ORIGINAL ARTICLE

Intertidal foraminiferal fauna and the distribution of Elphidiidae at Chupa Inlet, western White Sea

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Abstract

The bright colouration of the cytoplasm in intertidal rotaliid foraminifera and their particle-gathering activity reliably reveals live specimens in fresh samples, without any fixatives or dyes applied. Using this approach, we demonstrate that live representatives of three rotaliid species, all belonging to the genus Elphidium, were common on intertidal mud and sand beaches. Two species, E. excavatum clavatum and E. albiumbilicatum, lived close to freshwater outflows, whereas E. williamsoni occupied beaches bathed by waters with normal salinity (surface 26–27°C in the western White Sea). A least 13 species were found alive in the intertidal zone. Among non-calcareous foraminifera, Miliammina fusca, Ammotium cassi and Ovammina opaca were the most numerous.

Key words: Benthic foraminifera, Elphidiidae, intertidal, distribution, salinity, White Sea

Introduction

Intertidal foraminifera in the White Sea have been looked into occasionally alongside the subtidal fauna, but have never been the main objective of a separate study (see subsection featuring previous work below). The taxonomy of intertidal foraminifera remains controversial, and little is known of their distribution. In this first paper targeted on White Sea intertidal foraminifera, we focus on the calcareous fauna, aiming to clarify the taxonomy and to recognize distributional patterns. Additionally, we are compiling a list of foraminifera living in the White Sea intertidal zone.

Previous work

Intertidal foraminifera of the White Sea have never been the main goal of a study, but data are presented in publications by Stschedrina (1948, 1955, 1962), Mayer (1962, 1980) and Lukina (1985a, 1985b, 1988). The recorded taxa are listed in the first column of Supplementary material S1. Most of the samples came from localities adjacent to our study area, and only Lukina (1985a) obtained intertidal samples from the Onega Bay. There are no published data on the Dvina Bay or on the White Sea coast of the Kola Peninsula (see Figure 1 for location).

Stschedrina (1948) studied foraminifera of the Gridino Inlet (outer Kandalaksha Bay), examining 39 sediment samples, an unspecified number of which were intertidal. She found that Miliammina fusca Brady, 1870 was dominant in the intertidal and shallow subtidal zones and was the only foraminiferal species present in the estuary of the river. Stschedrina (1948) also gave a first description of Elphidium longipontis sp. nov., which was the most frequent calcareous foraminiferan. Later she presented a more complete account of these samples (Stschedrina 1962) and described E. longipontis in detail.

Mayer (1962) collected >100 intertidal sediment samples around the biological station of Moscow University (inner Kandalaksha Bay). Based on these data, she later delineated taxa occurring in the intertidal zone (Mayer & Korsun, 2008).

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Lukina (1985a, 1985b, 1988) examined 56 sediment samples from the Onega Bay, 73 sediment samples from a study area overlapping with ours, and 32 sediment samples from shores ~15 nautical miles east of our locality. Each of the three sets included intertidal samples, but their proportion was not indicated. The characterization of intertidal fauna was not among the aims of these studies; however, intertidal occurrences of taxa can be read from their depth ranges.

The cited authors shared their taxonomical views. They recorded a total of 24 species in the intertidal zone of the White Sea (see Supplementary material S1). Mayer (1962, 1980) applied the Rose Bengal dyeing. Thus, for the majority of species it is not certain whether live individuals have been found.

Study area

The White Sea is a subarctic marine basin about 400 km across (west to east) and > 300 m deep (Figure 1). This semi-isolated basin has salinities lower than normal marine areas. The surface water away from river mouths is 24–28%o; the deep water is 30–31%o. (Babkov & Lukanin 1985). From December to April, the inshore waters are covered with fast ice, the offshore with ice floes (Savoskin 1967). Snow-melt produces flooding in April–May, and the inshore surface waters may become nearly fresh (Babkov & Lukanin 1985).

The study area is located on the southwestern coast. Unlike the other coasts of the White Sea, which are mostly stretches of sand, this rocky coast is incised by fjord-type inlets, among which Chupa is one of the largest (Figure 1). There is little sand here; the intertidal zone is predominantly rock and boulders covered with kelp; mudflats are situated in sheltered embayments. The tide is semidiurnal with a 1.8-m range. The study area embraces the outer Chupa inlet and the adjacent nearshore waters of the Kandalaksha Bay.

Material and methods

Foraminiferal sampling

A total of 84 foraminiferal samples were collected on beaches within an 8-nautical-mile boat trip around the St. Petersburg University field station, which was the base of operation. A beach was defined arbitrarily as a stretch of intertidal mud or sand 30–300 m in strandline and usually separated from another beach by a rocky shore. We did not investigate any single intertidal area thoroughly; rather, we took 1–5 samples on each beach (aiming to reveal presence/absence of taxa). The whole sampling set consisted of 39 such clusters, which are hereafter called stations. Samples at a station were taken 2–20 m apart, but not randomly. We chose a sampling spot on a flat patch of mud or sand, avoiding Arenicola pits or mounds, away from scattered boulders with their kelp overgrowth, that sweeps the surrounding sediment, and away from mussel beds.

