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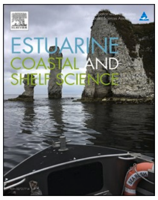

Saltmarsh foraminifera in the subarctic White Sea: Thrive in summer, endure in winter

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ABSTRACT

Abundance and diversity of intertidal benthic foraminifera decreases towards the poles. Well studied in the temperate zone, saltmarsh foraminiferal assemblages have only recently received attention at higher latitudes. We report modern foraminifera, including the taxonomy, abundance, and zonation, from a pristine saltmarsh in the subarctic White Sea, northern Europe. We sampled 10 stations (surface sediment, two replicates) from two high-tide flats covered with lush halophytic plants. Nine foraminiferal species found exhibited distinct vertical zonation confined to certain elevation levels. The high marsh assemblage comprised arenaceous *Balticammina pseudomacrescens*, *Trochammina inflata*, *Jadammina macrescens*, and monothalamous *Ovammina opaca*. This is the northernmost location where the first two species have been encountered alive. The low marsh assemblage was dominated by *Miliammina fusca* and *Elphidium williamsoni*. Summer abundances of live foraminifera were surprisingly higher than on other subarctic saltmarshes studied, mostly 100–500 and up to 3000 per 10 cm^3. In winter, under a 40 cm of ice, the abundances were only 15–20 ind./10 cm^3, but the species richness was the same. Unlike summer specimens of calcareous foraminifera, which are always brightly colored, winter *Elphidium williamsoni* all had bleak colorless cytoplasm, suggesting they discard kleptoplasts and abandon algal diet. We conclude that the insulating blanket of fast ice, which hardly moves on saltmarshes, prevents elimination of foraminifera in the harshness of winter, whereas the intense continental heating in summer lets them thrive on White-Sea saltmarshes. The composition of foraminiferal assemblages under local climatic conditions may thus deviate substantially from the latitudinal trend.

1. Introduction

While the latitudinal gradient in species richness is widely recognized in large-body-sized animals and plants across habitats and locations (Gaston, 2000; Hillebrand, 2004; Schemske et al., 2009), its manifestation in protists and meiofauna is less clear. The number of protist species can show weak (Hillebrand, 2004) or no consistency with latitudinal gradients, i.e. “everything is everywhere” (Finlay et al., 2004; Fenchel, Finlay, 2004). According to other studies, however, many protists are geographically restricted (Foissner, 2006; Pawlowski, Holzmann, 2008). Accurate biodiversity assessment is evidently hampered by undersampling, especially in remote areas of the world (Fenchel, Finlay, 2004; Foissner, 2006).

Benthic foraminifera are protists common in marine ecosystems from the deep sea to marginal habitats like intertidal mudflats and saltmarshes. Both deep-sea (Culver, Buzas, 2000; Buzas et al., 2002) and marginal (Lübbers, Schönfeld, 2018) foraminifera exhibit latitudinal diversity shifts. There are hundreds of species in tropical marginal settings (Debenay, 1990; Javaux, Scott, 2003) and fewer in mid latitudes (Goldstein, Watkins, 1999). Polewards in the mid latitudes, the number of species decreases to dozens (e.g. Alve, Murray, 1999; Lehmann, 2000). The northernmost surveys on live saltmarsh foraminifera from southern Scandinavia and Iceland (55–64°N) report 3 to 7 species (Alve, Murray, 1999; online supplementary materials in Murray, 2006; Lübbers, Schönfeld, 2018). Abundances of saltmarsh foraminifera also apparently drop with latitude: 18,000 ind./10 cm^3 at 37°N (Camacho et al., 2014), 16,000 at 47°N (Leorri et al., 2010), 600–2700 at 54°N (Lehmann, 2000), and 1–98 at 64°N (Lübbers, Schönfeld, 2018).

While the assemblages of temperate saltmarsh foraminifera have received much attention, relatively patchy (Scott et al., 2014) and

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narrow (Funk et al., 2004) saltmarshes from subpolar and polar coasts are much less studied. There are several sea-level reconstructions in southern Alaska, Canada's eastern coast, and northern Scandinavia, but they omit living foraminiferal data (Kemp et al., 2013; Barnett et al., 2015, 2019). Only three papers are available that deal with living saltmarsh foraminifera in the subarctic belt. They all report low diversities and low densities. Five species were recorded in the subarctic Canada (Hudson-James bays, 55°N): *Balticammina pseudomacrescens*, *Jadammina macrescens* and *Polysaccamina ipohalina* in the high marsh, and *Ammotium salsum* and *Miliammina fusca* in the low marsh (Scott, Martini, 1982, with the taxonomy amended after Murray, 2006). The densities were rather low, 50–180 ind./10 cm^3. In Iceland (64°N), Lübbers and Schönfeld (2018) recorded seven live species: *Jadammina macrescens*, *Miliammina fusca*, *Haynesina orbicularis*, *Trochammina adaperta*, *Trochammina astrifica*, *Trochamminita irregularis*, and *Deuterammina ochracea*. Densities were 1–98 ind./10 cm^3. Further north, at 68°N (Vesterålen Archipelago, Norway) Barnett (2013) observed two high marsh species: *J. macrescens* and *M. fusca*; densities were not reported. Clearly, there is a lack of data on subpolar regions, which impedes our progress in understanding the latitudinal diversity and abundance gradients in modern saltmarsh foraminifera.

In the subarctic White Sea, saltmarsh foraminifera have received little attention. As a part of sea-level reconstruction study, Kemp et al. (2017) reported dead saltmarsh foraminifera from the eastern White Sea. Here, we provide a thorough account of living saltmarsh foraminifera, including the taxonomy, abundance, and zonation, from pristine saltmarshes at 66°N and test the hypothesis that saltmarsh foraminiferal assemblages are uniform within subarctic latitudes.

In addition, as it is totally unknown what happens to saltmarsh foraminifera under winter ice, here we for the first time report the results of winter sub-ice samplings.

2. Study area

The White Sea is a glacially-eroded marginal basin, connected to the Barents Sea, with decreased surface salinities due to isolation and heavy runoff (Babkov, Lukanin, 1985), mostly covered with ice from November until April–May. The sites studied are located in its western part [Chupa Inlet of the Kandalaksha Bay (Fig. 1)], where mean annual air temperature is −0.4 °C, ranging from 14 to 15°C (up to +35 °C) in summer to −13°C (with a minimum of −47°C) in winter (Filatov et al., 2005). The sheltered parts of the intricate shoreline here have sandy or muddy flats edged landwards with upper intertidal meadows (saltmarshes). These are covered by dense stands of halophytic plants and may span hundreds of meters across. The high marsh is fully covered with seawater twice a month and the low marsh is exposed to seawater daily. The study area is affected by the discharge of the Keret river making surface waters brackish and nearly fresh in spring (Babkov, Lukanin, 1985). The thickness of the winter fast ice here is 40–50 cm (Naumov, 2013). Tides are semidiurnal, but the tidal cycle is remarkably asymmetrical (Howland et al., 1999). The spring tide amplitude is 1.6 m, and neap 1.0 m.

3. Material and methods

We sampled two saltmarshes (Fig. 1). One was a relatively large meadow (about 200 m perpendicular to the coastline) gently sloping from the head of the Sukhaya Salma embayment (66°18′ N, 33°40′ E). The other was steeper and narrower (some 100 m across) located on the isthmus of the Matrenin Island (66°18′ N, 33°38′ E). The crest of the isthmus only 1 m above the high tide was crowned with a narrow fringe of tundra vegetation. The environment is pristine. There are no roads, ports, or industry. The three small settlements shown on the map are accessible by sea only (Fig. 1). The sea traffic is of low intensity, exists in summer, consists of small boats driven by tourists and local dwellers.

In summer 2014, we collected vascular plants, identified them to the species level, and outlined vegetation belts. Then we set up one transect across the vegetation belts on each of the two marshes. We sampled vegetation belts. The Sukhaya Salma transect consisted of four stations and Matrenin of five. Plus, the *Plantago* belt lacking in the latter

