

**Environmental factors affecting recent benthic foraminiferal distribution  
in the south-eastern Baltic Sea**

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**Abstract.** The Baltic Sea is characterized by a restricted exchange of deep waters due to permanent stratification of the water column. The aim of the present study is to investigate the distribution of benthic foraminifera in the south-eastern part of the Baltic Sea in relation to environmental parameters. The distribution of benthic foraminifera was analyzed in 26 surface sediment samples collected in the south-eastern part of the Baltic Sea and in the Bornholm Basin during springtime and wintertime 2016. Foraminiferal diversity in the studied region was extremely low. Agglutinated specimens dominated the assemblages and were represented by small-sized individuals which belong to *Psammosphaera*, *Pseudothurammina*, *Saccammina*, and *Reophax* genera. Calcareous foraminifera were dominated by *Criboelphidium* genus. Micropaleontological data were compared to the environmental parameters characterizing bottom water (temperature, salinity, and dissolved oxygen content) and substrate conditions (grain size composition and total organic carbon content). Higher foraminiferal concentrations and diversity were found in deeper parts of the study region where fine-grained sediments with a higher total organic carbon content were accumulated under stable hydrographical conditions. Calcareous tests were found only at the stations with elevated salinity, indicating that bottom water salinity is the main factor limiting the distribution of calcareous foraminifera. On the other hand, substrate parameters and hydrodynamic conditions appear to play a major role in the distribution of agglutinated foraminifera.

**Keywords:** North Sea water inflows; grain-size composition; total organic content; Gdansk Basin; agglutinated foraminifera

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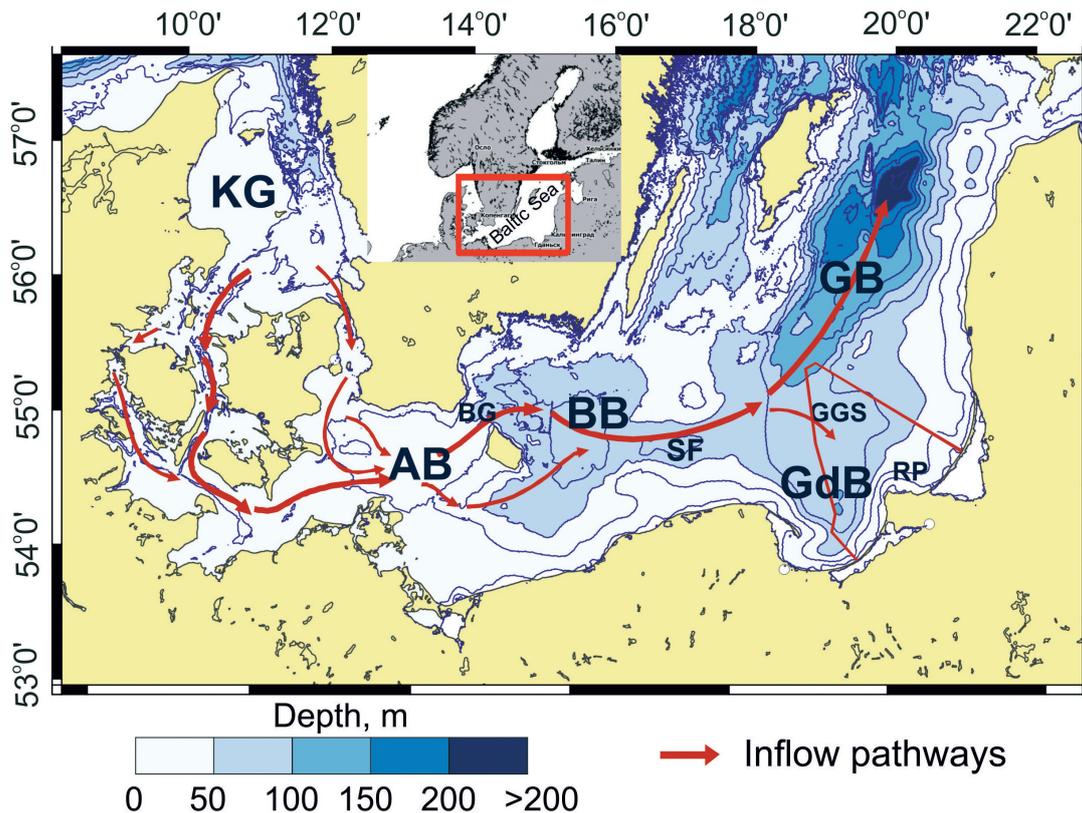
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## INTRODUCTION AND STUDY AREA

The Baltic Sea is a semi-enclosed brackish sea, with permanent stratification of the water column. Based on the sea floor topography, south-western and central Baltic can be divided into principal regions separated by submarine sills – the Danish Straits, the Arkona Basin, the Bornholm Basin, the Gdansk Basin, and the Gotland Basin (Hermelin 1987; Lepäranta, Myrberg 2009). The Gdansk Basin is separated from the Gotland Basin by the Gdansk-Gotland

Sill. Our study area comprises the Bornholm Basin, the Gdansk Basin, the Gdansk-Gotland Sill, and the south-eastern slope of the Gotland Basin (Fig. 1).

The Baltic Sea has a slow and restricted exchange of bottom waters via narrow and relatively shallow Danish straits. The hydrographic regime of isolated bottom water is strongly influenced by sporadic inflows of dense, high-saline, oxygenated North Sea water (Hermelin 1987; Kabel *et al.* 2012; Mohrholz *et al.* 2015). Due to a complex bottom topography, the propagation of inflow water is restricted, and the



**Fig. 1** Study area and direction of the North Sea water inflows (based on the combination by Matthäus 2006; Mohrholz *et al.* 2015). AB – Arkona Basin, BB – Bornholm Basin, BG – Bornholm Gatt, GB – Gotland Basin, GdB – Gdansk Basin, GGS – Gdansk-Gotland Sill, KG – Kattegat, RP – Rybachi Plateau, SF – Stolpe Furrow. The EEZR in the Baltic Sea is marked with red triangle

effect of inflows is always reduced by mixing (Matthäus 2006). With distance from inflow source increasing, the salinity in the Baltic decreases in the north-eastern direction. The general mechanism of inflow formation and further saltwater transport and transformation is relatively well studied and described (e.g. Mohrholz *et al.* 2018; Matthäus 2006; Mohrholz *et al.* 2015; Piechura *et al.* 1997; Paka 1996; Meier *et al.* 2004). Inflows are divided into two types – baroclinic and barotropic. Baroclinic events are driven by the salinity gradient between the Baltic and the North Sea. Barotropic ones are caused by sea level differences between the Kattegat and the western Baltic produced by wind forcing and air pressure differences. To impact deep-water conditions in the central Baltic to a significant degree, an inflow event must transport large amounts of highly saline (17–25 psu) water into the western Baltic. This water fills the chain of deep basins one by one. To describe this process, the term “Major Baltic Inflow (MBI)” has been introduced (Dickson 1971, 1973; Matthäus 2006; Mohrholz *et al.* 2018). To be characterized as a MBI, the main branch of dense and salty North Sea water has to flow from the Arkona Basin to the Bornholm Basin through the Bornholm Gatt. Then it has to spread further via the Stolpe Furrow all the way to Gotland and