The calcareous fauna, which was in the focus of this study, consisted exclusively of rotallids (see the Results). Rotallid foraminifera, especially the intertidal species, unlike the majority of foraminifera, commonly have brightly coloured cytoplasm and are usually motile (Langer et al. 1989). Live specimens can be recognized confidently by the presence of cytoplasm and by particle-gathering activity. Taking this opportunity, we forewent cytoplasm staining, such as the Rose Bengal technique, and counted live individuals in fresh unfixed samples. The advantage of this approach, as compared to Rose Bengal staining, is that the discrimination of live individuals and empty tests is more confident: tests filled with organic detritus rich in bacteria or tests containing metazoans are not mistaken for living specimens. Besides, less man-power is needed, because several procedures are omitted: fixative preparation, extra stain removal, drying, etc. The disadvantage is that the approach is not applicable to textulariids and miliolids, where the colourless cytoplasm is difficult to distinguish through the test wall. Also, precautions have to be taken to keep the foraminifera alive (see the Methods below).

Finally, unfixed samples have to be processed and counted within a few days. If the sample set is massive, several specialists should work in parallel.

The samples were sediment and seaweed. Surface sediment 0–1 cm deep was scooped out to a volume of 20 cm³. On remote mudflats that were not easy to revisit, we secured larger volumes, 40, 60 or 80 cm³. Beaches of coarse sand were avoided, as our previous observations (unpublished) showed that these sands were barren of live foraminifera. We sampled mud, sandy mud, or fine-to-medium sand. Unfixed sediment was sieved through 250- and 125-μm mesh screens with surface seawater within 3 h of collection. The residues were stored at 10°C (the ambient air temperatures were 15–25°C) and further processed within two days.

The intertidal kelp (four species of fucoid phaeophytes) was not sampled because our earlier observations had indicated that the kelp had been devoid of foraminifera. Yet, on certain mudflats densely grassed with Zostera, we took a few tufts, taking care not to
shake off the overgrowth of filamentous (Spirogyra-type) chlorophytes. These samples were processed on the spot. The seaweed was rinsed vigorously in a bucket of ambient water and put aside. The seaweed debris had to be removed, as it would have killed off all the metazoan fauna (and possibly the foraminifera) within an hour by depleting oxygen concentration. The bucket with the suspension was stirred, left undisturbed for a few seconds to let hard-shelled foraminifera settle, decanted, and refilled with a new portion of ambient water. This procedure, repeated several times, yielded a heavy residue consisting essentially of mussel spat, small gastropods and foraminifera. Yet, the remnant debris of filamentous algae sapped oxygen rapidly (as revealed by high mortality of crustaceans in stored samples). For this reason, we placed the residues in chilled water with normal surface salinity (27°C/15°C locally), transported them in a cooler, and counted the samples within 3 h of delivery to the laboratory.

The samples were obtained during low tides from 3 to 16 August 2011. The position of a station on the vertical scale was established visually, relative to the barnacle and kelp belts, and thus with an accuracy of ±20 cm. The majority of samples were collected from the lower intertidal zone (below the neap low tide). When this zone was flooded, samples were taken in the lower part of the middle intertidal. When large pools (>50 m across) were present in the middle and upper intertidal zones, those were sampled as a separate station. Each sieved residue was spread in a Ø 10-cm Petri dish and stored in a temperature-controlled room at 10°C. The Petri dishes were left untouched for at least 30 min, giving the foraminifera the time to deploy pseudopodia and grab particles. Counting was performed under dissecting microscopes, with incident light, at magnifications of ×16–52. As the samples needed to be dealt with immediately, several co-authors were employed to count the foraminifera simultaneously. We expected author-to-author taxonomic discrepancies to be negligible, because the species diversity was low and a dubious specimen could be agreed upon at once.

We chose to estimate foraminiferal population density semi-quantitatively, on the basis that (1) density on branching substrates such as seaweed cannot be measured with an accuracy sufficient for meaningful comparison with densities in sediment, and (2) our observation was aimed primarily on the presence/absence of taxa, and a semi-quantitative approach greatly reduced time. For each species, we distinguished three grades of population density. Abundant — there were several live specimens in each field of view (i.e. 20–80 specimens in a fraction >250 specimens per sediment volume 20 cm³). Common — one specimen in each third field of view (5–20 specimens per 20 cm³). Rare — a few specimens per sample (1–4 individuals per 20 cm³). For a station at which more than one sample was taken, we produced a mean value for each species. In a situation when all replicates were barren except one, which yielded a few specimens, the species occurrence at this station was rated as rare.

The criteria as to whether a specimen was alive were cytoplasm within the test (Figure 2) and a sheath of grabbed particles. Empty foraminiferal tests were noted but not quantified.