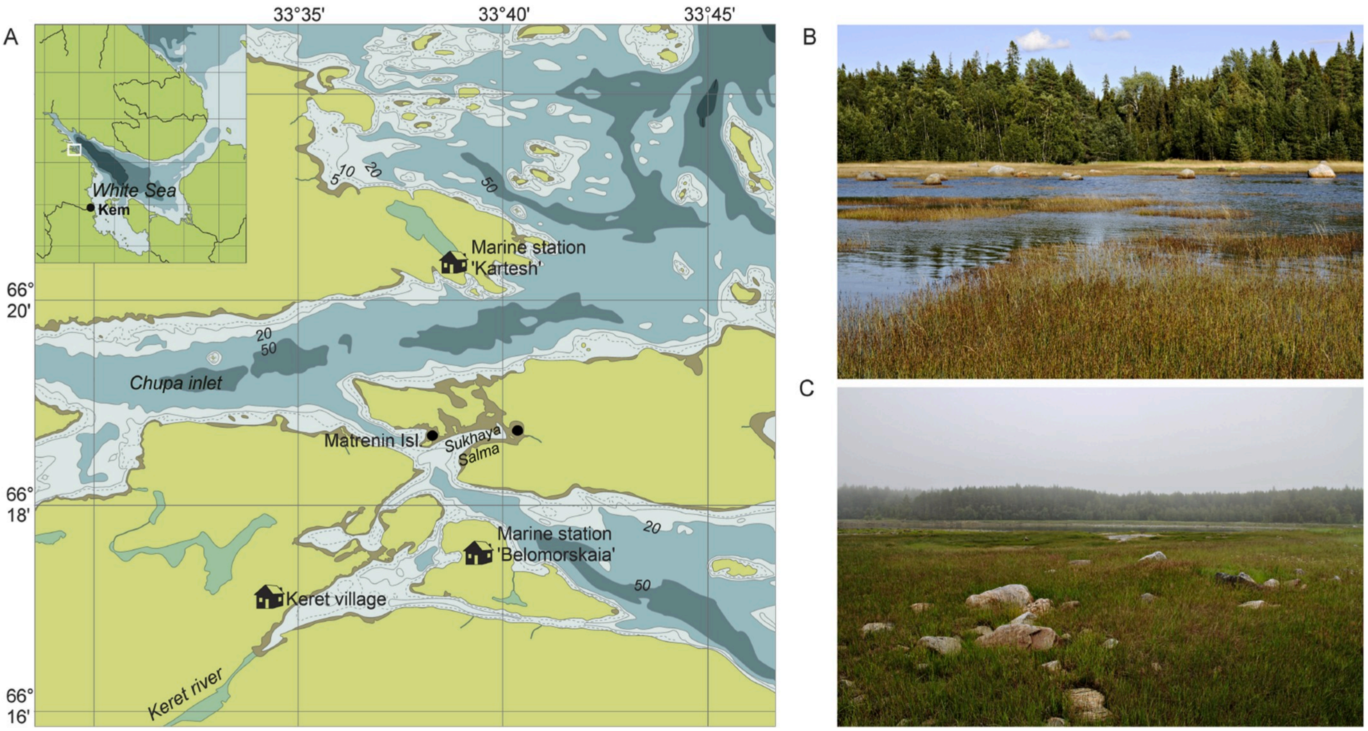

Fig. 1. A. Location of the studied saltmarshes (solid black circles) in the outer Chupa Inlet. The brown fringe marks the intertidal zone as it is shown on the nautical chart. The inset shows the White Sea with the study area boxed. **B.** Sukhaya Salma saltmarsh, high tide. **C.** Matrenin saltmarsh, low tide. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

vegetation sequence was sampled on the other slope of the Matrenin isthmus, 11.4 m away from the transect (Fig. 2). A metal tube with 3.5 cm inner diameter was pushed into the sediment. The core was immediately extruded and sliced with a 1 cm increment. Resultant 10 cm^3 samples were preserved with 70% ethanol and 2 g/l Rose Bengal stain. We obtained two replicate cores per station, ~30 cm one from the other. The surface 0–1 cm samples were used in this study. To compare the results with the winter campaign, we also included subsurface samples from one high-marsh station, which was nearest to the winter sampling site. All samples were wet sieved and wet counted. On the high marsh, we measured the salinity of pore water collected from a separate 10-cm deep pit after settling of suspended fines with a Hand-Held Salinity Refractometer "Atago MASTER-S/Mill Alpha" accurate to ±2 psu.

Preserved samples were washed with tap water through 0.5 mm (to remove plant debris) and 0.125 mm mesh sieves. The 0.125–0.5 mm fraction was retained for foraminiferal analysis. Samples were wet split into eight aliquots using Retsch PT II splitter before counting. Living and dead benthic foraminifera were counted wet in a Petri dish using the stereomicroscope Leica M205C. A minimum of 300 living and dead specimens were counted per sample or the whole sample was counted if the number of living specimens in seven aliquots was less than 300. We identified species using the illustrations of Mayer (1962), Stschedrina (1948), Brönnimann and co-authors (1984, 1989). We checked the accuracy of our identification against type material from the collection of the Natural History Museum in London. Juvenile specimens of *Jadammina macrescens, Balticammina pseudomacrescens* and *Trochammina inflata*, which are barely distinguishable, were assigned to "agglutinated indefinite". SEM images were obtained using a scanning electron microscope HITACHI TM3000.

Because of the logistic constraints there was a single quantitative under-ice sampling on the Matrenin high marsh during the oceanographic winter in March 2018 and a single qualitative under-ice sampling on the Sukhaya Salma low marsh in March 2019. We removed snow ~50 cm thick to clear the ice surface, cut through the ice with a chain saw, opened an ice window 50 × 50 cm and cut out thee replicate samples 10 cm^3 from the top centimeter of the soil. Since the top layer of soil with dead plants was frozen into the ice foot, we assume the sampled interval corresponded to 2–3 cm sediment depth in the summer cores. In 2018, samples were immediately preserved in rose Bengal stained ethanol. This technique may produce false positives (Murray, Bowser, 2000; Bernhard et al., 2006), so in 2019, we delivered an untreated sample in an insulated box to the field station, wet sieved it in cool sea-water, picked out foraminifera, left them in a cool room for half hour, then looked for deployed pseudopods to detect live specimens.

All tidal levels were acquired using WXTide32 program, and all elevation values were set to the regional chart datum. For the White Sea, WXTide32 refers to a single tide station, the port of Kem, about 160 km to the south, which has a >100 years long tide record. The tidal datum (mean high water at spring tides, mean high water at neap tides, etc.) was calculated following Frey and Basan (1978) for the period of the three summer months of the sampling year. Kartesh Marine Station situated in about 3 nautical miles from the studied marshes (see Fig. 1 for location) has a time offset of −1:03 h versus the Kem tide gauge for high water and −0:39 h for low water, whereas the tidal range is the same, as has been measured with a data-logger (Naumov, 2013, unpublished). We accepted these time offsets. Intricate shoreline and

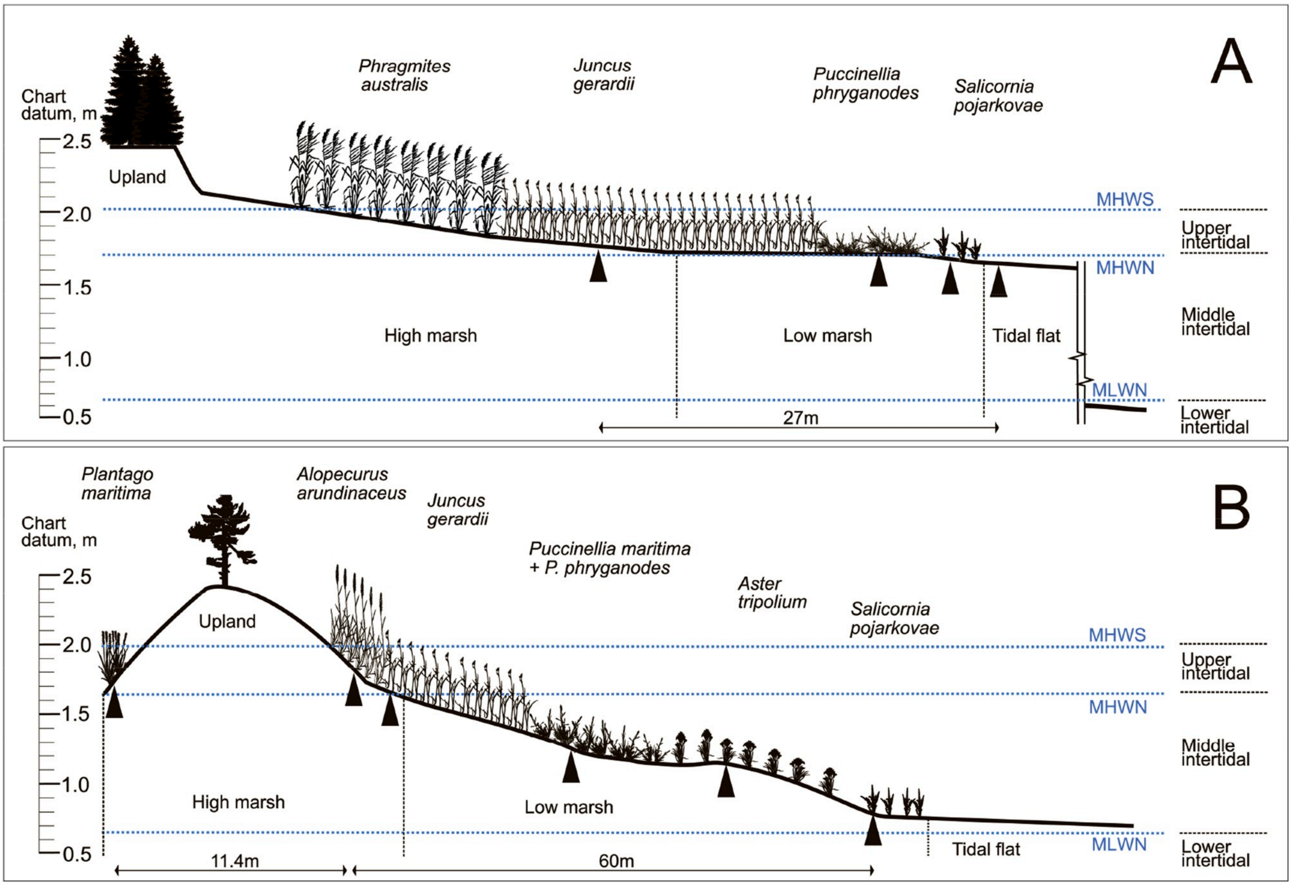

Fig. 2. Schematic transects of the White Sea saltmarshes. A. Sukhaya Salma. **B.** Matrenin. Vegetation belts are labeled above the transects. Arrowheads are foraminiferal sampling stations. Regional tidal levels calculated with WXTide32 are shown in blue color: MHWS mean high water at spring tides, MHWN mean high water at neap tides, MLWN mean low water at neap tides. The boundary between the high marsh and low marsh is MHWN. Intertidal zones are labeled on the right. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