Gdansk Basins in the central Baltic (Matthäus 2006; Kabel *et al.* 2012; Mohrholz *et al.* 2015; Hausler *et al.* 2017) (Fig. 1). Hence, the inflows which reach only the Bornholm Basin and do not propagate further to the central Baltic cannot be referred to as the MBIs.

A decreased MBI frequency observed since the 1980s has increased expansion of oxygen deficiency zones in the bottom water layer (Conley *et al.* 2002, 2009; Nausch 2008; Kabel *et al.* 2012; Jilbert and Słomp 2013; Carstensen *et al.* 2014). However, a lack of data on variations of hydrographic conditions in the past doesn't allow scientists developing a unified theory concerning MBI dynamic (Mohrholz *et al.* 2018).

Knowledge about the past variability of hydrographic conditions is required for understanding the changes in the Baltic Sea ecosystem, for identification of the natural component of these changes, and prediction of the future state under ongoing climate change. Paleoenvironmental reconstruction of highly dynamic brackish water environments, such as the Baltic Sea, requires a multidisciplinary approach involving micropaleontology, lithology, hydrography, and geochemistry. Foraminiferal analysis can play an integral role in reconstructing past environments; however, reliable interpretation of reconstructions

based on fossil foraminiferal assemblages requires knowledge of modern foraminiferal ecology in the study area. Previous studies showed that an average size, concentrations, and species diversity of benthic foraminifera in the Baltic Sea decrease north-eastward following the salinity gradient (Hermelin 1987). An exclusive economic zone of Russia in the south-eastern part of the Baltic Sea (hereinafter referred to as the “EEZR in the Baltic Sea”) is a relatively poorly studied area regarding the distribution and ecology of benthic foraminifera. Such studies are represented by few works (e.g. Saidova 1981; Lukashina 1995) due to low concentrations of shells in sediments and their poor preservation, which significantly complicates micropaleontological analysis (Frenzel *et al.* 2005).

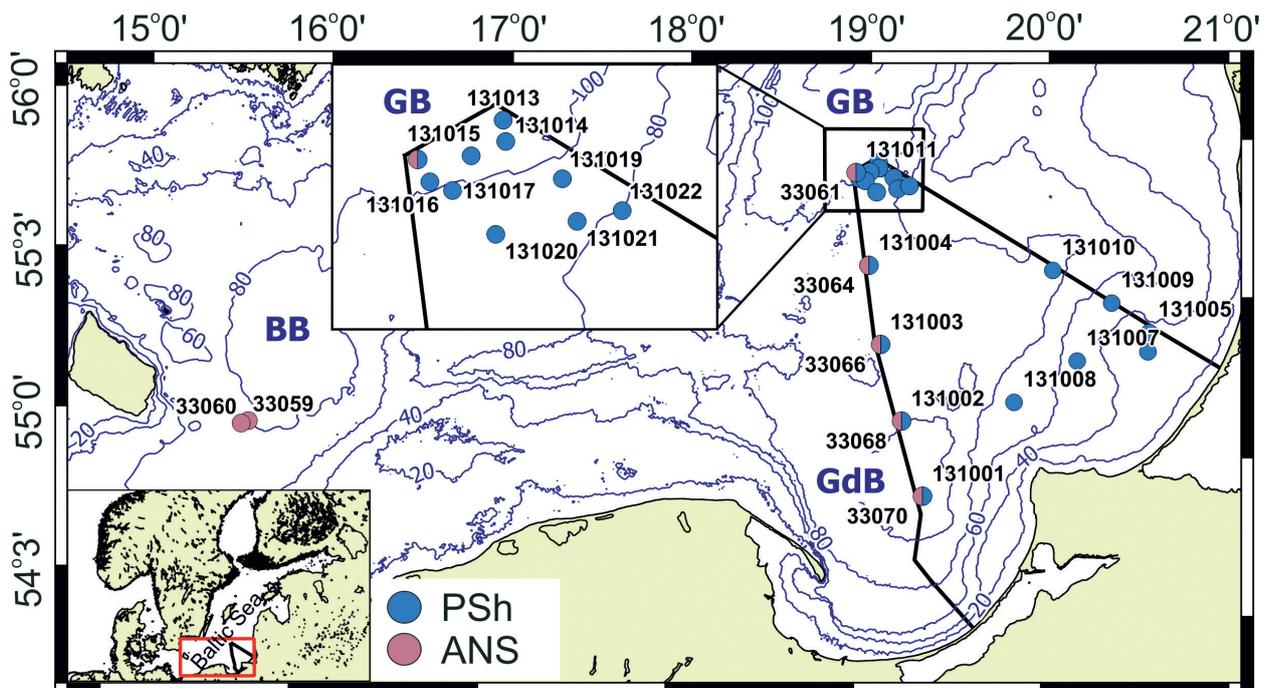
The present study is an extension of previous research focused on interrelation between the distribution of benthic foraminifera in the south-eastern part of the Baltic Sea and hydrography of bottom water (Ponomarenko and Krechik 2018). The aim of this work is to study the distribution of benthic foraminifera in the south-eastern part of the Baltic Sea (the EEZR in the Baltic Sea) in relation to bottom water (temperature, salinity, and dissolved oxygen) and substrate conditions (grain size and organic carbon).

## MATERIALS AND METHODS

This study is based on data obtained in the 131st cruise of the R/V “Professor Shtokman” (PSh, March–

April 2016) and 33rd cruise of the R/V “Akademik Nikolay Strakhov” (ANS, October–December 2016). In March–April 2016, samples of surface sediments were collected at 19 stations in the Gdansk Basin and on the south-western slope of the Gotland Basin using the “Ocean-50” grab. In October–December 2016, sampling stations were located along the western border of the EEZR in the Baltic Sea (5 stations) and in the Bornholm Basin (2 stations) (Fig. 2). The stations in the Bornholm Basin were used for a comparative analysis of changes in the benthic foraminiferal communities depending on the distance from the source of inflowing water. For subsequent analyses, the retrieved upper sediment layer of 0–1 cm was used. It should be noted that variation in sediment characteristics between springtime and wintertime results could be connected to seasonality, as well as to a simple difference in samples taken at the same stations due to the patchiness of foraminiferal distribution. Therefore, the data collected at the same stations in both cruises are presented and discussed together as an average for two samplings.