To obtain light-microscopy images, optical sections captured with a Leica M205-C dissecting microscope were stacked using Helicon Focus software. For scanning electron microscopy (SEM), dried foraminiferal tests were mounted on aluminium SEM stubs and ion-coated with 15 nm of Pt on a PECS device (Gatan Inc.). Imaging was performed on a ZEISS Merlin scanning electron microscope (accelerating voltage 3–10 kV).
Salinity sampling

We undertook salinity measurements because the foraminiferal data indicated that this could be a factor reflected in the foraminiferal distribution (see the Results). We measured surface water salinity with a portable refractometer, Extech RF20, with a precision of $\pm 1\%$. The low precision of this device was not considered to be a problem in our study area with its huge salinity gradient of $>20\%$. All water samples were taken with a pipette from a depth of 10 cm below the water surface. We took these samples from a small boat or by wading at the strandline. There were 63 salinity stations. They were positioned and numbered independently of the foraminiferal stations (the numbering is not shown). At each salinity station, one measurement was performed immediately in the field, and one 1.5-ml sample in a plastic tube was taken to the laboratory for measurement the same day. If the two replicates conflicted $>1\%$, a third and fourth measurement was carried out using the same 1.5-ml sample.

It is expected that surface salinity in areas absorbing freshwater runoff changes rapidly with tide and wind. Therefore, we planned 27 salinity stations to map the area where we found a prominent shift in the foraminiferal fauna. There were six surveys, three for high tide and three for low tide (9 August 2011). Each survey commenced within 1.5 h after a high- or low-water astronomical standstill and those samples were taken regardless of tidal phase. As we did not have contemporaneous support of vertical Conductivity–Temperature–Depth (CTD) data acquisition, we used a CTD profile obtained in the Keret estuary earlier, in 2003 (Valerian V. Kazaryan, St. Petersburg University, pers. comm.). The data were acquired in the Keret estuary off our foraminiferal station 32 with a ‘CTD-2002’ unit manufactured and calibrated at the Arctic and Antarctic Research Institute.

Results

Foraminifera

Intertidal foraminiferal fauna. There were live representatives of at least 13 foraminiferal species in the intertidal zone (the last column of Supplementary material S1). The first descriptions of all foraminiferal species mentioned in this article are listed in Supplementary material S2.

Three species of rotaliids occurred regularly on the studied beaches: *Elphidium williamsoni* Haynes, 1973, *E. excavatum* (Terquem, 1875) *clavatum* Cushman, 1930, and *E. albiumbilicatum* (Weiss, 1954) (Figure 3). Most specimens had brightly coloured cytoplasm, orange, yellow, light green, dark green, dirty green, or brown. After a few hours in a Petri dish they accumulated at the sediment surface and remained there afterwards, each partly concealed by a cocoon of silt grains. Specimens with brightly coloured cytoplasm but lacking grabbed particles were rare, <5%; we registered those dubious specimens as live. White empty tests of *E. williamsoni* were common but less frequent than live individuals. There were few empty tests of *E. excavatum clavatum* (hereafter shortened to *E. excavatum*) or *E. albiumbilicatum*. Other rotaliids were *Aubignyna* sp., occurring at two stations, and a single juvenile individual of *Haynesina orbiculare* Brady, 1881 (Supplementary material S3).

The others were non-rotaliid foraminifera with colourless cytoplasm, which was often difficult to distinguish. We did not make quantitative observations on these.

Of hard-shelled arenaceous forms, *Miliammina fusca* (Brady, 1870) was omnipresent. The cytoplasm was indistinguishable within the non-transparent agglutinated test, but the many specimens collecting detritus at the aperture were apparently alive. *Ammonia cassis* (Parker, 1870), including large specimens ~1 cm long $\times$ 0.5 cm tall, were numerous at certain stations. The specimens did not gather particles and remained motionless in Petri dishes. Tests containing transparent cytoplasm were difficult to distinguish from empty ones. Some specimens did contain cytoplasm and thus were alive, but which portion they accounted for remained uncertain. Empty tests of *Reophax dentaliformis* Brady, 1884, *Trochammina inflata* (Montagu, 1808), *T. lobata* Cushman, 1944, and *Balticammina pseudomacrescens* Brönnimann, Lutze & Whittaker, 1989 occurred sporadically.

Monothalamid foraminifera all had live representatives, with deployed pseudopodia. The silver saccamminid *Ovammina opaca* Dahlgren, 1962 was common; many tests had a circle of open hatches around the aperture, an indication of having undergone reproduction (Goldstein & Barker 1990). There were at least two undescribed saccamminids; *Hippocrepinella alba* Heron-Allen & Earland, 1932 and *Bathyphison* cf. *flexilis* Höglund, 1947 occurred; an undescribed large allogromiid was also common.
Distribution of *Elphidium*. The 250 and 125 μm fractions, when compared in ~20 samples, showed no perceptible difference in species composition and it therefore was unnecessary to count both fractions in all samples. As the larger specimens could be identified more reliably, we thoroughly processed the coarser fraction, whereas the fine fraction was only scanned for the presence of species.