complex sea-floor topography may modify tides, and the tidal dynamics at the marshes may deviate from that at the Marine Station. At the transects, we always checked WXTide32 time prediction, but did not make direct water level measurements and were unable to verify WXTide32 level prediction. Elevations were measured using the optical RGK-C20 level with a precision of ±2 mm per 1 km double levelling. Accuracy of levelling was ±5 mm. The stations were positioned with GPS-navigator Garmin Legend HGx, precision 0.001'. Our WXTide32 elevation values can be converted to topographic elevations by applying a −1.17m correction, which is the difference between the chart datum used by WXTide32 (lowest astronomical tidal level) and the mean sea level of the Baltic System of Heights (BSH-77) used in national topographic maps. Precise recalculation does not seem to be possible, as the levelling surveys for the topographic maps were performed in the 1960s. The residual glacial isostatic uplift in the western White Sea is 3–4 mm per year (Kolka et al., 2012; Romanenko, Shilova, 2012), which makes altitude points shown on topographic maps imprecise for +20 to +30 cm.

To visualize variation in foraminiferal assemblage composition (Legendre, Legendre, 2012) we used nonmetric multidimensional scaling (nMDS) based on Brey-Curtis dissimilarities calculated from square root transformed and double standardized abundances of living foraminifera. Double standardization (Bray, Curtis, 1957) by species and samples achieves a common scale for rare and abundant species and makes the stations with different number of samples comparable. Stress values <0.2 indicated an interpretable ordination. The analysis was performed in the `vegan` package (Oksanen et al., 2019) for R (R Core Team, 2019).

To classify the foraminiferal assemblages, we clustered the samples using unweighted pair group average method (UPGMA) on the matrix of chord distances computed on absolute abundance data, and compared it with relative abundances of species. To choose a distance metric, we tested performance of chord distance and Bray-Curtis dissimilarity in clusterization using cophenetic correlation (Pearson's correlation between the dissimilarity matrix recovered from the dendrogram and the original dissimilarity matrix). Chord distance was better reflected on the dendrogram. Cophenetic distances were computed using the `ape` package (Paradis et al., 2004). Branch support values were calculated using multiscale bootstrap resampling (Shimodaira, 2004) in the `pvclust` package for R (Suzuki, Shimodaira, 2015) with 50000 iterations to ensure accurate estimation of approximately unbiased p-values (AU p-values).

Shannon-Wiener index of species diversity was computed as $H' = \Sigma p_i \ln(p_i)$, where p_i is a proportion of an i-th species in a sample (Shannon, 1948). Buzas-Gibson evenness index was calculated as $E = \exp(H')/S$, where S is the total number of species (Buzas, Hayek, 2005).

Growing Degree Days (GDD) heat index was calculated as the integral of warmth above a base temperature using www.degreedays.net. In our comparison we used a 5-year-average (2013–2017) of growing degree days for a base temperature of 0.0 °C (Supplementary material 1).

4. Results

4.1. Saltmarsh description: elevations, vegetation, and salinity measurements

Vascular plants formed belts in both transects (Fig. 2). In the Sukhaya Salma, the highest belt was dense stands of the common reed *Phragmites australis* between 2 m and 1.8 m elevations. The wide carpet of the saltmarsh rush *Juncus gerardii* descended to 1.73 m. Seawards, *Puccinellia phryganodes* was followed by *Salicornia pojarkovae* below 1.69 m. The tidal flat without vascular plants stretched below 1.67 m. In the Matrenin saltmarsh, there were belts of the foxtail *Alopecurus arundinaceus* at 2.0–1.7 m, sea plantain *Plantago maritima* at 1.8–1.7 m, and *Juncus gerardii* at 1.7–1.4 m. There were mixed stands of *Puccinellia phryganodes* and *Puccinellia maritima* from 1.4 m down to 1.19 m. Scattered tufts of sea aster *Aster tripolium* occurred at 1.19–0.79 m and *Salicornia pojarkovae* at 0.79 m. There was a tidal flat below. The shore slope was 1.72 m/km in the Sukhaya Salma and 12.02 m/km in the Matrenin saltmarsh.

We calculated the tidal datum for the Chupa Inlet for the three summer months of 2014: Mean High Water Spring (MHWS) 2.0 m; Mean High Water Neap (MHWN) 1.67 m; Mean Low Water Neap (MLWN) 0.61 m; Mean Low Water Spring (MLWS) 0.39 m. The time of high waters did not deviate from WXTide prediction for Kartesh Marine Station. Porewater salinity of the high marsh soil was 19 psu in the Sukhaya Salma and 24 psu in the Matrenin Island.

4.2. Saltmarsh foraminiferal assemblages

4.2.1. Taxa, absolute abundance, relative abundance, and diversity of living foraminifera

We found eight living species in the Sukhaya Salma and seven in the Matrenin saltmarsh (Plate 1). With a six species overlap, it was a total of nine species.

Abundances of living foraminifera ranged from 74 to 3040 ind./10 cm^3 (Fig. 3; supplementary material 2). Highest in the middle of low marsh, it tended to decrease both towards the high marsh and tidal flat. Abundances of low marsh species were remarkably high: *Miliammina fusca* reached 1100 ind./10 cm^3 in *Puccinellia*, and *Elphidium williamsoni* had 2000 ind./10 cm^3 in *Salicornia*. Abundances of high marsh species did not exceed 300 ind./10 cm^3.

Either *Balticammina pseudomacrescens* or *Jadammina macrescens* dominated the high marsh (Fig. 4). The low marsh was dominated by *Miliammina fusca* and *Elphidium williamsoni.* This distinct change in the dominant taxa segregated the assemblages of the high marsh and low marsh. Subordinate species, which accounted for 1–10%, were the monothalamous *Ovammina opaca* (on both transects) and *Trochammina inflata* (on one transect). Other species were accessory with <1%.

The assemblages were monospecific sensu Hayward (2014). The high marsh dominant was *Balticammina pseudomacrescens* (>60%) in one marsh and *Jadammina macrescens* (>80%) in the other. The low marsh dominant was *Miliammina fusca* (>80%). The H' diversity ranged from 0.25 to 1.25, and high marsh was slightly more diverse than low marsh (Figs. 3 and 4).

4.2.2. Multivariate community structure

Ordination (nMDS) revealed two groups of samples, high marsh and low marsh. Elevated abundances of the agglutinated species *Jadammina macrescens*, *Balticammina pseudomacrescens*, *Trochammina inflata* were characteristic of the high marsh, whereas *Miliammina fusca* and *Elphidium williamsoni* of the low marsh (Fig. 5). Similarly, cluster analysis indicated two main clusters with AU p-values of 93% and 94%, respectively (Fig. 6). Cluster 1 consisted of 9 samples and comprised mainly high marsh stations with elevations between 1.6 m and 1.8 m. Cluster 1 was dominated by *J. macrescens* with relative abundances 46%–96%, co-dominated by *B. pseudomacrescens* (max 61%), and characterized by the presence of *O. opaca* (max 28%) and *T. inflata* (max 6%). Cluster 2 consisted of 11 samples and included only low marsh stations with elevations between 0.8 m and 1.7 m. This cluster was dominated by *M. fusca* (max 92%) and *E. williamsoni* (max 67%). Thus both ordination and cluster analysis revealed two distinct assemblages, high marsh and low marsh.

4.2.3. Absolute and relative abundance of dead foraminifera

The absolute abundances of empty arenaceous tests reached their maximum values at high marsh stations and decreased towards low marsh in both transects (Fig. 3). The proportions of arenaceous species were similar to those in the living fauna (Fig. 4) indicating little taphonomic bias. The Sukhaya Salma was barren of calcareous tests, and a few empty tests of *E. williamsoni* occurred in the Matrenin. The lack of empty calcareous tests suggests their quick postmortem dissolution.

