Original Article

The Baltic Sea scale inventory of benthic faunal communities

Mayya Gogina1*, Henrik Nygård2, Mats Blomqvist3, Darius Daunys4, Alf B. Josefson5, Jonne Kotta6, Alexey Maximov7, Jan Warzocha8, Vadim Yermakov9, Ulf Gräwe1, and Michael L. Zettler1

1Leibniz Institute for Baltic Sea Research (IOW), Warnemünde, Seestr. 15, 18119 Rostock, Germany
2Marine Research Centre, Finnish Environment Institute SYKE, PO Box 140, FI-00251 Helsinki, Finland
3Hafok AB, 179 61 Stenhamra, Sweden
4Coastal Research and Planning Institute, Klaipeda University, H. Manto Str. 84, LT-92294 Klaipeda, Lithuania
5Department of Bioscience, Aarhus University, Frederiksbergvej 399, 4000 Roskilde, Denmark
6Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia
7Zoological Institute Russian Academy of Science, Universitetskaja nab. 1, 199034 St Petersburg, Russia
8National Marine Fisheries Research Institute, ul. Kolłątaja 1, 81-332 Gdynia, Poland
9Latvian Institute of Aquatic Ecology, Daugavgrīvas Str. 8, LV-1048 Riga, Latvia

*Corresponding author: tel: +49 381 5197 393; fax: +49 381 5197 211; e-mail: mayya.gogina@io-warnemuende.de

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This study provides an inventory of the recent benthic macrofaunal communities in the entire Baltic Sea. The analyses of soft-bottom benthic invertebrate community data based on over 7000 locations in the Baltic Sea suggested the existence of 10 major communities based on species abundances and 17 communities based on species biomasses, respectively. The low-saline northern Baltic, characterized by silty sediments, is dominated by Monoporeia affinis, Marenzelleria spp., and Macoma balthica. Hydrobiidae, Pygospio elegans, and Cerastoderma glaucum dominate the community in sandy habitats off the Estonian west coast and in the southeastern and southern Baltic Sea. Deep parts of the Gulf of Finland and central Baltic Sea often experience hypoxia, and when oxygen levels in these regions recover, Bylgides sarsi was the first species to colonize. The southwestern Baltic Sea, with high salinity, has higher macrofaunal diversity compared with the northern parts. To spatially interpolate the distribution of the major communities, we used the Random Forest method. Substrate data, bathymetric maps, and modelled hydrographical fields were used as predictors. Model predictions were in good agreement with observations, quantified by Cohen’s $k$ of 0.90 for the abundance and 0.89 in the wet weight-based model. Misclassifications were mainly associated with uncommon classes in regions with high spatial variability. Our analysis provides a detailed baseline map of the distribution of benthic communities in the Baltic Sea to be used both in science and management.

Keywords: Baltic Sea, community analysis, large scale, macrozoobenthos, Random Forest, spatial distribution.

Introduction

In the recent decades, there has been a marked increase in benthic habitat mapping, largely inspired by the development and implementation of various research and monitoring programmes, management plans, and legislations, such as the 1992 EU Habitats Directive. This has resulted in an exponential accumulation of data hitherto stored as different non-standardized national datasets. Here for the first time, we bring much of these datasets together and harmonize them to address management issues on the large Baltic Sea scale. Similar large-scale efforts were previously reported for the North Sea in Rees et al. (2007), for the Barents Sea in Anisimova et al. (2010).

The focus of our study was identification, description, and basin scale mapping of major benthic macrofauna community distribution in the Baltic Sea. A number of works were previously published, describing and mapping the benthic macrofauna communities in different subbasins of the Baltic Sea (e.g. Warzocha, 1995; Laine, 2003; Glockzin and Zettler, 2008; Gogina et al., 2010). However,
we identified a lack of joint data analyses covering the entire Baltic Sea region based on new data collected since 2000.