In the Gdansk Basin, samples were taken at water depths of 25–42 m on the Rybachy Plateau and at the depths of 42 to 106 m on the slopes and in the centre of the Gdansk Basin (Gdansk Deep). The water depth of sampling points was 72–85 m at the Gdansk-Gotland Sill and 85–109 m at the slope of the Gotland Basin. The average water depth at the study site located in the Bornholm Basin was 89 m. For a detailed information about sampling stations see Table 1.



**Fig. 2** Map of the study area. Dots indicate sampling stations during the 131st cruise of the R/V “Professor Shtokman” (blue dots) and 33rd cruise of the R/V “Akademik Nikolay Strakhov” (red dots); BB – Bornholm Basin, GB – Gotland Basin, GdB – Gdansk Basin. The EEZR in the Baltic Sea is marked with black triangle

**Table 1** Location and water depth of sampling stations during the springtime (PSh) and wintertime (ANS) of 2016

Station number	Latitude	Longitude	Water depth, m
PSh-131001	54°51.935'	19°20.967'	109
PSh-131002	55°05.964'	19°13.496'	101
PSh-131003	55°20.282'	19°05.950'	78
PSh-131004	55°35.155'	19°01.483'	88
PSh-131005	55°23.649'	20°34.055'	34
PSh-131006	55°19.856'	20°33.648'	32
PSh-131007	55°18.006'	20°10.438'	47
PSh-131008	55°10.043'	19°49.958'	68
PSh-131010	55°35.008'	19°02.034'	81
PSh-131011	55°52.593'	18°56.240'	107
PSh-131013	55°54.645'	19°03.485'	109
PSh-131014	55°53.608'	19°03.758'	109
PSh-131015	55°52.861'	19°00.810'	102
PSh-131016	55°51.531'	18°57.314'	104
PSh-131017	55°51.138'	18°59.288'	85
PSh-131019	55°51.861'	19°08.733'	78
PSh-131020	55°49.059'	19°03.126'	95
PSh-131021	55°49.802'	19°10.101'	75
PSh-131022	55°50.380'	19°13.961'	72
ANS-33059	54°59.99'	15°40.78'	100
ANS-33060	54°59.4'	15°38.68'	83
ANS-33061	55°52.39'	18°57.14'	103
ANS-33064	55°35.16'	19°1.74'	84
ANS-33066	55°20.282'	19°05.950'	83
ANS-33068	55°05.964'	19°13.496'	101
ANS-33070	54°51.935'	19°20.967'	109

### Grain size analysis

Grain size composition of muddy sediments was determined with a laser diffraction particle size analyzer SALD-2300 (Shimadzu, Japan). Organic carbon was preliminarily removed from samples by treatment with hydrogen peroxide. The dispersion of sediments before measurement was carried out in an ultrasonic bath with the addition of sodium hexametaphosphate. Grain size composition of samples with a high content of the sand fraction was determined using a combined method. Fractions coarser than 63  $\mu\text{m}$  were sieved through 63, 90, 125, 180, 250, 355, 500, 1000, 1400, 2000, 2800 and 4000  $\mu\text{m}$  meshes. Then the grain size composition of the remaining fraction of less than 63  $\mu\text{m}$  was determined with a laser analyzer. The results were combined based on measured sediment moisture. For samples with a high content of sand and gravel material, only sieving was applied. Statistical processing was carried out in the program Gradistat (Blott, Pye 2001). The mean size and sorting were determined according to Folk and Ward (1957). The type of sediment was derived by the Folk classification (Folk 1954).

### Estimated sedimentation rates

The sedimentation rate reported for the Gdansk Basin varies from 1–2 mm/year (Emelyanov 2002) to

1.5 cm/year (Blazhchishin 1998). Significantly lower sedimentation rates were described for the Gdansk-Gotland Sill and the slope of the Gotland Basin – 0.1 cm/year and 0.03 cm/year, respectively (Emelyanov 2002). Therefore, a 1 cm thick sediment sample corresponds to the age of 5 to 33 years.

### Bulk sediment geochemistry

The total organic carbon (TOC) content in sediments was estimated by the coulometric method with carbon analyzer AN-7529M. Samples from the slope of the Gotland Basin and the Rybachy Plateau were excluded from the analysis. At these sites, only gravelly and sandy deposits depleted in organic matter suitable for geochemical analysis were found.

### Foraminiferal analysis

For foraminiferal analysis, surface sediments (a total of 26 samples) were washed on a 63  $\mu\text{m}$  sieve. The sieve with such cell size allows taking into account small shells of foraminifera, which are common in brackish-water environments. The concentration of benthic foraminifera was counted as a number of individuals per 10 grams of dry sediment (ind/10 g). For a detailed description of micropaleontological analysis see Ponomarenko and Krechik (2018). Since the objective of this study is to identify the general patterns of the distribution of benthic foraminifera, the entire community contained in the retrieved upper centimetre of sediments was used for micropaleontological analysis without distinguishing living and dead individuals. The total fauna of foraminiferal assemblages within the sediment upper layer provides an integrated, time-averaged view of the foraminiferal fauna (Schröder-Adams 2006), but it may also include individuals transported post mortem (Murray 2006). Living foraminiferal communities are influenced by seasonality and small heterogeneities of the environment, while combined assemblages (alive and dead) reflect averaged long-term conditions and can serve as an example of fossil material in the study area (Murray and Alve 2011). Most individuals were identified under a stereomicroscope to the genus level due to a small shell size, breakage, and severe dissolution of calcareous shells. Because of the general difficulty to identify foraminifera to species level, no diversity indices were calculated. Additionally, the extremely low abundance of shells in most samples did not allow picking the required amount of 100–300 individuals for indices calculation (Sen Gupta 1999; Fatela, Taborada 2002; Holbourn *et al.* 2005). Calculation of genus richness was the only possible approach to estimate the diversity of communities.