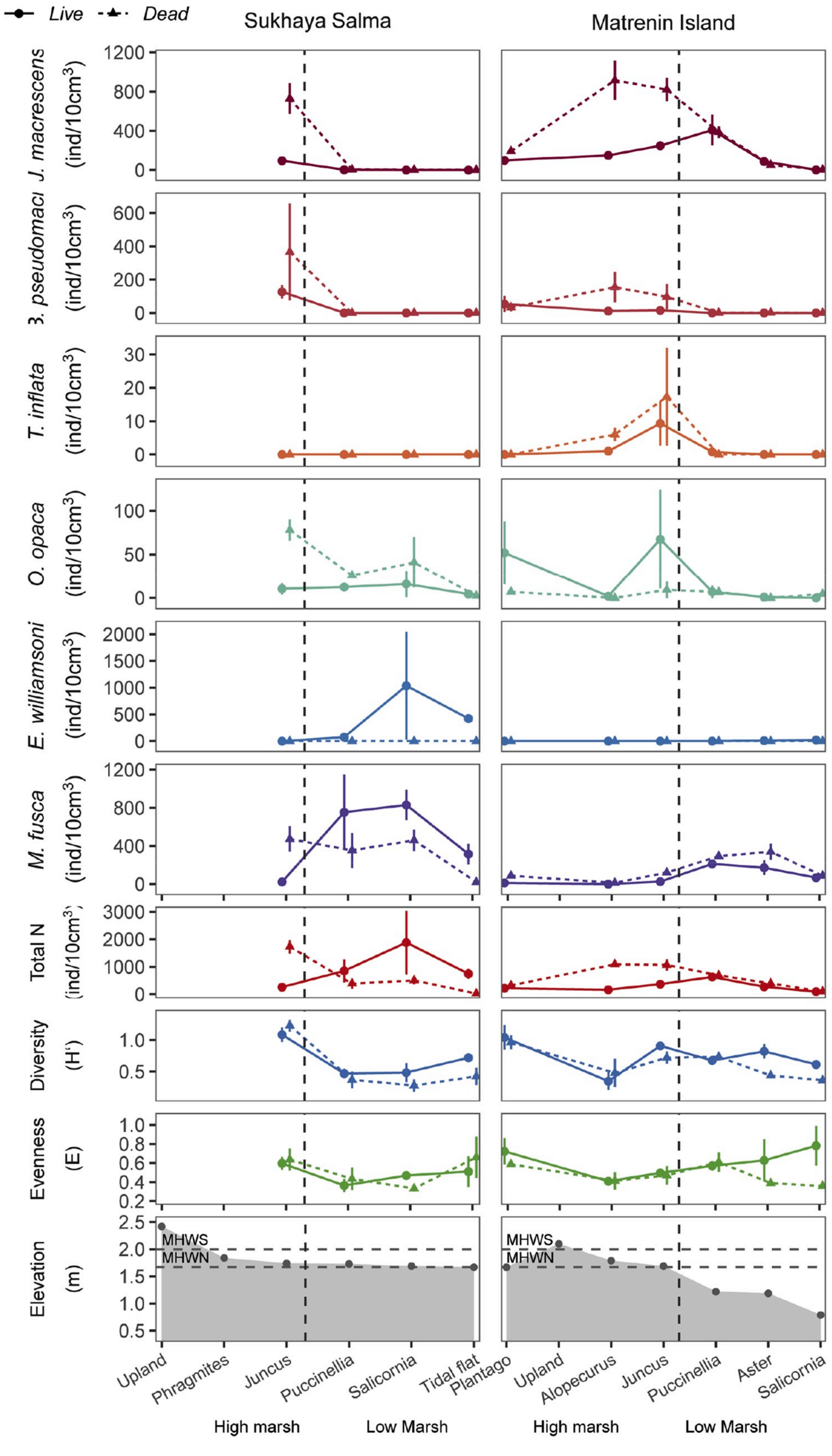

Fig. 3. Living and dead abundances (ind./10 cm^3) of common foraminiferal species on the two saltmarshes. Shannon-Wiener's diversity and Buzas-Gibson's evenness are shown. Vertical bars denote min/max range for replicate samples. The vertical dashed line separates high marsh and low marsh. Stations are arranged along the sampling transect. The elevation profile is shown at the bottom.

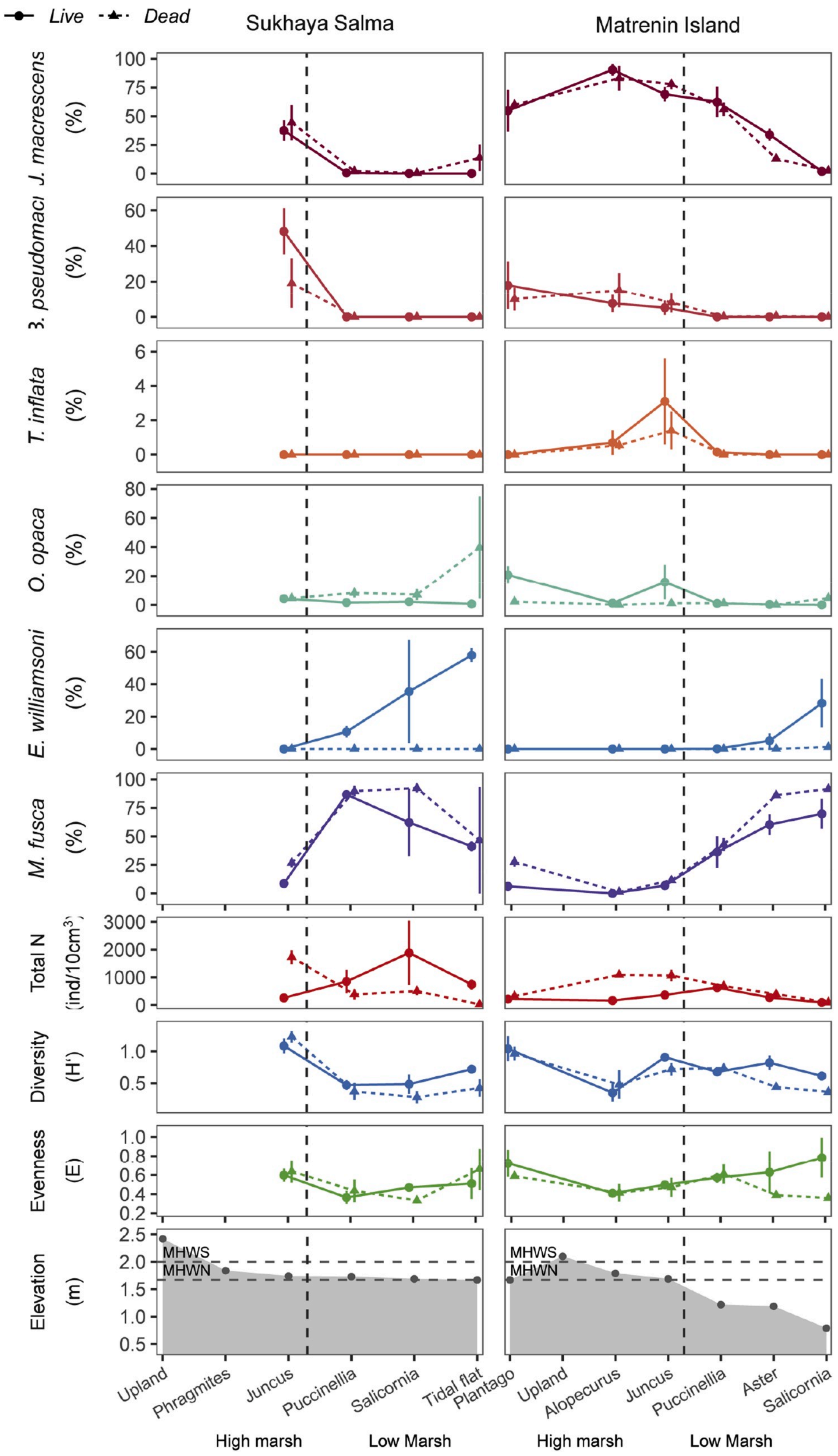

Fig. 4. Relative abundances of common foraminiferal species on the two saltmarshes. Shannon-Wiener's diversity and Buzas-Gibson's evenness are shown. Vertical bars denote min/max range for replicate samples. The vertical dashed line separates high marsh and low marsh. Stations are arranged along the sampling transect. The elevation profile is shown at the bottom.