At the beginning of the last century, Petersen (1913) introduced the concept of infraunal communities for the description and quantification of areas with similar fish food. He aggregated the infraunal species in relation to broad geographic areas of relatively uniform sediments, depth, and salinity. Petersen (1913) described various soft sediment benthic macrofauna assemblages in different regions of the Baltic Sea. The scale of the investigated area and its heterogeneity allowed for high resolution of classification detail, and the definition of a number of communities or assemblages. Summaries on the distribution of fauna in the Baltic Sea can be found in works of early investigators such as Hesde (1924), Valikangas (1933), Ekman (1933, 1935), and Segerstråle (1957). Based on the findings outlined by Zenkevitch (1963), Schiewer (2008) listed the most important Baltic Sea coenoses or assemblages of species. These were (i) Abra alba-coenosis with Corbula gibba, Arctica islandica, Lagis koreni, Nephys spp., Distylus rathkei, and Ophiura albida which predominate in the western Baltic. Towards the east (ii) Arctica-Astarte assemblages were increasingly found. In the shallow part of the Baltic Proper (iii) Macoma calcarea coenosis dominated, whereas in the deeper part (iv) Macoma calcarea coenosis (with Mya truncata and Astarte) occurred. Farther in the eastern soft-bottom areas (v) Saduria-Monoporeia-Pontoporeia coenosis with euryhaline species were found, and Gotland Deep, strongly affected by oxygen depletion, was colonized only by (vi) a species-poor hypolimnic community. One of the deepest basins in the Baltic Sea, the Landsort Deep, was characterized by long-term azoic, laminated hypolimnic community. One of the most significant macrofaunal taxa were grouped to genus or even higher taxa.

GIS databases were utilized for collating the distribution of benthic macrofauna covering the entire Baltic Sea basin. Most data (77%) were collected with a van Veen grab (covering a bottom area of 0.1 m²), 1–3 replicates per sampling were taken, sieved on a 1 mm mesh, preserved in 4% buffered formaldehyde–seawater solution, and identified in the laboratory to the lowest taxonomic level possible. Table 1 provides more details including specifications and the area covered by each laboratory. All species abundance and biomass data were recalculated to the area of 1 m². Biomass records were available for 75% of the samples. Wet weight (including calcaceous structures, without tubes) were only available for 2943 (39%) locations and ash-free dry weight for 2241 (29.7%) locations. Only wet weight were used for further analysis. Where only dry or ash-free dry weight data were available, in-house (IOW) biomass data conversion factors were used to calculate wet weight. The conversion factors are available upon request.

For the analyses, we used a 5 × 5 km grid (matching one-quarter of the European Environment Agency EEA 10 km reference grid size). Inner coastal fjords, estuaries, and lagoon regions were omitted from the analysis due to higher macrofauna variability, and because these areas contained a large part of freshwater organisms not representative for the broadscale picture of the entire Baltic. Average taxonomic unit abundances were calculated to account for all samples within one grid cell. Biomass records were obtained for 2268 of 5 × 5 km grid cells. Such aggregation of data neglects fine-scale spatial differences in the community structure and ignores temporal variation within the study period in the favour of capturing the most important large-scale patterns.

Community analysis
Cluster analysis (group-average linking) and nMDS (not presented here for brevity) were conducted to reveal similarities between stations. For multivariate analyses, we used taxa determined to the species level, where possible. Difficult taxa such as oligochaetes and chironomids were not identified to lower taxonomic level. Some characteristic Baltic Sea taxa were grouped to genus or even higher taxonomic level (Diastylis, Harmathoe, Exogone, Hydrodriidae, Idotea, Nephys, Ophiura, Phoronis, Polydora, Diptera) to overcome taxonomic inconsistencies. For abundance-based analysis, only taxa that occurred at more than ten sampling events and contributed to the top 90% of the cumulative abundance per sampling event were retained. This reduction was done for better detection of the underlying community similarities and resulted in 272 taxa. For biomass analysis, taxonomic units were selected based on two criteria: either among top five species with highest biomass recorded at any sampling event or contributed to 80% of the cumulative total biomass. It resulted in the selection of 381 taxa. Abundance and biomass data matrices can be found in the Supplementary material.

All abundance data were fourth-root transformed, and biomass data were log(x + 1)-transformed to account for the biasing effect of few high and low data values. Zero-adjusted Bray–Curtis similarities were calculated between stations. Clarke et al. (2006) suggested solving the problem of denuded samples in data (i.e. no common species among two sites) by using a dummy variable being equal to 1 for all objects allowing for the coefficient to be defined in these cases, thus avoiding bias. We used the dissimilarity matrix to perform a