### Hydrographical data

A statistical analysis of a five-year dataset (2014–2018) of bottom water parameters (temperature, sa-

linity, and dissolved oxygen) was performed by using STATISTICA 10 software to study the hydrographical regime in the south-eastern part of the Baltic Sea. The analysis was based on data obtained in 15 scientific cruises of IO RAS run from July 2014 to July 2018 (Kuleshov 2014a, b; Dorokhov 2015, 2016a, b, c, d; Paka 2016; Sivkov 2016; Krek 2017a, b, c, 2018). The high time resolution and period measurements allow describing spatial variation of average hydrographical conditions in the study region. The measurements of hydrographical parameters in the Gdansk Basin were carried out at the sampling points located on a transect along the western border of the EEZR in the Baltic Sea (Fig. 2). Hydrographical data for the Bornholm Basin were measured during the 33rd cruise of the R/V “Akademik Nikolay Strakhov” (December 2016) simultaneously with sediment sample collection.

The temperature and salinity of bottom water were measured using the Sea & Sun Tech CTD 90M and Idronaut Ocean seven 316. Dissolved oxygen in the bottom water layer was determined according to the Winkler titration method. Samples were taken using the HYDRO-BIOS Multi Water Sampler MWS 12 Slimline rosette.

## RESULTS

### *Grain-size composition and TOC content of sediments*

In the Bornholm Basin, surface sediments were represented by well-sorted fine material such as clayey silts and silts (mean grain size is 6–30  $\mu\text{m}$ ). The sediments found at the station ANS-33060 from the Bornholm Basin had a slight odour of hydrogen sulfide. The TOC content in sediments was 5%.

On the slope of the Gdansk Basin, poorly sorted silty-clayey sands with the mean diameter of 24  $\mu\text{m}$  were found. Clayey silts and silts with the mean grain size of 4–5.5  $\mu\text{m}$  and a smell of hydrogen sulfide were typical of the stations located in the centre of the Gdansk Basin. The TOC content varied from 4 to 5.6%.

At the stations of the Rybachy Plateau, the presence of boulders and different-grained sand with the inclusion of gravel and pebbles was registered. The mean grain size varied from 212 to 8041  $\mu\text{m}$ .

Finally, the sediments of the Gdansk-Gotland Sill and the slope of the Gotland Basin were represented by poorly sorted different-grained sands and clayey-sandy silts with admixture of coarse material, pebbles, and gravel. The mean grain size ranged from 6 to 635  $\mu\text{m}$ . The TOC content varied from 0.7% in poorly sorted coarse-grained material to 4.3% in clayey-sandy silts. The bottom surface of the slope of the Gotland Basin was covered with a thin layer of

fine-grained soupy and soft mud with TOC content of up to 6.7%.

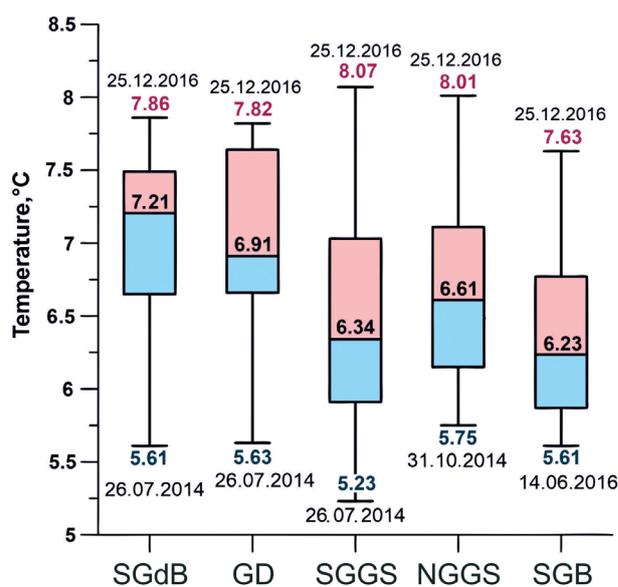
### *Hydrographical and hydrochemical conditions*

On the slope of the Gdansk Basin and in the Gdansk Deep (the deepest part of the basin), at the depths of more than 90 m, the salinity and temperature of the bottom water mass were similar (Figs 3, 4). On the slope of the Gdansk Basin, the temperature range of 5.6–7.9°C and salinity range of 11.9–14.4 psu were recorded. Oxygen showed a variability of 0.2 to 2.8 ml/l. In the Gdansk Deep, temperature varied between 5.6 and 7.8°C, while salinity showed the range of 11.8 to 14.4 psu. Bottom water oxygen varied between 0.2 and 3.8 ml/l (Fig. 5).

At the southern part of the Gdansk-Gotland Sill, the temperature of bottom water changed from 5.2 to 8.1°C, while salinity varied between 10.3–12.9 psu (Figs 3, 4). The northern part of the Gdansk-Gotland Sill was characterized by the temperature range of 5.8–8.0°C and salinity range of 11.7–13.4 psu. Within the Gdansk-Gotland Sill, the lowest dissolved oxygen was >1.6 ml/l (Fig. 5), while the highest oxygen concentration recorded was 6.84 ml/l.

The slope of the Gotland Basin was characterized by the lowest variability in temperature and salinity (Figs 3, 4). The temperature range of 5.6–7.6°C and salinity range of 11.5–12.6 psu were recorded. Bottom water oxygen showed the variability of 0.4–3.9 ml/l (Fig. 5).

In December 2016 in the Bornholm Basin, the salinity and temperature of bottom water were considerably higher (> 18 psu and 7.5–10.3°C, respectively)



**Fig. 3** Boxplot of temperature in the bottom water layer at the transect located along the western border of the EEZR in the Baltic Sea; SGdB – slope of the Gdansk Basin, GD – Gdansk Deep, SGGS – southern part of the Gdansk-Gotland Sill, NGGS – northern part of the Gdansk-Gotland Sill, and SGB – slope of the Gotland Basin

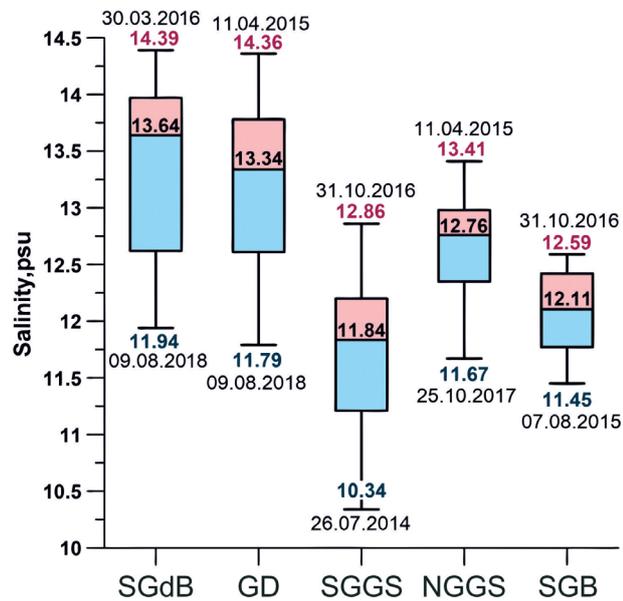
compared to averaged values for the south-eastern part of the Baltic Sea. The content of dissolved oxygen in bottom water was 3.1 ml/l.