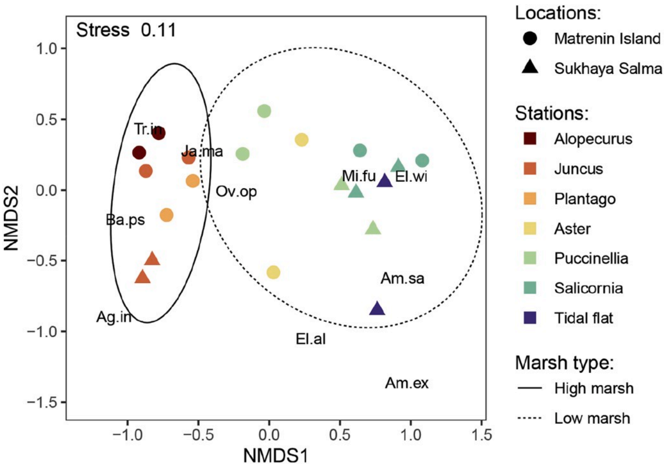

Fig. 5. Ordination of foraminiferal assemblages using the nonmetric multidimensional scaling. Distances between points are proportional to Brey-Curtis dissimilarities. Stress value estimates the goodness of fit. Shapes code location; color codes vegetation belts. The abbreviations in the plot stand for foraminiferal species; their position indicates the association of abundances with vegetation. 95% confidence ellipses are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4.2.4. *Winter densities of saltmarsh foraminifera*

In March 2018, the Matrenin high marsh was covered with a 40 cm of ice and 50 cm of snow. The sampled soil was soft, moist, and salty. Rose Bengal stained specimens were bright and did not differ from those fixed in summer, so we considered the coloration real. In total, five species were found beneath the ice, three among them had rose-Bengal-stained individuals. Abundances of stained individuals at 2–3 cm core depth beneath the upper frozen layer were 15–20 ind./10 cm^3, which were comparable to 30–80 at the same core depth in summer (Table 1). Abundances of dead individuals were high and similar to those observed in summer (Table 1; supplementary material 2). The qualitative unpreserved samples from the Sukhaya Salma low marsh in March 2019 contained *Elphidium williamsoni*, *Miliammina fusca*, and *Ovammina opaca*. The content of their tests lacked coloration, and the specimens looked dead. However, after being left alone for 10–30 min in a cool room, all specimens deployed pseudopods and thus were alive (Fig. 7).

5. Discussion

Plant species on the studied marshes were typical of the White Sea (Sergienko, 2013). In both marshes, the vascular plants formed distinctive monospecific belts, though the dominant species somewhat varied between the two marshes (Fig. 2). This taxonomic change in the dominant taxa reflects their tolerance to inundation by saline or brackish water and subaerial exposure (e.g., Pennings et al., 2005; Porter et al., 2015). The vertical expansion of the belts also differed. The belts were compressed in the Sukhaya Salma saltmarsh and were essentially restricted to the upper intertidal zone, whereas the vegetation belts descended to as low as the mid middle intertidal zone in the Matrenin (Fig. 2). We suppose the difference is explained by the inundation time. The time of high waters did not deviated from WXTide32 prediction, and the level of high waters assumingly did not deviate

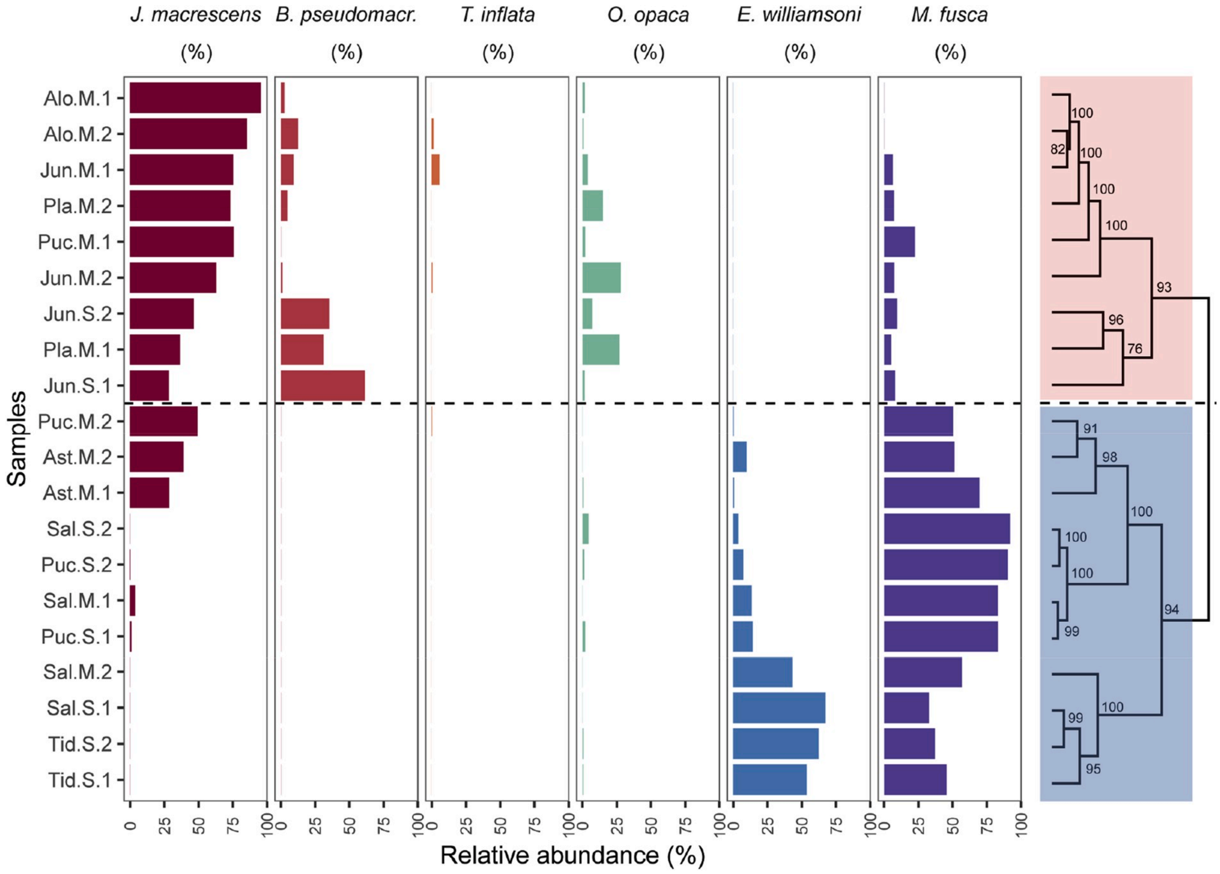

Fig. 6. Clusterization of samples, based on relative occurrence of living foraminifera. Strength of the cluster support by data is expressed in approximately unbiased p-values (AU p-values). The stations are arranged according to the cluster analysis results (station labels: plant species_saltmarsh_replicate). Pink codes the high marsh stations (upper cluster), blue – low marsh (lower cluster). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Winter and summer abundance of living and dead foraminifera (ind./10 cm^3) at 2–3 cm core depth in the Matrenin high marsh.

Location	Matrenin Island									
Vegetation belt	*Juncus gerardii*									
Season, year	Winter 2018						Summer 2014			
Replicate ID	Ma-Ju-1		Ma-Ju-2		Ma-Ju-3		Ma-Ju-1		Ma-Ju-2	
Living/Dead	**L**	**D**	**L**	**D**	**L**	**D**	**L**	**D**	**L**	**D**
Jadammina macrescens	13	653	13	843	14	1257	72	835	15	74
Balticammina pseudomacrescens	1	55	2	107	4	158	1	2		
Trochammina inflata	1	3		1	1	5				
Miliammina fusca		255		279		263	5	583	11	403
Ovammina opaca		1		2	2	6		7	2	
Forams counted	**15**	**967**	**15**	**1232**	**21**	**1689**	**78**	**1427**	**28**	**477**
Portion counted	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Forams/10 cm^3	**15**	**967**	**15**	**1232**	**21**	**1689**	**78**	**1427**	**28**	**477**
Number of species	**3**	**5**	**2**	**5**	**4**	**5**	**3**	**4**	**3**	**2**
Sediment volume, cm^3	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**