Methods
Joint dataset
The standardized dataset comprised over 1000 taxa from over 7000 locations (17 000 visit events) mostly sampled in period 2000–2013 for species abundance and partly for biomass (Figure 1). Overall, 1176 taxonomic units (accepted in the World register of Marine Species WoRMS) were included in the final dataset. Over 70% of the samples were collected from May to July and therefore, the dataset is biased towards spring and early summer.
hierarchical cluster analysis (group-average). Community clusters were determined by selecting a distance where stations were grouped in well-defined clusters (arbitrary based on expert judgement). The classification results were tested with a one-way PERMANOVA based on the Bray–Curtis similarity matrix using 999 random permutations (Anderson, 2001). See Anderson and Walsh (2013) for the warning on usage of this test for unbalanced designs where heterogeneity of dispersions is known to occur. These analyses were conducted in PRIMER v6 (Clarke and Warwick, 2001).

Finally, we applied Similarity percentage analysis (SIMPER, Clarke and Warwick, 2001) and Indicator value analysis (IndVal

Table 1. Sampling equipment used for different datasets included and availability of biomass.

| Source | Sampler | Sampler area (m^2) | Mesh size (mm) | n sampling events | Biomass                   |
|--------|---------|--------------------|----------------|-------------------|--------------------------|
| DK     | Haps    | 0.0143             | 1              | 191               | To species               |
|        | van Veen| 0.1                | 1              | 313               |                          |
| EST    | Ekman-Birse | 0.021            | 0.25           | 2153              | Dry weight, to species   |
|        | Box     | 0.04               | 0.25           | 19                |                          |
|        | Lenz    | 0.021              | 0.25           | 627               |                          |
|        | Petersen| 0.044              | 0.25           | 344               |                          |
|        | van Veen| 0.1                | 0.25           | 427               |                          |
| DE     | van Veen| 0.1                | 1              | 1370              | To species               |
| LT     | van Veen| 0.1                | 0.5            | 313               | Fresh weight             |
| LV     | van Veen| 0.1                | 0.5            | 195               | –                        |
| PL     | Reineck | 0.0225             | 1              | 48                | To species               |
|        | van Veen| 0.1                | 1              | 298               |                          |
| SE     | SM      | 0.1                | 1              | 21                | To species               |
|        | van Veen| 0.1                | 1              | 6738              |                          |
| FI     | Box     | 0.04               | 1              | 57                | To species               |
|        | Ekman-Birse | 0.0225–0.1445 | 1              | 247               | To species               |
|        | van Veen| 0.1                | 1              | 1425              |                          |
| RU     | van Veen| 0.025              | 0.4            | 25                | To species               |
| Literature | van Veen mainly | 0.1       | 1              | 1536              | Partly, to species       |
| ICES   | van Veen| 0.1                | 1              | 42                | –                        |

Figure 1. Temporal variability within the joint dataset: (a) only data collected starting with the year 2000 is shown; (b) with data collected before 2000 included. Data from different periods are shown in different colours. Considering the older data (that contributes to only 9% of the overall sampling events and are up to 98% collected after 1990 which considerably increases spatial resolution and coverage especially in the northern and central regions). This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.
The Baltic Sea scale inventory of benthic faunal communities

Increasingly used for benthic ecological studies (Wei et al., 2010), random forests are a machine learning algorithm developed by Breiman (2001) to generate full-coverage community maps. This method is implemented in the R package “randomForest” (Liaw and Wiener, 2002), a machine learning algorithm comprising an ensemble of randomly constructed decision trees (500 classification trees predicting class membership). A brief description of how the algorithm works can be found in Diesing et al. (2014). The model runs efficiently on large datasets, and can handle thousands of input variables without variable deletion. Moreover, the algorithm avoids the problem of overfitting. Another advantage of the Random Forest algorithm is that there is no need for additional cross validation or a separate test set to reach unbiased estimate of the test set error. This is internally estimated by the OOB (out-of-bag) error estimates, using a different bootstrap sample from the original data (one-third), during the construction of the tree. OOB data are also used to get estimates of variable importance. After building each tree, proximities are computed for each pair of cases. If two cases occupy the same terminal node, their proximity is increased by one. At the end of the run, proximities are normalized by the number of trees. Proximities are used to replace missing data, locate outliers, and to create low-dimensional views of the data. For this case study, it was essential that the algorithm balanced the error in class population unbalanced datasets. Due to the differing data sources used in this study, communities towards the entrance of the Baltic Sea are represented by considerably smaller number of sampling events and grid cells. Thus, no random stratified sampling design is possible to be achieved without a loss of spatial resolution.

