
	17.5-20	live			10	1	57				11	6.2	2
	17.3-20	dead	1		75	22	65	2	2		167	93.3	6
		total	1 1		85	22	65	2 2	2 2		178	100.0	6
	20-22.5		1		85			2	2		178	5.8	
	20-22.5	live				1	1						3
		dead			59	22	74	1 1	6		162	94.2	5
	22.5.25	total			67	23	75	1	6		172	100.0	5
	22.5-25	live	•		2	22	22		~		2	1.7	1
		dead	3		40	33	33		5		114	98.3	5
		total	3		42	33	33		5		116	100.0	5
	25-27.5	live			1	1			1		3	3.1	3
		dead	4	2	22	15	47		7	1	98	97.0	7
		total	4	2	23	16	47		8	1	101	100.0	7
	27.5-30	live			1						1	0.9	1
		dead	10	2	22	17	31	2	24		108	99.1	7
		total	10	2	23	17	31	2	24		109	100.0	7
	30-32.5	live			1				1		2	1.8	2
		dead	6	2	28	11	42		19		108	98.2	6
		total	6	2	29	11	42		20		110	100.0	6
	32.5-35	live			3	1					4	3.9	2
		dead	2		20	26	39	1	10		98	96.1	6
		total	2		23	27	39	1	10		102	100.0	6
	35-37.5	dead			40	15	58		2		115	100.0	4
	37.5-40	dead			50	10	51				111	100.0	3
	40-42.5	dead			88	43	46	2	2		181	100.0	5
	42.5-45	dead	1		88	37	70	7			203	100.0	5

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Table B6 Numbers of living and dead foraminifera for Core BAM M