Semi-quantitative data on distribution were acquired on cytoplasm-colored rotallids, the vast majority of which were the three species of *Elphidium* (Supplementary material S3; Figure 4).
Thirteen of the 39 foraminiferal stations yielded no *Elphidium*. We revisited certain beaches, and some stations that had appeared barren yielded *Elphidium* after all (Supplementary material S3; stations 20, 21, 27, 29). Thus, it remained unclear whether the 13 stations with zero counts were truly barren or just lacked replicates.

The population density varied greatly between beaches (Supplementary material S3; Figure 4). When *E. williamsoni* or *E. excavatum* ranked ‘abundant’ or ‘common’ in a sediment sample, they were represented by specimens of nearly identical size, indicating that these were offspring of a single reproduction pulse. The same species when clinging to seaweed were diverse in size. There was no other discernible pattern in population density.

The main effort was to reveal presence or absence of a species on a beach. *E. williamsoni* occurred on most beaches. There were only four stations where this species was absent, whereas the other two
Elphidium species (either or both) were present (stations 29, 30, 31, 32; Figure 4). These four stations were situated close to each other and were most proximal to the Keret River mouth. This suggested a possible effect of salinity on the distribution.

**Salinity**

The non-recurrent surface salinity survey showed that the Keret River was the major source of fresh water in the Chupa fjord and its surroundings (Figure 5b). The surface brackish layer formed by river influx, however, was only 1 m thick. In the Keret estuary, it capped the typical high-latitude water column: the seasonally warmed mixed layer (15 m thick in this case) underlain by winter-chilled water (Figure 5a).

The foraminiferal stations of interest (stations 29, 30, 31, 32) were located in or near the outer Swan Cove (see Figure 6 for location), a small basin connected by an intertidal channel to the Keret estuary and by a shallow subtidal channel to the outer straits. A station grid for the recurrent surface salinity survey was aimed at tracing the short-term variability in the Swan Cove and the adjacent water bodies. The surface salinity was changing perceptibly with tide and wind (Figure 6). (1) During high tide, brackish water poured from the Keret estuary to the outer Swan Cove. The easterly wind upwelled saltier water at the eastern shore of the Keret estuary. (2) Retarded by the wind, low-salinity water ($<20\%_o$) was not released from the estuary at low tide (in support, we observed little ebb in the estuary). The wind again upwelled saltier water at the eastern shoreline. (3) The brackish water poured from the estuary to the Swan Cove at high tide again. The $5\%_o$ isoline had the broadest spread. When the wind had died down, the brackish water flushed out of the estuary overcoming the high tide. (4) This survey showed the broadest spread of low-salinity water ($<20\%_o$) in the adjacent straits. The water that had accumulated in the estuary during the easterly wind was dissipating in the straits. (5) The westerly wind upwelled saltier water at the northwestern shoreline of the estuary. (6) The weakest gradients were observed after calm weather. Overall, during the recurrent survey, foraminiferal stations 29, 30, 31, 32, where *E. williamsoni* was lacking (see Figure 4 for location), had lowest surface salinities.

**Discussion**

**Intertidal foraminiferal fauna**

_Taphonomic considerations._ Before comparing the published species lists with the data obtained in...
this study, we will estimate how probable it is that foraminiferal tests are redeposited and accumulated in the intertidal zone.

Empty tests of calcareous foraminifera in our samples were less numerous than live specimens and all belonged to the taxa dwelling in the intertidal zone, i.e. they were produced locally. The reproduction period in White Sea Foraminifera has not been studied. The only species studied in the vicinity is the intertidal *Elphidium williamsoni* on the Barents Sea coast of the Kola Peninsula, which has been shown to reproduce once a month during summer (Korsun et al. 1994). Our study area is at a lower latitude and is characterized by higher water temperatures in summer. It is reasonable to assume that the generation time of intertidal rotaliids in the White Sea in summer is also a month or possibly somewhat less. Considering that empty calcareous tests were several times less abundant than live individuals in our samples, the half-decay period for empty calcareous tests must be a week or two. Other carbonate remains in the sediments were mollusk shells and debris of coralline algae, both non-abundant and both etched by corrosion, and hence also indicative of strong CaCO₃ dissolution. We did observe empty arenaceous tests but never en masse, which indicates that they decay too but last longer than calcareous ones, perhaps months.

The coastline where our and the cited data sets have been obtained is Precambrian rock scraped by the last glacier (Svendsen et al. 2004) and draped with a thin veneer of late-glacial and post-glacial deposits. Within our study area, there is a site (c. 1 km east of foraminiferal station 4), where thick-walled valves of *Hiatella arctica* (Linnaeus, 1767) and *Astarte borealis* (Schumacher, 1817), probably Mid- or Early-Holocene in age, occur just above the spring tide. Thus, the shoreline deposits in our study area and probably along the southwestern coastline of the White Sea are a lean source of washed-out fossil foraminiferal tests.