Elith et al. (2010) showed that results of such machine learning algorithms should be treated with caution if extrapolated outside of the training area. However, we assume that the spatial cover of our data is sufficient and that we are not going beyond interpolation.

To assess the accuracy of the spatial prediction, we derived measures of classification accuracy from an error matrix. These measures were overall OOB estimate, error rate, purity, and representation. Additionally, we applied Cohen’s (1968) \( \kappa \) coefficient of agreement calculated using “psych” R library (Revelle, 2015). This statistic measures inter-rater agreement typically used for categoric-al data to compensate for the chance agreement and is thought to be a more robust measure than simple per cent agreement calculation in this kind of study (Diesing et al., 2014).

Environmental variables

To support the spatial modelling, we used environmental variables, which represent direct or indirect linkage to the distribution of benthic macrofauna. We limited ourselves to datasets that were available for the entire Baltic Sea. We identified five major environmental predictors: bathymetric maps, near-bottom hydrographic fields (temperature, salinity, and flow speed), sediment type maps, and particulate organic carbon content of surface sediments. We tested bathymetry datasets originating from the EU-BALANCE project (Al-Hamdani and Reker, 2007) and from Seielt et al. (2001). The latter showed to be more useful for our purposes, and was used to calculate the slope and indices of northness and eastness, describing the orientation of the slopes (based on first derivate of the bathymetry).

Hydrographic near-bottom fields of temperature, salinity, and flow speed were extracted from the model simulations of Gräwe et al. (2015), covering the entire North Sea and Baltic Sea for the period 1997–2015. The numerical model has a spatial resolution of 1 nm (~1.8 km), data were provided as either monthly or annual means, minimum or maximum values. Additionally, we used monthly or annual standard deviation to quantify the natural variability. To account for extremes, monthly 5 and 95% percentiles were used. From the original dataset, only the period from 2000 to 2014 was used. The averaging of the hydrographical variables helped to reduce the variance in the resulting fields.

The only available data on seabed sediments covering the whole Baltic Sea region were produced by the EU-BALANCE project. The dataset was categorized in five categorical sediment classes: 1, bedrock; 2, complex sediments; 3, sand; 4, hard clay; 5, mud and clay. As these substrate data are available at a 200 × 200 m resolution, for model training, we down-sampled the data to the final 5 × 5 km grid. This was done by choosing the sediment class with highest coverage within the 5 km grid. Note that this strategy can lead to a mismatch between the dominating sediment class (within a 5 km grid cell) and the actual sediment type sampled for macrofauna. However, we believe that this error caused by the local heterogeneity occurs only at a small number of occasions and the entire Baltic picture aimed at should not be essentially biased.

Full coverage map of particulate organic carbon content in surface sediments with a resolution of 5 km was published by Leipe et al. (2011). All other variables were resampled before the prediction to match the sediment type data resolution to avoid information loss.

Estimate of total biomass distribution

To estimate the distribution of total benthos wet weight biomass over the Baltic Sea basins based on the available data, we utilized ordinary kriging on the log-transformed data averaged per 5 × 5 km grid cell. The resulting raster was then back-transformed to display biomass in gramme per square metre.

Results

Communities based on abundance data

Based on the hierarchal cluster analysis of abundance data, we identified ten major communities inhabiting the Baltic Sea (Figure 2). We placed a cut off at 23% of Bray–Curtis similarity, clusters with a minimum number of ten cells considered as major...
communities. It should be noted that we have chosen an arbitrary level of classification to provide an entire Baltic picture. We have tested various arbitrary cut-off similarity levels and decided on the reported one based on expert judgement. The higher the chosen similarity level, the larger the number of delineated groups (communities). Our aim was to determine a reasonable number of communities that can be well visualized and distinguished. Community structure differed significantly between the delineated communities (PERMANOVA $F_{10,2656} = 175.32, p = 0.001$). The results of the indicator species and SIMPER analyses revealed that certain species contributed to observed pattern and helped to determine group distinctions. The characteristics of major communities and characteristic species are listed in Table 2 and the observed distribution aggregated to the 5 km grid cell scale is shown in Figure 3. Grid cells classified outside the major groups are treated as a separate class of “diverse/patchy/variable” community and will be referred to as “other” throughout the text. Distribution of the oxygen minimum zone was used to mask out regions with frequent absence of macrofauna (grey areas in Figure 3). A full-coverage map of the model prediction is presented in Figure 4.