Core site	Depth (cm)	Status	M. fus.	A. sal.	T. inf.	T, com.	T. mac.	H. man.	A mex.	P ipo.	T earl.	Egg.	Calc.	Total		Species	Cal. P. orb.	Cal. E. exc.	Cal.	Cal. A. bec.
BAM M	0-2.5	live	<u>jus.</u> 4	2	<u> </u>	1	5	mun.	1	ιро.	eari.			19	age 17.3	6	P. OID.	E. exc.	Quel.	A. Dec.
Mudflat	0-2.5	dead	13	8	28	8	32		1		1			91	82	7				
S. altern		total	17	10	34	9	37		2		ì			110	100.0	7				
	2.5-5.0	live	6	1	12	4	7	3						33	28.0	6				
		dead	9	10	17	7	40		2					85	72.0	6				
		total	15	11	29	11	47		5					118	100.0	6				
	5.0–7.5	live	4	4	8	3	10				1			30	26.8	6				
		dead	8	8	21	2	43							82	73.2	5				
	7.5-10	total	12 2	12 1	29 13	5 2	53 7		4		1			112 29	100.0	6				
	7.3-10	live dead	2 9	18	13 30	2 8	21		4 5					29 91	26.4 82.7	6 6				
		total	11	19	33	10	28		9					110	82.7 109.1	6				
	10-12.5		11	19	5	4	1		,					10	9.8	3				
	10 12.5	dead	9	25	24	5	28	1						92	90.2	6				
		total	9	25	29	9	29	Î						100	100.0	6				
	12.5-15	live	-		7	2		-	1					10	8.8	3				
		dead	5	15	33	13	34		4					104	91.2	6				
		total	5	15	40	15	34		5					114	100.0	6				
	15-18	live			7	1	4		1					13	12.9	4				
		dead	4	14	25	7	35		3					88	87.1	6				
		total	4	14	32	8	39		4					101	100.0	6				
	15-20	live	_	_	5	1	1		1					8	6.8	4				
		dead	7	7	51	8	33		2			1		109	93.2	7				
		total	7	7	56	9	34		3			1		117	100.0	7				
	20-22.5	live	10	15	2	0	1		1					4	3.8	3				
		dead	12	15	44	8	16		5				1	101	96.2	7				1
	22.5-25	total	12	15	46	8	17 4		6				1	105 15	100.0	7				1
	22.3-23	live dead	9	23	10 40	1 5	4 37		1					115	11.5 88.5	3 6				
		total	9	23	50	6	41		1					130	100.0	6				
	25-27.5		í	25	8	ĩ	4		2					16	15.1	5				
	20 27.5	dead	6	11	30	5	31		4				3	90	84.9	8	2	1		
		total	7	11	38	6	35		6				3	106	100.0	8	2	1		
	27.5-30	live	1		3	1	3							8	7.0	4				
		dead	7	6	30	9	32		2				20	106	93.0	8	15	5		
		total	8	6	33	10	35		2				20	114	100.0	8	15	5		
	30-32.5	live			5	1	2							8	7.0	3				
		dead	11	4	42	3	19						27	106	93.0	8	18	8	1	
		total	11	4	47	4	21						27	114	100.0	8	18	8	1	
	32.5-35	live			4	_								4	3.7	1				
		dead	11	9	31	7	21		1				25	105	96.3	8	21	4		
	26 27 6	total	11	9	35	7	21		1				25	109	100.0	8	21	4		
	35–37.5	live	0	42	2	1	22		I				4	3 124	2.4 97.6	2 9	3			
		dead total	9 9	42 42	31 33	13 14	23 23		1			1 1	4	124	97.6 100.0	9	3	1		
	37.5-40	live	2	42	33	2	1		I			1	4	6	5.8	3	3	1		
	57.5-40	dead	5	10	30	17	29		3				4	98	94.2	7	4			
		total	5	10	33	19	30		3				4	104	100.0	7	4			
	4042.5	live	1	10	2	1	50		D					4	3.8	3				
		dead	6	8	32	12	36		4				3	101	96.2	8	2	1		
		total	7	8	34	13	36		4				3	105	100.0	8	2	I		
	42.5-45	live			3		1							4	3.8	2				
		dead	2	7	33	14	45					1		102	96.2	6				
		total	2	7	36	14	46					1		106	100.0	6				
	45-50	live			1		t							2	1.8	2				
		dead	9	1	40	14	33		4				10	111	98.2	8	6	4		
	50 	total	9	1	41	14	34		4				10	113	100.0	8	6	4		
	50-55	total	8	4	22	20	35		3				3	105	100.0	7	3			
	55-60	total	7	16	31	17	31		1					103	100.0	6				

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Table B7 Dry weights of various size fractions for samples from cores HE, 3KMH, and 5KMH

Core HE				Core KMH	13			Core KMH 5				
Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked wt (g)	Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked wt (g)	Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked w (g)	
0.00	6.110	7.250	0.043	0.00	3.511	6.536	0.021	0.00	2.056	6.370	0.030	
0-2.5	3.999	1.442	0.015	0-2.5	3.044	1.386	0.061	0-2.5	0.278	1.555	0.031	
2.5-5.0	2.980	3.577	0.011	2.5 - 5.0	3.565	1.995	0.058	2.5-5.0	0.557	2.184	0.009	
5.07.5	4.469	5.800	0.073	5.0-7.5	2.808	2.382	0.054	5.0-7.5	0.643	1.925	0.046	
7.5-10	3.595	2.180	0.013	7.5-10	0.188	1.695	0.072	7.5-10	1.133	1.822	0.109	
10-12.5	3.158	2.099	0.011	10-12.5	1.828	1.082	0.018	10 - 12.5	1.085	1.538	0.890	
12.5-15	3.172	1.675	0.012	12.5-15	1.960	0.775	0.023	12.5-15	0.601	1.165	0.029	
15-17.5	4.559	2.137	0.010	15-17.5	1.258	0.512	0.065	15-17.5	1.343	2.218	0.024	
17.5-20	3.940	2.315	0.006	17.5-20	2.655	0.540	0.007	17.5-20	1.238	2.161	0.031	
20-22.5	5.359	4.035	0.036	20-22.5	3.367	0.973	0.093	20-22.5	1.362	3.080	0.042	
22.5-25	3.650	4.755	0.010	22.5-25	2.135	1.205	0.024	22.5-25	2.089	6.900	0.236	
2527.5	3.567	7.011	0.005	25-27.5	1.961	2.608	0.051	25-27.5	0.860	3.404	0.084	
27.5-30	2.035	4.785	0.035	27.5-30	1.855	1.477	0.072	27.5-30	1.702	1.872	0.087	
30-32.5	2.312	3.124	0.060	30-32.5	0.911	1.316	0.200	30-32.5	0.008	3.964	0.033	
32.5-35	2.034	1.719	0.007					32.5-35	2.020	2.496	0.033	
35-37.5	1.963	4.585	0.197					35-37.5	1.502	2.956	0.017	
								37.5-40	1.354	4.390	0.042	