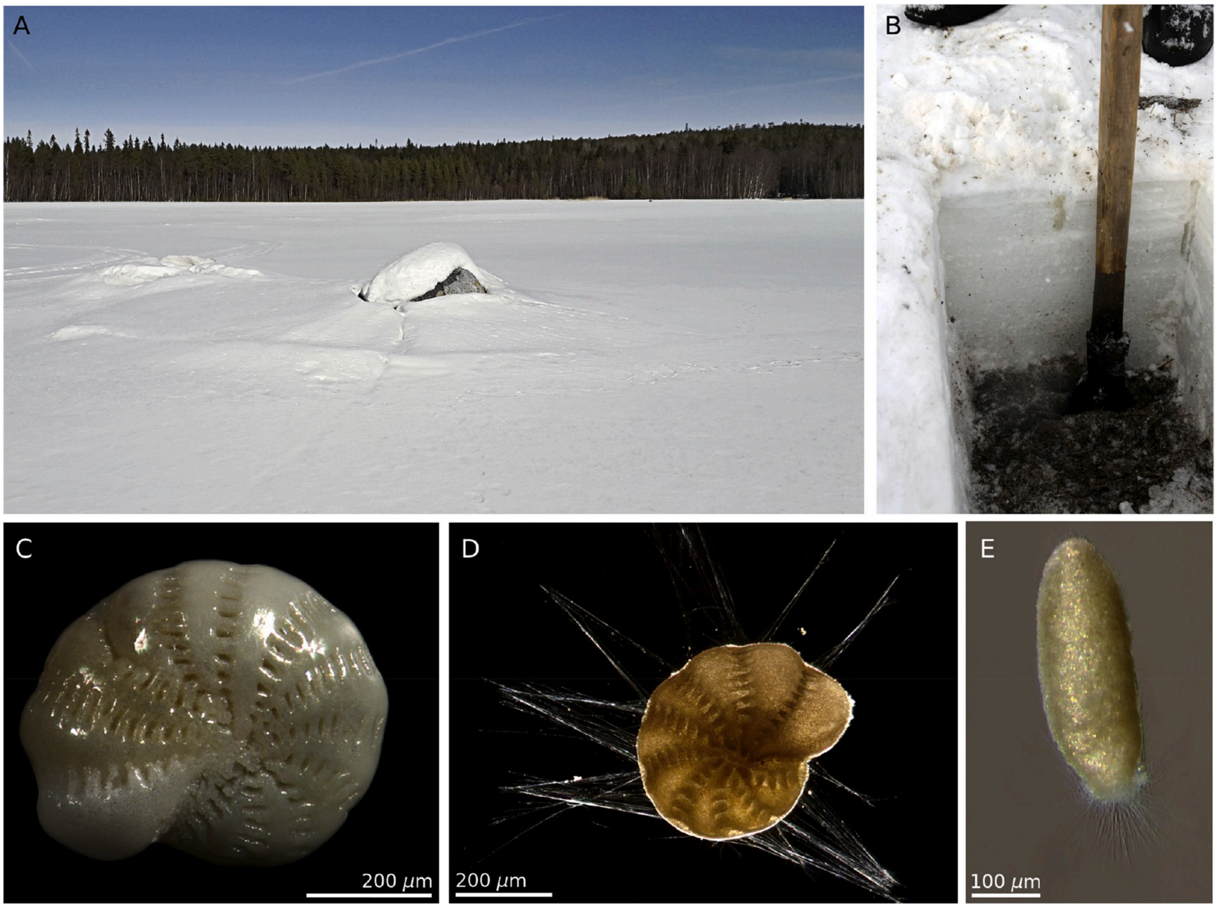

Fig. 7. Saltmarsh and its foraminifera in winter. A. The Sukhaya Salma covered with ice and snow. The continuous plate of fast ice is only disturbed by erratic boulders. **B.** The sampling site in the Matrenin high marsh. **C.** A specimen of *Elphidium wiliamsoni* with colorless cytoplasm. **D.** The same *E. williamsoni* specimen deploying pseudopods. **E.** Pseudopodial activity of *Ovammina opaca* (C, D, E. Light microscopy).

either. We did not measure low water levels though. The Sukhaya Salma marsh has a small slope. A dense line of boulders, lying where an ice pressure ridge builds in winter, isolates the marsh meadow from the outer embayment. The boulders retard water outflow. It is plausible that the ebb lags, and the mean tidal level, as the result, is higher than WXTide32 prediction. The plants are flooded for an extended period, and the belts of vegetation are compressed into the upper intertidal zone. The Matrenin marsh is steeper, has no barricade of boulders retarding the ebb, and the low boundary of saltmarsh vegetation descents to the mid middle intertidal zone, which is the mean tidal level calculated with WXTide32.

We found 9 species of foraminifera on the White Sea saltmarshes studied. This is more than have ever been found on subarctic saltmarshes and even more than recorded for several temperate locations (e.g., Alve, Murray, 1999; Saad, Wade, 2017). Standing stock we observed (up to 3000 ind./10 cm^3) is also an order of magnitude higher than any subarctic records and is comparable to temperate locations (e.g., Lehmann, 2000). Our null hypothesis is therefore rejected, since the White Sea

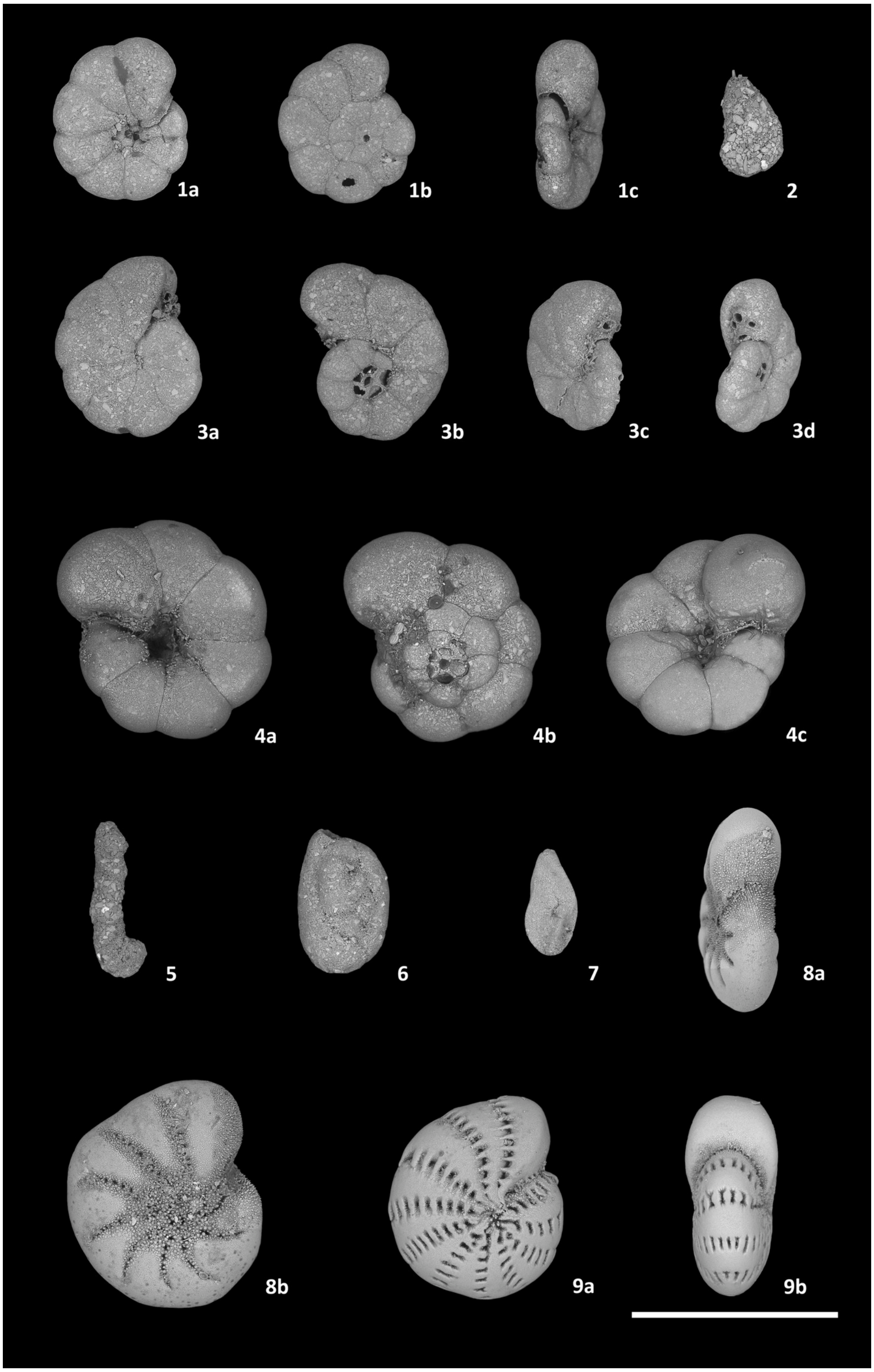

Plate 1. SEM images of living saltmarsh foraminifera of the White Sea. **1**, *Balticammina pseudomacrescens*. **2**, *Ammotium salsum*. **3**, *Jadammina macrescens*. **4**, *Trochammina inflata*. **5**, *Ammobaculites balkwilli*? **6**, *Miliammina fusca*. **7**, *Ovammina opaca*. **8**, *Elphidium albiumbilicatum*. **9**, *Elphidium williamsoni*. Scale bar 500 μm.

looks an outlier in terms of living abundances among other known subarctic saltmarsh foraminiferal assemblages. Below we discuss the potential mechanisms allowing saltmarsh foraminifera to thrive in subarctic latitudes.

5.1. *Living foraminiferal abundances and species richness*

Both standing stock and taxonomic diversity of saltmarsh foraminifera tend to decrease polewards (Lübbers, Schönfeld, 2018). Temperature is the most important abiotic factor of those correlated with latitude (Tittensor et al., 2010). Water high heat capacity makes temperatures in the marine realm, particularly in the deep sea, extremely stable. Distribution of benthic fauna often reflects the presence of certain water masses rather than latitudinal zonation. An example is the warm-water fauna that goes into the Arctic following the warm North Atlantic current (Skirbekk et al., 2010; Matul, Mohan, 2017). Of course, temperature may be just the identifier of a water mass whereas foraminiferal distribution is actually controlled by other factors, the first of which is food supply (e.g. Schnitker, 1994), yet in this paper we discuss temperature as a climatic driver that affects foraminiferal assemblages directly. The thin wedge of intertidal water has small volume and responds promptly to sunlight heating (latitude-driven) and air temperature (regional climate). We assess potential influences of latitudinal zonation and regional variability on the distribution of intertidal foraminifera taking into account several climatic variables (Table 2).