### Foraminiferal distribution

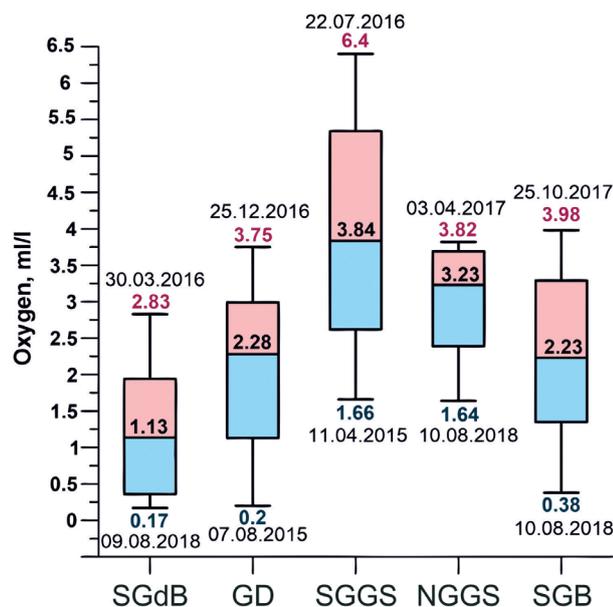
Based on our data, distribution of benthic foraminifera demonstrates low abundances and diversi-

ty. The concentrations of benthic foraminifera varied greatly: from 0.2 to 453.4 individuals per 10 grams of sediment (Table 2). The lowest foraminiferal concentrations were found in the sediments of the Rybachy Plateau (0.2 and 0.6 ind/10g). On the slopes of the Gdansk Basin, foraminiferal concentration was 3.7–18.7 ind/10g. The concentration of 101.4 ind/10 g was observed in the Gdansk Deep. The highest shell concentrations of 83.7 and 453.4 ind/10 g were found in the sediments of the Gdansk-Gotland Sill. On the slope of the Gotland Basin, the concentration of foraminifera in sediments increased with depth, changing from 0.6 to 144.4 ind/10 g. In the sediments collected in the Bornholm Basin, the concentration of foraminifera was considerably higher compared to average values obtained for the Gdansk Basin and varied from 347.9 to 369.5 ind/10 g.

Altogether 11 genera were identified in the samples (see faunal list in Appendix 1). Agglutinated foraminifera dominated the assemblages and were represented in 9 of 11 genera. Among them, small-sized individuals (less than 100 µm) with simple unilocular tests were the most abundant. Only one genus was found in the sediments of the Rybachy Plateau (Table 2). The highest genus richness of 7 genera was identified in the Gdansk Deep. On the slopes of the Gdansk Basin, genus richness varied from 1 to 4



**Fig. 4** Boxplot of salinity in the bottom water layer at the transect located along the western border of the EEZR in the Baltic Sea; SGdB – slope of the Gdansk Basin, GD – Gdansk Deep, SGGS – southern part of the Gdansk-Gotland Sill, NGGS – northern part of the Gdansk-Gotland Sill, and SGB – slope of the Gotland Basin



**Fig. 5** Boxplot of oxygen in the bottom water layer at the transect located along the western border of the EEZR in the Baltic Sea; SGdB – slope of the Gdansk Basin, GD – Gdansk Deep, SGGS – southern part of the Gdansk-Gotland Sill, NGGS – northern part of the Gdansk-Gotland Sill, and SGB – slope of the Gotland Basin

**Table 2** The concentration of benthic foraminiferal shells and genus richness in studied samples

Sample name	Shell concentration (ind/10 g)	Genus richness
PSh-131001 / ANS-33070	101.4	7
PSh-131002 / ANS-33068	17.9	4
PSh-131003 / ANS-33066	453.4	4
PSh-131004 / ANS-33064	83.7	2
PSh-131005	0.2	1
PSh-131006	0.6	1
PSh-131007	3.7	2
PSh-131008	4.9	2
PSh-131010	18.7	1
PSh-131011 / ANS-33061	144.4	6
PSh-131013	10.4	4
PSh-131014	0.6	1
PSh-131015	4.6	3
PSh-131016	1.6	3
PSh-131017	4.7	3
PSh-131019	2.3	2
PSh-131020	2.1	2
PSh-131021	2.5	5
PSh-131022	1.9	1
ANS-33059	369.5	6
ANS-33060	347.9	4

genera per sample. In the sediments of the Gdansk-Gotland Sill, genus richness showed variability of 4 to 6 genera per sample. On the slope of the Gotland Basin, genus richness grew with depth from 1 to 6 genera per sample. In the sediments of the Bornholm Basin, genus richness varied from 4 to 6 genera per sample.

The most numerous genera were *Crithionina*, *Pseudothurammina*, *Psammosphaera*, *Saccammina*, and *Reophax*. Other genera occurred only sporadically in extremely low abundances, so they were left out of discussion. *Crithionina* sp. was present in the sediments of the slope of the Gotland Basin only (Figs 6, 7), and its tests concentration in the sediments increased with water depth. *Psammosphaera* sp. was found at all studied locations except for the Gdansk Deep (Figs 6, 7). The highest shell concentration of this genus was identified at the slope of the Gotland Basin. Individuals of *Pseudothurammina* sp. were distributed in the sediments of the entire study region, with the exception of the Rybachy Plateau (Figs 6, 7). High shell concentration was found in the sediments of the Gdansk-Gotland Sill and in the Bornholm Basin. Individuals of *Reophax* genus were found at all stations, except for the Rybachy Plateau, with the highest shell concentrations recorded on the Gdansk-Gotland Sill and in the Bornholm Basin (Figs 6, 7). *Saccammina* sp. individuals were absent in the sediments of the Gdansk Deep and the Rybachy Plateau. The highest shell concentration of this genus was recorded in the Bornholm Basin. The calcareous foraminiferal assemblage was dominated by *Cribrorbulina* (*Elphidium*) genus. In the south-eastern part of the Baltic Sea, carbonate shells were found only in the Gdansk Deep, while in the Bornholm Basin they were present at all stations (Figs 6, 7).