Table B8 Dry weights of various size fractions for samples from cores BAM BR, BAM 8C, BAM M

Core BAM	1 BR			Core BAM	I 8C			Core BAM M				
Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked wt (g)	Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked wt (g)	Depth (cm)	Coarse wt (g)	Fine wt (g)	Picked wt (g)	
0-2.5	0.384	0.85	0.004	0-2.5	1.054	1.543	0.013	0-2.5	0.514	41.910	0.260	
2.5-5	1.01	0.505	0.003	2.5-5	2.665	3.890	0.008	2.5-5	1.923	62.775	0.257	
5-7.5	1.06	1.059	0.012	5-7.5	1.033	2.239		5-7.5	1.965	64.457	0.244	
7.5-10	1.309	0.925	0.009	7.5-10	2.078	4.746	0.024	7.5-10	1.799	72.792	0.366	
10-12.5	1.214	0.61	0.002	10-12.5	1.275	1.681	0.017	10-l2.5	0.623	57.170	0.185	
12.5-15	1.763	2.027	0.004	12.5-15	2.040	3.641	0.125	12.5-15	0.562	43.168	0.226	
15-17.5	1.156	2.101	0.005	15-17.5	2.226	9.565	0.199	15-17.5	0.731	66.122	0.186	
17.5-20	1.088	2.17	0.006	17.5-20	1.770	6.311	0.096	17.5 - 20	0.680	52.971	0.210	
20-22.5	1.023	2.18	0.005	20-22.5	0.938	4.535	0.027	20-22.5	0.434	46.877	0.182	
22.5-25	0.675	1.612	0.016	22.5-25	1.454	10.293	0.307	22.5-25	1.279	55.538	0.325	
25-27.5	0.934	1.891	0.017	25-27.5	1.247	4.428	0.219	25-27.5	4.904	63.248	0.200	
27.5-30	0.476	1.543	0.013	27.5 - 30	1.540	5.564	0.451	27.5 - 30	9.519	37.386	0.213	
3032.5	0.533	1.326	0.014	30-32.5	1.156	4.422	0.237	3032.5	19.298	31.872	0.222	
32.5-35	0.531	1.217	0.014	32.5-35	0.942	6.808	0.415	32.5-35	33.792	46.832	0.174	
35-37.5	0.57	1.325	0.011	35-37.5	0.567	2.736	0.048	35-37.5	1.801	42.691	0.209	
37.5-40	0.359	1.45	0.011	37.5-40	0.628	2.161	0.017	37.5-40	0.581	41.191	0.193	
40-45	1.42	2.721		40-42.5		1.191	0.010	40-42.5	1.305	51.034	0.241	
45-50	2.413	2.005		42.5-45		1.090	0.039	42.5-45	1.587	30.516	0.164	
5055	1.071	2.013						45-50	5.461	53.423	0.282	
55-60	4.744	1.308						50-55	6.432	49.050	0.148	
60-65		1.476						55-60	0.900	100.731	0.237	
65-70	1.829	2.942										
70-75	1.335	3.156										
7580	0.977	2.107										

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