Saltmarsh foraminiferal diversities and abundances apparently are not uniform within the subarctic climatic zone. Species richness varied from 2 in northern Norway to 9 in the White Sea (this study). Foraminiferal abundances in subarctic marshes were 1–180 individuals per 10 cm^3 in Hudson Bay, 1–98 in Iceland, and not reported for northern Norway (Table 2). Foraminiferal populations were surprisingly rich in the White-Sea study area (up to 3000 living specimens per 10 cm^3) that is comparable to abundances on temperate saltmarshes (e.g., Lehmann, 2000).

Table 2

Regional climatic characteristics and foraminifera in subarctic saltmarshes. The four saltmarshes, for which living foraminiferal data are available, are arranged according to increasing latitude. Foraminiferal values are from Scott, Martini (1982) for Hudson Bay, Lübbers, Schönfeld (2018) for Iceland, Barnett (2013) for Norway, n/a not available. [1]source: NOAA (Fort Severn) for Hudson Bay; Hanna et al. (2006), Björnsson (2003) for Iceland; Filatov et al. (2005) for White Sea; www.weatherbase.com for Norway. [2–5] Maxwell (1986) for Hudson Bay; Björnsson (2003), Lübbers, Schönfeld (2018) for Iceland; Filatov et al. (2005) for White Sea; Barnett (2013) for Norway. Extreme air temperatures obtained from www.weatherbase.com (st. Winisk for Hudson Bay, st. Borgarnes for Iceland, st. Narvik for Norway) and Filatov et al. (2005) for White Sea. [6–9] Sea surface temperatures for Hudson Bay, Iceland and Norway and[6,8] data for White Sea are from www.seatemperature.org (St. Rankin Inlet for Hudson Bay, Borgarnes for Iceland, Chupa for White Sea, Harstad for Norway), and [7,9] for White sea are from Filatov et al. (2005). [10] Ice thickness is Gagnon, Gough, 2006 for Hudson Bay; Naumov (2013), Levakin et al. (2013) for White Sea. [11] Precipitation is Stewart, Lockhart (2004) for Hudson Bay; Lübbers, Schönfeld (2018) for Iceland; Filatov et al. (2005) for White Sea; www.weatherbase.com (Vesteralen) for Norway. [12] Celsius-based 5-year-average (2013–2017) growing degree days for a base temperature of 0.0 °C with data obtained from www.degreedays.net for weather stations Churchill (Hudson Bay), Reykjavik (Iceland), Umba (White Sea), Harstad (Norway).

	Hudson Bay, Canada (55°N)	Iceland (64°N)	White Sea (66°N), this study	Northern Norway (69°N)
Number of salt marsh species of foraminifera	2–5	1–7	9	2
Max living abundance of foraminifera, ind./10 cm^3	180	98	3040	n/a
[1]Mean annual temperature, °C	−4.4	4.3	−0.4	4.4
[2]Mean winter air temperature, °C	−20–22	0	−13	2
[3]Minimum winter air temperature, °C	−45–50	−3	−47	−7.5
[4]Mean summer air temperature, °C	10–12	8–10	14–15	13
[5]Maximum summer air temperature, °C	32	25	35	31
[6]Mean winter sea temperature, °C	−1.6	4.1	−1	3.8
[7]Minimum winter sea temperature, °C	−1.7	2.9	−1.7	2.7
[8]Mean summer sea temperature, °C	6.8	10.6	14.6	12.2
[9]Maximum summer sea temperature, °C	9.3	12	18.9	14.2
[10]Sea ice thickness, m	0.9–2.4	–	0.5–1.5	–
[11]Annual precipitation rate, mm	200–800	800–1300	500–550	1017
[12]Growing degree days (above 0 °C)	1412	2134	1877	2092

Climatic differences may explain the disparity in the foraminiferal diversities and abundances from the four subarctic locations. Iceland and northern Norway are adjacent to the core of Gulf Stream derivatives, and both have maritime climate with mild ice-free winters and cool wet summers. Precipitation rates are high, mean annual air temperatures are about 4 °C. Winter surface water temperatures never drop below 2 °C, despite negative air temperatures. Hudson Bay and the White Sea, on the other hand, have relatively continental climate with larger seasonal differences. Both water bodies are away from warm oceanic currents, receive heavy runoff, have a well-developed pycnocline and are covered with fast ice for at least 7 months a year. Winter temperatures are similar, while in summer Hudson Bay is cooler due to the direct inflow of Arctic water through the Fury and Hecla straits (Stewart, Lockhart, 2004), which makes it almost an arctic basin. The White Sea has no such influx of cold Arctic waters, hence warmer summers (Table 2).

In subpolar and polar regions, long severe winters and sea ice are the key factors that affect coastal communities (Dionne, 1989). Ice ploughing (see below) eliminates macroscopic life on the shore (Conlan et al., 1998). Simultaneously, ice is a thermal insulator that protects intertidal organisms from sub-zero temperatures and wind. Air temperatures below intertidal ice have been shown to be consistently higher than those on nearby ice-free shorelines (Kuznetsov, 1960; Scrosati, Eckersley, 2007). In the White Sea, air temperatures under intertidal ice do not fall below −2 °C (Krell et al., 2003; Naumov, 2013). In spring, when the sun rises higher, under-ice temperatures can substantially exceed those of ambient air (Kuznetsov, 1960; Scrosati, Eckersley, 2007). This prevents littoral organisms from experiencing lethal thermal stress in cold regions (Scrosati, Eckersley, 2007). The top 2 cm of saltmarsh soil at our winter sampling site was frozen into the ice foot. Moist soil immediately below contained live foraminifera (Table 1). Quick deployment of pseudopods indicated the specimens were not dormant

Table 3

Living foraminiferal species recorded on subarctic saltmarshes. The locations are arranged according to increasing latitude. The data are from Scott, Martini (1982), Lübbers, Schönfeld (2018), this study, and Barnett (2013) respectively.

List of species	Hudson Bay, Canada (55°N)	Iceland (64°N)	Western White Sea (66°N)	Northern Norway (69°N)
Jadammina macrescens	✓	✓	✓	✓
Balticammina pseudomacrescens	✓		✓	
Trochammina inflata			✓	
Trochammina adaperta		✓		
Trochammina astrifica		✓		
Trochamminita irregularis		✓		
Deuterammina ochracea		✓		
Haynesina orbicularis		✓		
Polysaccamina ipohalina	✓			
Ammotium salsum	✓		✓	
Ammobaculites balkwilli?			✓	
Miliammina fusca	✓	✓	✓	✓
Ovammina opaca			✓	
Elphidium williamsoni			✓	
Elphidium albiumbilicatum			✓	

(Fig. 7). Noteworthy, the winter *Elphidium* specimens had colorless cytoplasm. They probably discard kleptoplasts and switch to a non-algal diet. The winter rose-Bengal density at 2–3 cm was comparable to summer density at the same core depth (Table 1), but was one order of magnitude lower than summer density at the surface (0–1 cm). Saltmarsh foraminifera do dwell deep in soil (Ozarko et al., 1997; Saffert, Thomas, 1998), and their densities decrease significantly downcore (Lutze, 1987). In our case, the subsurface part of the population can serve as a winter surviving pool that proliferates then in spring. The question remains open whether freezing eliminates live foraminifera in the surface soil. Little is known of how freezing affects foraminifera. Antarctic planktonic foraminifera in seasonal ice live in brine channels, not frozen into the solid phase (Spindler, Dieckmann, 1986). Richter (1965) reported survival of intertidal foraminifera frozen into ice that forms sporadically on the tidal flats of the North Sea. It is not clear whether the latter finding is applicable to the subarctic White Sea, where winter is much more severe, and tidal ice is dry and lasts seven months a year. The issue needs further studying.

Protection by ice can explain survival of foraminifera during severe winter in the White Sea and the Hudson Bay, but it does not explain higher summer abundances in the White Sea. Moving ice is extremely destructive. The sediment of the upper intertidal zone, including vegetated parts of saltmarshes, freeze into ice (Martini et al., 2009; Naumov, 2013) and can be bulldozed when it moves (Naumov et al., 2009). In New England, plant assemblages need a long time to recover after ice ploughing (Ewanchuk, Bertness, 2003). Such ploughing will leave the marsh surface with small depressions that persist for several years (Dionne, 1969, 1974). The terrain of the western White Sea has a veneer of erratic boulders, composed of extremely hard granitoid rock of the Baltic Shield (Chuvardinskij, 1971), which are frequent on saltmarshes. Boulders absorb ice movement and prevent destruction of adjacent soft sediments and organisms (Kuznetsov, 1960). Rocks of Hudson Bay are, in contrast, relatively weak (Martini, 1981; Scott, Martini, 1982) and cannot withstand ice ploughing. However, Naumov's (2013) and our unpublished observations show that ice pressure ridges lie at lower and mid intertidal zones, whereas little ice movement occurs at upper intertidal where saltmarshes develop. Thus, protection from ploughing ice is unlikely to be responsible for the high foraminiferal abundances observed.