Community 1 was the dominating type in the northern area. Characteristic species in community 1 were Monoporeia affinis, Marenzelleria spp., and Macoma balthica. Their abundance are well correlated with the occurrence of muddy to sandy sediments. There are some interspersed patches of community 2 found in sandy areas characterized by Hydrobiidae, Pygosia elegans, and Cerastoderma glaucum species. This community was mainly found in sandy habitats off Estonian west coast and in the southwestern Baltic Sea. Figure 3 shows group 4 in the Gulf of Finland and central Baltic down to Arkona Basin. Group 4 is strongly linked to the oxygen conditions in the deeper basins. Beggiatoa-periphytons occur frequently in these areas during periods of hypoxia or low oxygen content. After increase in oxygen levels, the motile Bylgides sarsi is the one to arrive first.

Communities in the southern part are more diverse than the benthic communities of the Northern Baltic Sea. The Bay of Mecklenburg is mostly inhabited by sandy community 2 in shallower areas and community 3 (Diastylis sp., C. gibba, Dipolydora quadrilobata, A. islandica, Aricidea suecica, Abra alba) in the deeper part. Communities 5 (characterized by Amphiura sp., Abra nitida, Galathowenia oculata, Eunucula tenuis, Thyasira flexuosa, Nucula nitidosa, Diplocirrus glaucus), 7 (Phoromis sp., Tellina fabula, Thracia phaseolina, Ophelia borealis, Spiophanes bombyx, Branchiomotoma lanceolatum, Spio arndti) and 8 (Tellina tenuis, Ensis directus, Haustorius pacifica, Lamprops fasciatus) are mostly found in the Kattegat region. Community 9, probably a degraded habitat (with L. koreni, Cerastoderma edule, Polydora sp., Halicryptus spinulosus), is typical for the Flensburg Fjord. The occurrence of community 10 (characterized by Echinocyamus pusillus, Harmnothoe sp., Bittium reticulatum, Oligochaeta, Alitta virens, Turritella communis, Asterias rubens) is well restricted to the Great Belt region.

**Communities based on biomass data**

The hierarchal cluster analysis of biomass data identified 17 major communities in the Baltic Sea. Results are shown in Figure 5 (cut-off at 28%), clusters with minimum number of ten cells were considered as major communities, see Table 3 and Figure 6 for characteristic species). The significance of differences in species composition of 17 distinct communities was confirmed by PERMANOVA ($F_{17,2250} = 91.255, p = 0.001$). Figure 7 shows full-coverage map resulting from the model prediction.

Biomass-based community 1 covers most of the northern areas. It appears on both muddy and sandy sediments and has Saduria entomon, Ma. balthica, M. affinis, H. spinulosus, Pontoporeia femorata as characteristic species. Community 2 is characterized by Hediste diversicolor, Mya arenaria, Hydrobiidae, and C. glaucum and can be classified as the third largest community, based on predicted spatial coverage. Community 2 mostly appears on sandy sediments and can be found in patches in the Archipelago Sea, in shallower parts of the Gulf of Riga, and on the edge of the Eastern Gotland Basin. However, the preferred habitats occur in the Pomeranian Bay, the Rügen-Falster-Plate, and in the northwestern part of the Sound. The second largest coverage was community 5,
Table 2. Characteristics of major communities delineated based on abundance.