The White Sea is too small for the long oceanic swell to build up. Even on the outer islands, on boulder pavements facing the open sea, the beach wrack is only 2–3 m above the spring tide, indicating that the surf is not very powerful. Soft-sediment beaches inhabited by foraminifera are situated in sheltered straits and inlets where the swell, which comes with the easterly winds, dissipates. Wrack piles here are <0.5 m above the spring high tide, indicating that the stormy waves carry little energy. For example, in the Keret estuary, where the narrow entrances let no swell in, the thickness of the brackish layer shows that waves developing in this restricted area (only 3.5 km long) are able to stir the water to a depth of <1.5 m, as revealed by the CTD profile (Figure 5a). In support of this single CTD measurement, our experience of snorkelling in the estuary confirms that the thickness of the topmost warm layer in summer is always 1–1.5 m. Storm waves outside the estuary apparently are somewhat longer and stir the water column deeper; still, at the sheltered beaches the surf is unlikely to stir and pick up sediment from water depths exceeding 5 m (the maximum water depth of sorted fine-to-medium sands we have seen in the study area). The foraminiferal fauna in such shallow subtidal habitats differs little from that in the intertidal zone (Stschedrina 1962; Lukina 1985a, 1985b).

Based on the above considerations, we conclude that the vast majority of foraminiferal tests found in the intertidal area are not winnowed and either remain in situ or are transported for a short distance (metres). The intertidal foraminiferal fauna does not vary much between oceans, less than one would expect intertidal fauna to vary within the White Sea. Moreover, all the data sets excluding Lukina (1985a) have been obtained within 60 nautical miles of the coastline. Therefore, the species lists must match.

**Taxonomic considerations.** The results (Supplementary material S3) and our unpublished preliminary observations in this study area, as well as on other coasts of the White Sea, convince us that only four rotaliid taxa occur regularly in the intertidal zone: *Elphidium williamsoni*, *E. excavatum*, *E. albiumbilicatum*, and *Aubignyna sp.* (Supplementary material S1; Figure 4).

*Elphidium longipontis*, according to Stschedrina’s (1962) description and contour drawings, is identical to *E. williamsoni*. We see no morphological differences between specimens from the White Sea (Figure 3-3, 3-4) and *E. williamsoni* collected in the Skagerrak. In our opinion, the two names are synonymous. The senior synonym formally is *E. longipontis* (International Code of Zoological Nomenclature, article 23.9), but *E. williamsoni* is legacy of the much earlier description, *Polystomella umbilicatula* (Walker) var. *incerta* Williamson, 1858. We have no impetus to discuss taxonomic priority in this article and adopt the name *williamsoni*, which has been in much broader use.

*Elphidium excavatum clavatum*, when small, had typical ‘clavatum’ morphology, with a single umbilical boss and a few ponticuli on the sutures (Figure 3-8). In large tests, however, a split boss was present in the umbilical area, the intraseptal interlocular spaces were bridged by many ponticuli, and the ponticuli themselves became elongated and regularly spaced (Figure 3-7). This latter form was difficult to distinguish from *E. williamsoni*. The diagnostic
differences were the somewhat irregular shape of the ponticuli and the large pores maculating the wall in *E. excavatum*, but these features were readily seen only using high-magnification optics and powerful light sources. We therefore suppose that *E. williamsoni* and the intertidal *E. excavatum* have been partially confused in the published record.

*Elphidium subarcticum* Cushman, 1944 is reported by all earlier authors for the intertidal zone of the White Sea (Supplementary material S1). This form has a most confused taxonomy. It is probably synonymous with *E. hallandense* (Brotzen, 1943), and many authors seem to lump *E. frigidum* (Brotzen, 1943), and many authors confused taxonomy. It is probably synonymous with Sea (Supplementary material S1). This form has a most earlier authors for the intertidal zone of the White Sea. On the other hand, Stschedrina (1948, none of these forms have been seen dwelling in the of our knowledge, all literature available indicates that our experience with arctic foraminifera and, to the best species. Regardless of the taxonomic complications, all our experience with arctic foraminifera and, to the best of our knowledge, all literature available indicates that none of these forms have been seen dwelling in the intertidal zone. On the other hand, Stschedrina (1948, (1948) never mention *E. albiumbilicatum*, which is morphologically similar to and often confused with *E. subarcticum/hallandense*. When Stschedrina (1948) studied the first intertidal samples from the White Sea, *E. albiumbilicatum* (Weiss, 1954) had not yet been described. She probably found *E. albiumbilicatum* in her samples, named it *E. subarcticum*, choosing the closest morphological match, and her students Mayer and Lukina picked up this misidentification.