## DISCUSSION

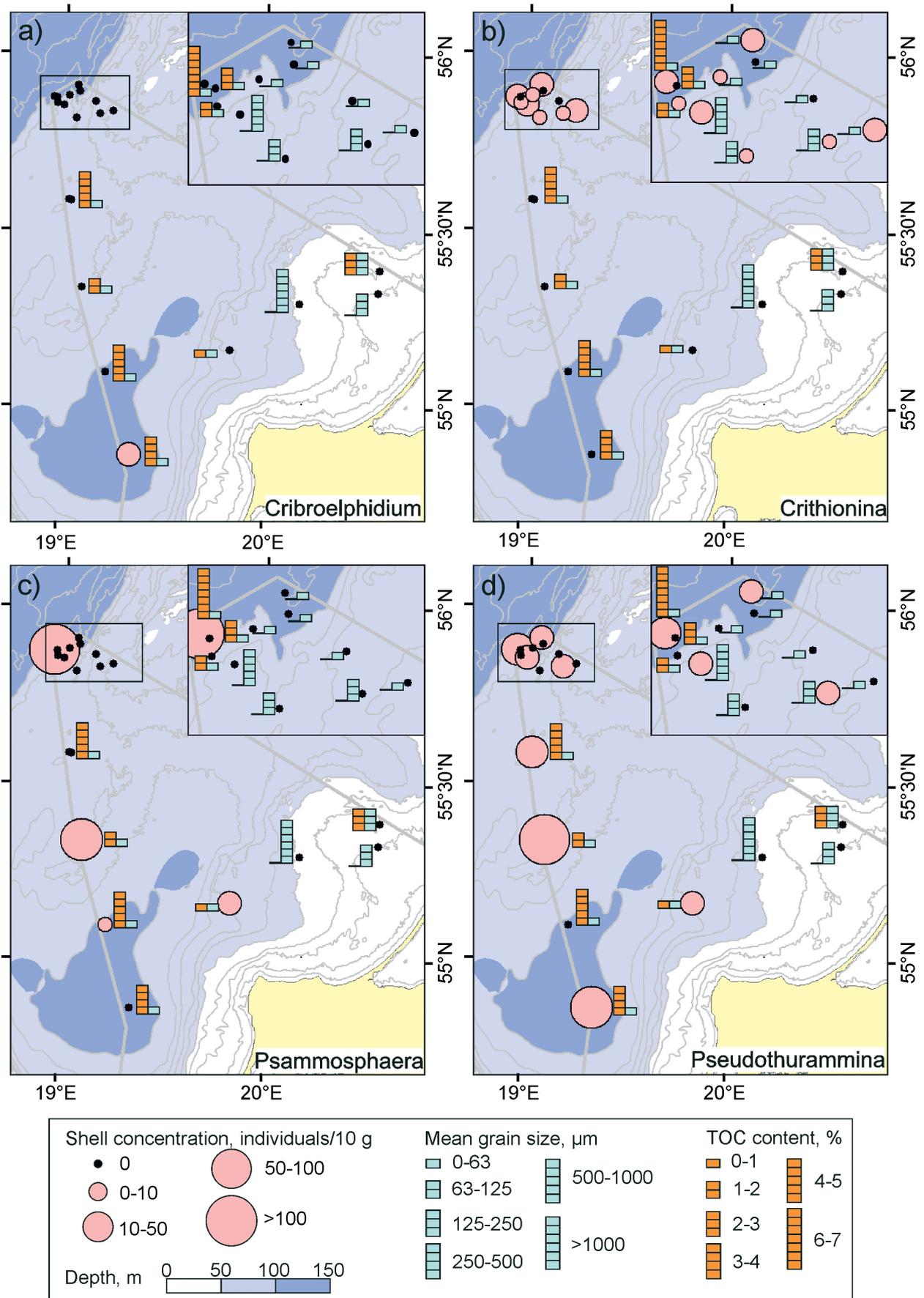
Though foraminiferal communities in the EEZR in the Baltic Sea were characterized by low diversity, they included a high amount of opportunistic and common infaunal genera. Similar assemblages were described as common for brackish-water environments (Schroder-Adams 2006). Depleted species richness of the Baltic Sea was also noted in the studies performed for the western regions (Polovodova *et al.* 2009; Brodniewicz 1965; Murray 2006; Binczewska *et al.* 2017). Investigated surface sediments were strongly dominated by agglutinated genera. Among them, small individuals with simple unilocular tests were the most common. A similar trend has been identified in the studies of benthic foraminiferal distribution in the western Baltic Sea (e.g. Hermelin 1987; Brodniewicz 1965). A size decrease of benthic foraminifera in the Baltic Sea is likely to be a

response of organisms to low salinity (Brodniewicz 1965; Hermelin 1987; Binczewska *et al.* 2017).