| Community | Key species                                                                 | n cells | n visits | Mean n species/station (overall) | Mean abundance/station (ind. m⁻²) | Mean biomass/station (g m⁻²) | Predicted area km² × 10³ | Depth | Av. salinity (min–max) | Sediment class (balance) |
|-----------|------------------------------------------------------------------------------|---------|----------|--------------------------------|-----------------------------------|----------------------------|---------------------------|-------|-----------------------|----------------------------|
| 1         | Monoporeia affinis, Marenzelleria, Macoma balthica                          | 1415    | 9977     | 5 (338)                         | 1345                              | 83                         | 245.26                    | 5–65  | 6.1 (0.9–19.4)        | Mud to sand                 |
| 2         | Hydrobiidae, Pygospio elegans, Cerastoderma glaucum                         | 557     | 3827     | 14 (463)                        | 4797                              | 193                        | 28.59                     | <30   | 9.5 (0.1–27.7)        | Sand                        |
| 3         | Diastylis, Corbula gibba, Dipolydora quadrilobata, Arctica islandica, Arcidea suecica, Abra alba | 208     | 1434     | 38 (543)                        | 3288                              | 358                        | 12.03                     | 10–25 | 20.7 (13.5–30.8)      | Sand                        |
| 4         | Bylgides sarsi, Pontoporia femorata                                         | 205     | 855      | 7 (202)                         | 485                               | 54                         | 74.97                     | 20–120| 12 (2.4–24.9)         | Mud                         |
| 5         | Amphiura, Abra nitida, Galathowenia oculata, Ennucula tenuis, Thyasira flexuosa, Nucula nitidosa, Diplocirrus glaucus | 84      | 600      | 44 (580)                        | 1903                              | 204                        | 14.33                     | 3–40  | 28.3 (19.1–34.7)      | Mud                         |
| 6         | Mytilus spp., Amphibalanus improvisus                                        | 39      | 77       | 7 (143)                         | 2986                              | 20                         | 0.27                      | 2–70  | 7.6 (4.1–21.4)        | Hard bottom complex          |
| 7         | Phoronis, Tellina fabula, Thracia phaseolina, Ophelia borealis, Spiophanes bombyx, Branchiostoma lanceolatum, Spio arndti | 38      | 127      | 29 (391)                        | 1508                              | 466                        | 5.58                      | 8–40  | 30 (25.4–34.1)        | Sand                        |
| 8         | Tellina tenuis, Ensis directus, Haustoria arenaria, Lamprops fasciatus       | 17      | 22       | 21 (159)                        | 1542                              | 44                         | 0.81                      | <25   | 26.4 (20.1–32.8)      | Sand                        |
| 9         | Lagis koreni, Cerastoderma edule, Polydora, Haliclyptus spinulosus           | 12      | 45       | 11 (105)                        | 1385                              | 41                         | 0.22                      | <20   | 18.9 (13–22.3)        | Sand                        |
| 10        | Echinocyamus pusillus, Harmothoe, Bittium reticulum, Oligochaeta, Alitta virens, Turritella communis, Asterias rubens | 11      | 12       | 29 (147)                        | 1719                              | 16                         | 0.20                      | 2–20  | 24.2 (19.4–28.1)      | Gravelly                    |
| Other     |                                                                               | 70      | (394)    |                                |                                   | 0.00                       |                           |       |                       |                            |
| No fauna  |                                                                               | 50      | 291      |                                |                                   | 11.59                      |                           |       | 11.3 (5.9–15.4)       | Mud                         |
which is characterized by \textit{B. sarsi} and corresponds to abundance-based community 4 (i.e. macrobenthic community attributed to the area when conditions are oxic). The accuracy estimates for the abundance-based classes are summarized in Table 4. The overall accuracy achieved by the spatial model prediction based on abundance data derived communities...
was 93% However, attempts failed to predict community 10 as well as community assemblages named “other”, where the representation was zero for both of these two classes. A slightly better, but still low, representation is achieved for communities 6 and 9 (see Table 2 and Figures 3 and 4 for respective details on characteristic species, observed and predicted distribution).

Figure 4. Full coverage map of abundance-based communities distribution predicted with Random Forest. See Figure 3 for colour legend, Table 2 for community characteristics, and Table 4 for accuracy estimates. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.
The accuracy achieved for the model based on biomass data was 92%. Table 5 shows the confusion matrix for the Random Forest biomass run-based classes (classes 1–17 are recognized as communities 1–17). Community 18 included all “other” pooled variable communities. Based on our available predictors, the model predicted community assemblages 1–3, 5, 9, 11, 13–16 quite well (see Table 3 and Figures 6 and 7 for respective details on characteristic species, observed and predicted distribution).

**Estimated distribution of total wet weight biomass**

Interpolation of total wet weight biomass over the Baltic Sea basins derived using ordinary kriging are shown in Figure 8. Areas where biomass data were lacking produced interpolation artefacts: for example, the very low values at the shallow parts of the Eastern Gotland Basin at the west coast off Latvia.