Similarly, all the earlier authors reported *Buccella frigida* (Cushman, 1921) for the littoral zone (Supplementary material S1), whereas all trochospiral specimens we found in the intertidal samples were similar to *B. frigida* or *B. tenerrima* (Bandy, 1950) but differed from those by the depressed umbilicus (Figure 3-10–11). Currently, the taxonomy of *Buccella* in the White Sea is not resolved; it is not clear how many species there are. Depressed umbilici occur in the genus *Aubignyna*, which is closely related to *Buccella* (Murray et al. 2000), and we provisionally named our morph *Aubignyna* sp. According to the Loeblich & Tappan (1987) classification, *Aubignyna* differs from *Buccella* in that the aperture extends all the way from the umbilicus to the periphery. However, Murray et al. (2000) conclude that differentiation of *Buccella* and *Aubignyna* is still uncertain. Indeed, they describe *Aubignyna hamblensis* sp. nov. as having a short *Buccella*-type foramen. In our specimens, the aperture was always concealed by papillae in live individuals (Figure 3-10). The foramen, which was readily seen in dead specimens with the broken off ultimate chamber, was a relatively short *Buccella*-type interiomarginal slit (Figure 3-11). We suppose that the earlier authors have seen *Aubignyna* sp. in their samples and have named it *B. frigida* or *B. tenerrima*. It seems highly unlikely that a relatively large foraminiferal species (Ø 300–400 μm in adults, Figure 3-9–3-11) from shallow waters around Europe remains undescribed. We still hesitate to suggest the species affinity. As has already been stated, the morph in question differs from the sublittoral representatives of *Buccella* in the depressed umbilicus. *Aubignyna hamblensis* is a small species, Ø < 130 μm in adults (Murray et al. 2000). *A. perlucida* (Heron-Allen & Earland, 1913) has a flattened spiral side, a long aperture, and the sutural depressions of the umbilical side becoming shallow toward the periphery (unlike our morph, Figure 3-13).

*Haynesina orbiculare* has been reported by earlier workers for the intertidal zone (Supplementary material S1). This species with its rather distinct morphology is unlikely to be misidentified for the other planispiral calcareous foraminifera occurring in the White Sea. Besides, we did find one specimen in our intertidal samples (Supplementary material S3). Moreover, this species, although referred to as *Haynesina germanica* (Ehrenberg 1839), has been recorded in the North Sea on a saltmarsh near Schobull, Germany (Joachim Schönfeld, pers. comm.). Therefore, it seems probable that *H. orbiculare* sometimes does dwell intertidally in the White Sea, but this needs future verification.

*Elphidium frigidum* (Cushman, 1933), recorded by Lukina (1988), is a sublittoral species that adheres to elevated substrates (Poag 1982 referred to it as *E. subarcticum*). First, we do not know a single permanently attached foraminiferal species in the White Sea intertidal zone. Probably, dry air or sporadic freshening (precipitation and flooding) make the intertidal environment too hostile for foraminifera that cannot escape to temperature-moderated salty pore-water (cf. Langer et al. 1989). Second, the sublittoral *E. frigidum* is often abundant on ramose red and brown algae (e.g. *Ptilota* and *Chaetopteris*, our unpublished observations in the White Sea). Sublittoral macrophytes are tossed ashore by stormy waves, apparently together with the attached foraminifera. The foraminifera die, the thalli decay, and the tests fall off into the intertidal sediments. We have often seen skeletons of sublittoral macrobenthos (crab carapaces; *Hiatella arctica* valves, etc.) picked up by gales with wrack clumps and thrown around. Dry foraminifera tests are probably also redistributed with the wind. Thus we conclude that *E. frigidum* tests are allochthonous.

*Elphidium bartletti* Cushman, 1933 is a morphologically distinct species, which we have never seen in the intertidal zone. The specimens Lukina (1985b, 1988) recorded were possibly winnowed from Holocene deposits.
E. advena authors working in the White Sea list Lukina (1985a, 1985b, 1988) in all her data sets. All perhaps, saw scrutinized. Lukina used a in the White Sea and adjacent basins has not been fact, the taxonomy of three-serial arenaceous forms this is a rare species and was possibly washed out very north of the White Sea (unpublished). Thus, Korsun2008). We have also observed it once in the station in the inner Kandalaksha Bay (Mayer &

Miliammina fusca tests occurred on all beaches, but as the live/dead ratio was not estimated, we could not judge whether its live individuals were more or less abundant than those of the rotaliid foraminifera. Mayer’s (1962) new species M. fungidens, described from a location 15 nautical miles west of ours, differs in the form of the tooth. We did not try to discriminate these two forms. The third miliolid foraminiferan, Siphonaperta agglutinata Cushman, 1917, is a shallow-water species and as such may be found in the intertidal zone; it is not yet known living or dead from our region.

Among textulariid foraminifera, Ammotium cassis Parker, 1870 was by far the largest and most conspicuous species and commonly occurred alive. This species was also extremely abundant in shallow subtidal soft sediments (our unpublished data). This foraminiferan is common in shallow seas in northern Europe (Olsson 1976). Already Stschedrina (1948) noted that the large specimens from the White Sea deviated morphologically from the type material and from A. cassis occurring in other Arctic seas. The chambers of the linear portion develop ventral protuberances, often irregular in shape. The other textulariid foraminifera the earlier authors had mentioned for the White Sea intertidal were either absent from our samples or rare and dead. Ammobaculites exigus Cushman and Bröniman, 1948 was absent from our samples and had been recorded only once in the White Sea intertidal zone (Galtsova et al. 1989). The species is considered estuarial, littoral and sublittoral, typical of sandy bottoms (Ellison & Murray 1987; Hayward & Hollis 1994).