The cause of high summer densities recorded could be differences in summer temperatures. Although both Hudson Bay and the White Sea have continental climates their summers differ. Direct influx of Arctic water resulting in cold spells in summer occurs only in Hudson Bay. Summer air temperatures near our research sites are 5–8 °C higher than at other mentioned subarctic locations, and sea surface temperatures are also highest (Table 2). Southeasterly winds from the continent occasionally bring warm air up to +30 °C (Filatov et al., 2005). Pore-water from the top centimeter of sediment on a local tidal flat averaged 17 °C in midsummer 2001–2002 with eventual maxima of 23–27 °C (Golikova, Fateev, 2003). Growing Degree Days (GDD), a climate index calculated as the integral of warmth above a base temperature (Prentice et al., 1992; Grigorieva et al., 2010), is substantially higher for the White Sea than for Hudson Bay (Table 2), meaning more cumulative heat in summer, which boosts the whole saltmarsh system including foraminifera.

Saltmarsh foraminifera are less diverse and abundant in milder Iceland and northern Norway than at colder subarctic Hudson Bay and White Sea locations. The vicinity of a warm oceanic current makes a subarctic coastline predominantly ice-free. Lack of ice exposes intertidal biota to eventual cold spells, commonly killing intertidal fauna during cold winters in mid latitudes (Crisp, 1964). We suggest that the lack of insulating ice blanket may cause winter elimination of intertidal foraminifera beyond the capability of the populations to recover in summer.

5.2. Species composition of living foraminiferal assemblages

Assemblages of saltmarsh foraminifera consisted of 9 species. *Jadammina macrescens, Balticammina pseudomacrescens, Miliammina fusca,* and *Elphidium williamsoni* were omnipresent and most abundant in the study area. *Trochammina inflata, Ovammina opaca, Ammotium salsum, Ammobaculites balkwilli*? and *Elphidium albiumbilicatum* were accessory. This is the northernmost record of live *B. pseudomacrescens, T. inflata, A. salsum, A. balkwilli*? and *O. opaca* in Europe to date. The morphospecies we found are cosmopolitan or nearly cosmopolitan (Supplementary material 3). The only species with restricted distribution is *E. albiumbilicatum,* presently never found south of Baltic and North Sea (Murray, 2006; Korsun et al., 2014 and references therein). On the saltmarshes studied *E. albiumbilicatum* was rare, being though quite abundant on adjacent tidal flats (Korsun et al., 2014).

Discussing species richness in the subarctic belt, we take into consideration only living data arrays, because dead and total assemblages commonly used in sea-level reconstructions may contain subtidal taxa washed ashore or subfossil taxa from outcrops. Subarctic saltmarsh foraminiferal faunas are moderately similar across locations. The two locations with cold winters (Hudson Bay and the White Sea) are most close in species composition. Four of the five species recorded in Canada also occur in the White Sea marshes, namely *J. macrescens, B. pseudomacrescens, M. fusca,* and *A. salsum* (Table 3). The fifth species, *Polysaccamina ipohalina*, is common in North America and recorded on European, Malaysian and New Zealandean saltmarshes (Hayward, Hollis, 1994; Camacho et al., 2015), but absent in our samples. The Icelandic saltmarsh fauna has only two of the seven species in common with the White Sea (*J. macrescens* and *M. fusca*). *Trochamminita irregularis* is found widely around the globe (Hayward, Hollis, 1994; Debenay, 1990; Guilbault, Patterson, 2000; Lehmann, 2000; Jennings et al., 1995), and its range excludes the White Sea for unknown reason. The other taxa found in Iceland do occur in the White Sea, but are shallow subtidal: *Haynesina orbicularis*, *Deuterammina ochracea*, *Trochammina adaperta* and *Trochammina astrifica* (Stschedrina, 1948; Voltski et al., 2015). The latter two had been originally described as forms of *Trochammina squamata*, while the White-Sea *Trochammina squamata* depicted by Lukina (1988) resembles much *T. adaperta* from Iceland. The comparison with Iceland shows that intertidal foraminifera may become subtidal in ice-covered seas. This commonly happens with macrofauna, e.g. mussels (Mathiesen et al., 2017; Leopold et al., 2019). The northern Norway species list contains only two species, *J. macrescens* and *M. fusca*. Both are cosmopolitan and occur at all the locations discussed. Cosmopolitan species mostly compose the faunas of all the four subarctic marshes discussed. Wide zoogeographic range of these species likely implies their tolerance for harsh environmental conditions.

There were two plainly different foraminiferal assemblages (Figs. 3–6). The boundary between them corresponded approximately to the elevation of neap tides (MHWN), and laid within the belt of the saltmarsh rush (*Juncus*, Fig. 2). The plant belts showed variation between the two marshes (Fig. 2) whereas the foraminiferal assemblages were much more similar (Fig. 5). Thus, the two foraminiferal assemblages obviously differ in their tolerance to inundation time and have no strong link to the vegetation. This weak link to plant communities has been already noticed in the pioneering study of subarctic saltmarsh foraminifera (Scott, Martini, 1982).

The high-marsh assemblage was dominated by *Jadammina macrescens* and *Balticammina pseudomacrescens* while low-marsh by *Miliammina fusca* (Figs. 4 and 6). Kemp at al. (2017) have revealed the same two distinct assemblages in the eastern White Sea. So this set of assemblages is characteristic of the whole White Sea. In northern Norway, Barnett with co-workers (2015) have described similar pair of assemblages, only *Balticammina pseudomacrescens* declines. North American assemblages are known from southern Alaska, Hudson Bay, and several localities on Canada's eastern coast (Scott, Martini, 1982, Kemp et al., 2013, Barnett et al., 2016; 2019). *Balticammina pseudomacrescens* is the omnipresent dominant of the high marsh, whereas *Miliammina fusca* dominates the low marsh except for several locations in Hudson Bay. North American *Jadammina macrescens* has a broader vertical range as a dominant. It prevails often not only in the high marsh, but also in the low marsh. Another difference of the North American marshes is that additional dominants may be present, namely *Haplophragmoides manilaensis* and *Polysaccammina ipohalina* in the high marsh and *Tiphotrocha comprimata* in the low marsh. *Trochammina inflata* is eventually subdominant in the high marsh or low marsh in both North America and Europe, but we see no consistent pattern. The assemblages from Iceland (Lübbers, Schönfeld, 2018) are an outlier. There is little similarity to the above mentioned dominants from North America and Europe. All the subarctic assemblages demonstrate a very high dominance, often exceeding 80%, which indicates stressful environment (e.g., Hayward, 2014). In summary, the common features of subarctic saltmarshes appear to be the clear vertical separation of two foraminiferal assemblages, high dominance, and nearly ubiquitous dominants being *Balticammina pseudomacrescens*, *Jadammina macrescens*, and *Miliammina fusca*.

Saltmarsh vegetation exists further north and has been extensively explored in northern Alaska, Canadian Arctic, Spitsbergen, and Siberian Arctic (Walton, 1922; Jefferies, 1977; Funk et al., 2004; Sergienko, 2013; Martini et al., 2019). Foraminiferal record is yet lacking there. We predict the presence of saltmarsh foraminifera further north with the wide-spread *Balticammina pseudomacrescens*, *Jadammina macrescens,* and *Miliammina fusca* as the last forms to disappear polewards.

6. Conclusions

We undertook a pilot winter sampling campaign and obtained the first record of saltmarsh foraminiferal populations under the ice. The uppermost 2 cm layer of soil was frozen into the ice foot, and live foraminifera occurred at low abundances (15–20 ind./10 cm^3) in the moist subsurface soil, which was comparable to summer values at the same core depth. Colorless cytoplasm in calcareous foraminifera (*Elphidium williamsoni*) suggests that they discard kleptoplasts and abandon algal diet under the winter ice.

In summer, the White Sea saltmarsh assemblages were surprisingly abundant (hundreds of living specimens per 10 cm^3, up to 3000x10 cm^3), far exceeding those of Hudson Bay and Iceland. We infer the insulation blanket of fast ice maintains constant about-zero temperatures underneath and allows the foraminifera to endure the harsh winter. A relatively warm continental summer in the White Sea makes saltmarsh foraminifera thrive during the vegetation season.

The studied White Sea fauna comprised 9 species, much fewer than a typical 15–40 on mid-latitude saltmarshes. Like other subarctic saltmarshes, those from the White Sea host a taxonomic subset of mid-latitude fauna. With the single exception of *Elphdium albiumbilicatum*, all the taxa found here have nearly cosmopolitan zoogeographic ranges. There were two distinct foraminiferal assemblages. *Jadammina macrescens* and *Balticammina pseudomacrescens* prevailed on the high marsh whereas *Miliammina fusca* on the low marsh. Dominance in both assemblages was remarkably high, often exceeded 80%. The boundary between the assemblages was controlled by water level (neap tides) rather than by vegetation belts. These coupled high-marsh and low marsh assemblages vary little throughout the subarctic belt of Europe and North America.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Elena Golikova: Conceptualization, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Marina Varfolomeeva:** Data curation, Formal analysis, Visualization, Software. **Eugeniy Yakovis:** Formal analysis, Visualization, Writing - review & editing. **Sergei Korsun:** Supervision, Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106685.

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