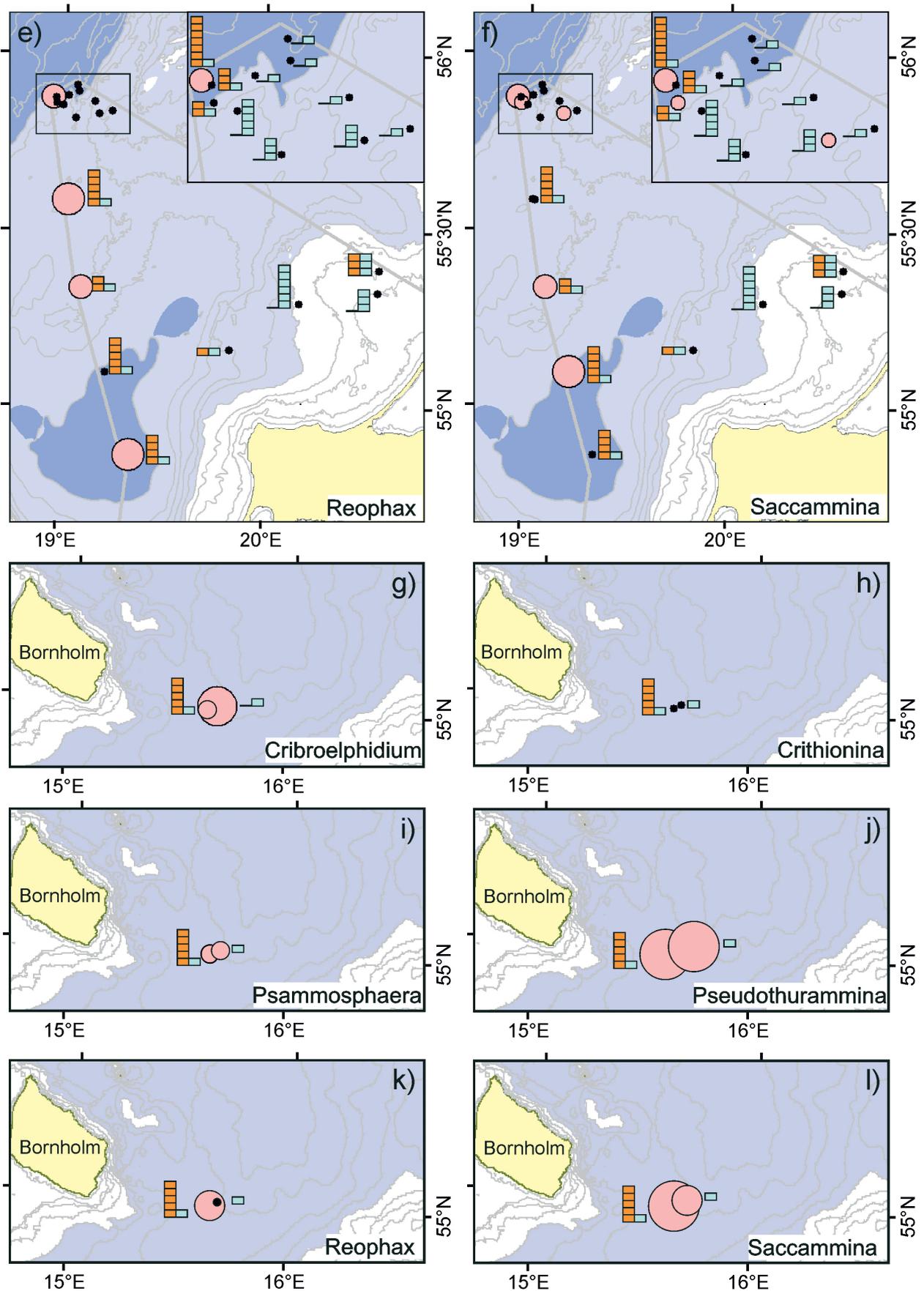
Minimum foraminiferal concentrations and genus richness were found in the sediments of the Rybachy Plateau, where only occasional rare tests of *Psammosphaera* sp. were found. It is likely that highly dynamic conditions of the shallow nearshore zone and coarse-grained sediments with a low TOC content create an extremely unfavourable environment for foraminifera. *Psammosphaera* was described as a genus being found in intertidal-subtidal environments (Baccaret 1987; Murray, Alve 2011) and in the perireefal area, and it is rare to common in the lagoon (Baccaret 1987). Murray and Alve (2011) reported *Psammosphaera* from the shelf and shelf deeps. The latter species depth range of 16–1600 m was reported from shelf and slope settings by Stefanoudis (2016). Thus, *Psammosphaera* sp., usually associated with sandy sediments in areas of intense near-bottom hydrodynamic (Baccaret 1987; Murray, Alve 2011), is the only genera able to survive in the sandy sediments of the Rybachy Plateau.

In the Gdansk Basin and on the slope of the Gotland Basin, increased foraminiferal concentrations and a relatively high genus richness, in comparison with other sampling stations, were recorded indicating close environmental conditions at these sites. Foraminiferal concentrations and genus richness increased with water depth, with simultaneous increase in TOC content in sediments and with grain size change from sandy to fine-grained, soft silty and muddy sediments. The temperature measured in these locations showed little variability. The slope of the Gotland Basin was also characterized by a less variable salinity indicating relatively stable hydrographical conditions. In our study, individuals of agglutinated genus *Crithionina* were found only on the slope of the Gotland Basin. *Crithionina* was reported from the shelf and slope settings at the water depth of 16–1600 m rather than at abyssal depths (Stefanoudis 2016). This genus lives in an infaunal habitat, being found in the uppermost centimetre of the sediment (Thies 1990). Together with our results, this can serve as evidence that this genus prefers stable hydrographic conditions with soft fine-grained sediments and high food availability.

Agglutinated individuals of *Psammosphaera*, *Pseudothurammina*, *Reophax* and *Saccammina* genera occurred all over the Gdansk Basin and on the slope of the Gotland Basin. All these genera were found in the shallow-water habitats with pronounced variations in physical and chemical conditions as tidal inlets, upper estuary banks, bays and lagoons. Variable sediment grain size from mud with variable amounts of sand to fine and coarser sand was reported for these genera (Lagoe 1979; Goldstein 1988; Gold-



**Fig. 6** Distribution of benthic foraminiferal genera in the surface sediments of the EEZR in the Baltic Sea (a–d) in relation to water depth, grain size, and TOC content in sediments



**Fig. 7** Distribution of benthic foraminiferal genera in the surface sediments of the EEZR in the Baltic Sea (e, f) and the Bornholm Basin (g–l) in relation to water depth, grain size, and TOC content in sediments. For legend see Fig. 6. The position of the sampling area in the Bornholm Basin is shown in Fig. 2

stein and Harben 1993; Hayward and Hollis 1994). Adaptation to a wide range of environmental conditions favoured the distribution of these genera in the Gdansk Basin and on the slope of the Gotland Basin. Concentration of *Psammosphaera*, *Pseudothurammina* and *Saccammina* tests increased with water depth following a change to a more fine-grained sediment, increase in TOC content and hence better food availability, and less intense hydrodynamic. *Saccammina* genus is found in environments with a wide salinity range of 28–32 psu (Lagoe 1979; Goldstein 1988). Our study confirms these findings and shows that this genus can tolerate salinities as low as 10.3 psu.

Carbonate shells of *Criboelphidium* (*Elphidium*) sp. were found only in the Gdansk Deep and Bornholm Basin. In the Gdansk Deep, the range of salinity is rather large; and the highest salinity of the EEZR in the Baltic Sea was recorded in the Gdansk Deep. The variability of hydrographical conditions indicates sporadic pulses and accumulation of saline water induced by the MBIs, which creates preferable salinity levels for the *Criboelphidium* genus. However, the lowest dissolved bottom water oxygen close to zero was also found in this area, indicating re-occurring anoxic conditions. A combination of these parameters explain why *Criboelphidium* (*Elphidium*) sp. sharply dominated among calcareous fauna found in the study area. *Criboelphidium* (*Elphidium*) genus occurs in brackish (12 psu) to normal marine waters (35 psu) worldwide. This genus is usually the most abundant calcareous form in moderately brackish settings (Hayward, Hollis 1994). *Criboelphidium* (*Elphidium*) was reported by numerous authors from seaward parts of estuaries, enclosed harbours and inlets, intertidal zones, marginal marine locations, and shallow areas adjacent to straits (Hermelin 1987; Conradsen 1993; Hayward, Hollis 1994; Polovodova *et al.* 2009). It is known as an extremely tolerant genus which can stand high fluctuations in salinity and temperature and is relatively insensitive to oxygen depletion (Conradsen 1993 and references therein; Binczewska *et al.* 2017; Brodniewicz 1965; Hausler *et al.* 2017; Kaiho 1994; Lutze 1965; Murray 2006).