Reophax indivisus Mayer, 1974 had been mentioned from shallow subtidal settings (Lukina 1985b, 1988). We sporadically found dead specimens in intertidal samples. This species is morphologically similar to R. dentaliformis Brady, 1884 and is possibly synonymous to the latter.

Turritellella shoneana (Siddall, 1878) has been reported only once for the modern White Sea sediments; it was found in littoral and sublittoral settings near the Moscow University biological station in the inner Kandalaksha Bay (Mayer & Korsun 2008). We have also observed it once in the very north of the White Sea (unpublished). Thus, this is a rare species and was possibly washed out from Holocene deposits.

Eggerella advena (Cushman, 1921) is recorded by Lukina (1985a, 1985b, 1988) in all her data sets. All authors working in the White Sea list E. advena. In fact, the taxonomy of three-serial arenaceous forms in the White Sea and adjacent basins has not been scrutinized. Lukina used a >50 μm fraction and, perhaps, saw Eggerella europea (Christiansen, 1958), which is, unlike E. advena, a small species occurring in shallow waters (Murray 2003). Because we focused on the >250 μm fraction, we could have missed this species.

Trochammina inflata (Montagu, 1808) specimens that had been recorded intertidally in the White Sea (Mayer 1962) differed from the type description and from subtidal specimens, and Mayer (1962) preliminarily described the subspecies maris-albi. We had a few empty tests and cannot say whether they deviated from the typical T. inflata.

Stschedrina (1955) discerned a secondary aperture in White Sea representatives of Trochammina lobata Cushman, 1944. As this trait did not fit Cushman’s description, she erected the new genus and new species Trochamminula fissuraperta Brönnimann et al. (1983), using SEM, examined specimens from the T. lobata type locality, detected the Trochamminula-specific secondary aperture, and concluded, ‘It is now evident that Cushman’s species is a Trochamminula and almost certainly a senior synonym of T. fissuraperta.’ We adopt this view. Lukina (1985a, 1988) used both names for her material from the White Sea (Supplementary material S1).

Trochammina macrescens Brady, 1870, Jadamma macrescens (Brady, 1870), J. polystoma Bartenstein & Brand, 1983, and Balticammina pseudomacrescens Brönnimann, Lutze & Whittaker, 1989 – their taxonomy has been debated for decades (Gehrels & van de Plassche 1999). The genera principally differ in secondary apertures. Trochammina has the single aperture as an interiomarginal slit and no secondary apertures. Balticammina has secondary umbilical apertures. In Jadammina, the secondary apertures are areal pores. One approach is to consider the forms with various secondary apertures as ecomorphs of the single species Trochamrina macrescens (Scott & Medioli, 1980); the other approach is to discriminate two valid taxa, J. macrescens and B. pseudomacrescens (Brönnimann & Whittaker 1984; Brönnimann et al. 1989). Stschedrina’s specimens from White Sea intertidal samples had a secondary aperture as a single areal opening, and she erected the new genus and new species Trochamminisca cyclostoma Stschedrina, 1955. She said the presence of the secondary aperture was the only difference from Trochammina inflata var. macrescens Brady 1870 (modern name J. macrescens) and, if this secondary aperture were to be found in the Trochammina inflata var. macrescens types, both species would be conspecific or at least congenic. Indeed, Brönnimann & Whittaker (1984) found secondary areal apertures (although multiple, not single) in lectotype from the Brady collection. We treat Stschedrina’s species as a junior synonym of J. macrescens. Lukina (1988) studied her material before Brönnimann et al. (1989) erected the genus Balticammina,
and it is unclear whether she saw *J. macrescens* or *B. pseudomacrescens*. Both species are present in the White Sea. The first species was recorded previously (as forms with areal openings: *T. cyclostoma*, *Jadammina cyclostoma* or *J. polystoma*, see Supplementary material S1), the second species occurred in our material.

*Balticammina pseudomacrescens* is a typical salt-marsh foraminiferan (Alve & Murray 1999; Gehrels & van de Plassche 1999; Gehrels & Newman 2004). Live specimens were certainly absent from the lower intertidal zone, for which we had good station coverage during this sampling campaign. The regular occurrence of empty tests in our samples suggests this species dwelled somewhere nearby. It is a task for the future to find out which habitats its populations occupy at these subarctic latitudes.

Monothalamous foraminifera lack diagnostic morphological features. For this reason, we do not try to compare species lists. Based on the limited data obtained, monothalamids seem as diverse as hard-shelled foraminifera in our samples. This fauna deserves a dedicated investigation.

**Elphidium distribution**

The differences between beaches in the foraminiferal fauna may be driven by a variety of environmental factors, including the dry period, sediment type, ice ploughing, availability of food, and so on. We either lack data to evaluate these factors or their effects appear minor in the study area. Only salinity has a consistent and large gradient, which is why we discuss only salinity, disregarding for the time being the other factors.