In the sediments of the Gdansk-Gotland Sill, genus richness of benthic foraminifera was low. At the same time, the sill was recorded to have the highest foraminiferal concentration. Surface sediments were represented by poorly sorted sandy silts with a variable TOC content and corresponded to the outcrops of relict glacial till (Emelyanov 2002; Dorokhov *et al.* 2018). Highly variable hydrographic conditions at the sill are caused by the proximal position of the halocline to the bottom. Low temperature and salinity values as well as oxygenated bottom water indicate the influence of a cold intermediate water layer lying above the halocline. According to Emelyanov, Grit-

senko (1999), the Gdansk-Gotland Sill is on the pass of the North Sea water inflows, which is reflected in a high range of hydrographical parameters. The absence of muddy sediments on the sill may be explained by a high activity of inflows or inner waves occurring at the halocline (Blazhchishin 1998).

*Pseudothurammina* and *Psammosphaera* genera were found at the Gdansk-Gotland Sill in highest concentrations as compared to the entire study region. *Saccammina* and *Reophax* genera were less abundant in the sediments of the sill. According to previous studies, *Pseudothurammina* and *Reophax* genera are reported to have infaunal habitats in marshes, subtidal locations, estuaries, enclosed harbours, perireefal stations and brackish pans of fjords (Baccaret 1987; Goldstein, Harben 1993; Hayward, Hollis 1994). Egger *et al.* (2003) described *Saccammina* and *Psammosphaera* genera as epi- and infaunal passive deposit feeders. Due to infaunal habitats, these genera are likely to be better adapted to variable hydrographic conditions caused by the proximity of the halocline, such as those found at the Gdansk-Gotland Sill. Individuals of *Pseudothurammina* and *Psammosphaera* are also found to be associated with sandy sediments depleted in organic matter (Goldstein, Harben 1993). In many studies, *Reophax* is related to fine-grained muddy sediments (Hayward, Hollis 1994; Goldstein, Harben 1993). However, according to Murray, Alve (2011), this genus is usually found in sandy sediments formed under intensive bottom currents. *Saccammina* is found in muddy sediments with variable amounts of very fine to coarse sand (Lagoe 1979). The described substrate preference can serve as an explanation of high shell abundance in poorly sorted sediments with varying organic content found at the sill in our study. Oxygen is always present in bottom water at the Gdansk-Gotland Sill because of its shallower depths in comparison with surrounding basins, the influence of the intermediate water layer, and North Sea water inflows. It is also likely that the proximity of the halocline to the bottom favours suspended matter accumulation and hence food availability at the sill. Hence, well oxygenated near-bottom water and the presence of food can explain high foraminiferal concentration found in the sill.

In the Bornholm Basin, foraminiferal concentrations were higher than the average for the entire south-eastern Baltic observed in this study. Furthermore, a high genus richness was found in the basin, with all genera, except for *Crithionina*, present in its sediments. Calcareous tests of *Criboelphidium* (*Elphidium*) sp. were present at all stations. The basin also exhibited the highest concentration of *Saccammina* genera. In the Bornholm Basin, silty and muddy sediments with a high TOC content and considerably higher near-bottom water salinity due to the proxim-

ity to the inflow source most likely present favourable environmental conditions for the most of foraminiferal genera reported herein.

## CONCLUSIONS

Our data from the south-eastern part of the Baltic Sea indicate that the geographic distribution of benthic foraminifera follows the variability of environmental parameters such as bottom water (temperature, salinity, and dissolved oxygen content) and substrate conditions (grain size composition and total organic carbon content). The foraminiferal genus richness in the studied region was rather low due to brackish conditions. Agglutinated specimens of small size and with simple unilocular tests dominated the assemblages. Increase in foraminiferal concentrations and diversity was found in the deeper parts of the study region. For example, in the Gdansk Deep, the slope of the Gotland Basin and Bornholm Basin, silty and muddy sediments with a higher TOC content were accumulated under more stable and calm hydrographic conditions, whereas higher salinity of bottom water created favourable conditions for foraminifera. Calcareous tests of *Criboelphidium* (*Elphidium*) sp. were present only at the stations with increased salinity in the Bornholm Basin and Gdansk Deep, which confirms salinity to be the main factor limiting calcareous foraminiferal distribution in the Baltic Sea. Thereby, the North Sea inflow frequency and volume are crucial parameters for the presence of calcareous foraminifera in the south-eastern part of the Baltic Sea. At the same time, grain size composition and organic content of substrate appear to play a major role in the distribution of agglutinated foraminifera, as it has been shown for the Gdansk-Gotland Sill and Rybachy Plateau. The revealed relationship can be used as a baseline for the application of the distribution of benthic foraminifera in sediment cores for the paleoreconstruction of environmental conditions in the Baltic Sea.

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#### APPENDIX A. FAUNAL LIST OF SPECIES FOUND DURING THIS STUDY

- Bathysiphon* sp. Sars, 1872
- Cribrulephidium* sp. Cushman & Brönnimann, 1948
- Cribrulephidium excavatum* Terquem, 1875 (*Polys-tomella excavata* Terquem, 1875)
- Cribrulephidium incertum* Williamson, 1858
- Crithionina cf. pisum* Goës, 1896
- Melonis* sp. Montfort, 1808
- Miliammina fusca* Brady, 1870 (*Quinqueloculina fusca* Brady, 1870)
- Psammosphaera* sp. Schulze, 1875
- Pseudothurammina* sp. Scott, Mediolli & Williamson, 1981
- Reophax* sp. Montfort, 1808
- Reophax regularis* Höglund, 1947
- Reophax mankowskii* Brodniewicz, 1965
- Rhabdammina* sp. Sars in Carpenter, 1869
- Saccammina* sp. Sars in Carpenter, 1869
- Thurammina cf. papillata* Brady, 1879