Within the variability revealed by the recurrent salinity survey, there was a consistent pattern: brackish water (\(<10\%_o\)S), overlying the estuary, dissipated in the adjacent straits (Figure 6). This consistency suggested that the broader picture based on non-recurrent data (Figure 5b) also was rather stable, despite the effect of tide and wind, and thus could be compared to the foraminiferal distribution. The four stations where *Elphidium excavatum* and/or *Elphidium albumblicatum* occurred but *E. williamsoni* was lacking indeed had the lowest surface salinity (Supplementary material S4). The only station situated within the Keret estuary (station 32) and characterized by the lowest salinity values yielded only *E. albumblicatum*.

The presence of elphidiids in areas mapped for the constant presence of brackish water (\(<10\%_o\)S), such as station 32, does not mean the foraminifera withstand such low salinities. The surface brackish layer is thin (Figure 5a), and therefore the intertidal zone is flooded with much saltier subsurface water every high tide, or at least during spring tides. When the tide ebbs and the overlying brackish layer impacts on the lower intertidal bottom, the littoral foraminifera may dig into the sediment where the pore water retains a high salinity (Langer et al. 1989).

The *Elphidium* distribution (Supplementary material S4) supports the notion that *E. excavatum* and *E. albumblicatum* tolerate decreased salinities (Conradsen 1993; Austin & Sejrup 1994; Hald et al. 1994; Alve 1995; Polyak et al. 2002). Besides, *E. albumblicatum* has been repeatedly mentioned as a brackish- and shallow-water species (e.g. Lutze 1965; Gehrels & Newman 2004). One would seek confirmation of the pattern at other river mouths. We did not find such in our study area. The Pulonga river mouth (see Figure 4 for location) had no soft-sediment beaches in its vicinity. The discharge of the Letnyaya river was weak; the brackish water even at low tide spread only a 100 m from the mouth (Supplementary material S4). The pattern, however, seems to be confirmed in other seas. On the Barents Sea coast of the Kola Peninsula, *E. williamsoni* occurs on beaches with normal marine salinity, whereas *E. albumblicatum* is found at river mouths (Korsun et al. 1994). At the Tana delta of northern Norway, *E. albumblicatum* is characteristic of the brackish setting (Corner et al. 1996). In the North Sea and Baltic Sea, all three *Elphidium* in different combinations have been reported from the intertidal zone (Alve & Murray 1999; Gehrels & Newman 2004; Horton & Edwards 2006), with *E. albumblicatum* reported from low-salinity environments (Nikulina et al. 2007; Polovodova et al. 2009). Further south, *E. albumblicatum* does not occur (Alve & Murray 1999), whereas the taxonomy of *E. excavatum* becomes complicated (Wilkinson 1979).

Surface salinity in the study area apparently varies throughout the year, but the data are scarce for seasons other than summer. According to accounts of personnel wintering over, the surface water under the fast ice (December–April) is drinkable (i.e. \(S = 0\%_o\)) even in the distal part of the Keret estuary (as compared to \(3\%_o\) measured over there during our recurrent survey in August, Figure 6). Apparently, the ice shields the sea from the wind, and the discharge of the Keret river flows undisturbed. The thickness of this freshwater layer is unknown. It probably wedges out seawards. During the flood (late April—early May), the surface salinity in the whole study area may plummet to \(<10\%_o\) as indicated by the oceanographic data from the multi-year monitoring station of the Zoological Institute (Babkov & Lukarin 1985), positioned axially in the outer Chupa inlet (between our foraminiferal stations 6 and 10 in Figure 4). However limited the local data are, they demonstrate that the seasonal change in the surface salinity is profound and that the lowest values are characteristic
of the oceanographic spring. It is not known how the seasonal salinity affects the foraminiferal distribution. Even though the distribution of the three *Elphidium* species in the intertidal zone appears coupled to the salinity (Supplementary material S4), neither our study nor those cited above have demonstrated that salinity controls the foraminiferal distribution directly in a physiological way. In fact, a survey along the profound salinity gradient at the coast of the Skagerrak (Alve & Murray 1999) has not revealed that *E. williamsoni* is any less frequent at low salinities than *E. excavatum* or *E. albuimbilicatum*. This may indicate that salinity preferences of the three species differ in certain regions only. That would mean that the effect of salinity is indirect. It may be mediated by another factor, e.g. the availability of preferred fresh- or brackish-water prey diatoms (cf. Alexander & Banner 1984; Knight & Mantoura 1985; Bernhard & Bowser 1999) or the longevity of the ice-cover period (decreased salinity facilitates freezing).

To conclude, the distribution of the intertidal *Elphidium* appears coupled to salinity. Yet the physiological nature of the link is not understood; the effect of salinity may be indirect. Of textulariid foraminifera, only *Ammotium cassis* is shown with certainty to inhabit the studied lower intertidal settings. The specific living conditions of the typical intertidal taxa, such as *Trochammina inflata*, *Jadammina macrescens* and *Balticammina pseudomacrescens* remain unknown. Monothalamids account for at least half of the species richness; most of the taxa are undescribed. The monothalamid fauna deserves a targeted study.

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