**Discussion and conclusions**

**Community analyses**

The present study describes the major benthic communities inhabiting the Baltic Sea in terms of both abundance and biomass. Community structure is often used to assess changes along environmental gradients. Abundance is often used as the response variable in community data analyses. Biomass, however, is generally used to indicate the functionality of a species within a community, as it is strongly correlated with metabolism (Saint-Germain et al., 2007). Biomass is also a decisive metric in recently developed biotope classifications (such as HELCOM HUB Underwater Biotope and Habitat classification system, Schiele et al., 2015), and is especially relevant for the implementation of Marine Strategy Framework Directive (MSFD) and other legislative directives.

The question of using either abundance (count) or biomass as a response variable always emerges in community analyses. Generally, this dilemma is an understudied question. Which biodiversity “currency” is more relevant for different aspects of ecosystem functioning, and what is the relative importance of the two in relation to the effect they have in ecosystem processes (see Norkko et al., 2013)? Communities themselves are not abundances or biomasses, but both, and a statistical workflow should be developed in the future to combine these two approaches.

The whole northern area of the Baltic Sea is dominated by abundance-based community 1, characterized by *M. affinis*, *Marenzelleria* spp., and *Ma. balthica*. This is expected as all the three species are typical for the Baltic Sea according to previous studies (Laine, 2003; Perus and Bonsdorff, 2004). *Monoporeia affinis* is a limnic species, with highest densities observed for salinities between 5 and 9, and only in rare occasions, it occur at stations with salinity values above 10 (e.g. Gogina and Zettler, 2010). *Marenzelleria* spp. are among the most successful non-native benthic species in the Baltic Sea (Maximov et al., 2015). After first appearance in 1985, they quickly colonized the entire sea, now occupying a dominant position in the zoobenthos. Although the distribution of *Ma. balthica* is limited by salinity of ~3 (Väinolä and Varvio, 1989), community 1, with *Ma. balthica* as a typical constituent species, reaches the whole Bothnian Bay and eastern part of Gulf of Finland. Some sources (e.g. Elmgren, 1978) imply that in contrast to most parts of the Baltic Sea where *Ma. balthica* is most common, bivalves are absent and meiofauna plays the most important role in the Bothnian Bay and the easternmost Gulf of Finland. Since we focused on soft-bottom macrofauna communities, the similarity analysis suggests that these areas still belong to that most typical community 1 cluster. Thus, the similarity of community structure despite the absence of bivalve species is still overall very high. However, if a finer level of classification was considered, these areas would indeed be allocated into a separate class. Laine (2003) analysed large-scale distribution of soft-bottom macrofauna in the open Baltic Sea based on biomass data collected in 1996/1997, thereby representing the momentary state in distribution for that period. He showed that zoobenthos in the Bothnian and central part of the Bothnian Sea is dominated by the isopod *Saduria entomon* and the amphipods *Monoporeia/Pontoporeia*. This is confirmed by our data, with *Ma. balthica* as another characteristic species of community 1 (both abundance and biomass based) increasing in importance where salinity is higher (above 4.5).

Standardized taxonomic units in abundance/biomass matrices are essential to ensure ecologically meaningful interpretation of clustering of stations. Unresolved taxonomic units are a problem that was
Table 3. Characteristics of major communities delineated based on biomass.

| Community | Key species | n cells | n visits | Mean n species/station (overall) | Mean abundance/station (ind. m$^{-2}$) | Mean biomass/station (g m$^{-2}$) | Predicted area km$^2$ | Depth | Av. salinity (min–max) | Sediment class (balance) |
|-----------|-------------|---------|----------|---------------------------------|----------------------------------------|-----------------------------------|-----------------------|-------|------------------------|--------------------------|
| 1         | Saduria entomon, Macoma balthica, Monoporeia affinis, Halicryptus spinulosus, Pontoporeia femorata | 951     | 8549     | 5 (255)                         | 1452                                   | 111                               | 244.2                 | 2–86  | 9.1 (1.8–25.5)         | Mud to sand              |
| 2         | Hediste diversicolor, Mya arenaria, Hydrobiidae, Cerastoderma glaucum | 682     | 4327     | 13 (448)                        | 4108                                   | 180                               | 43.3                  | <30   | 20.1 (14.3–28.1)       | Sand                     |
| 3         | Diastylis, Astarte, Mya truncata, Dendrodoa grossularia, Abra alba, Lagis koreni, Trochochaeta multisetosa, Lineus ruber | 159     | 1156     | 41 (481)                        | 3383                                   | 414                               | 10.0                  | 10–46 | 5.8 (2.4–9.6)          | Mud                      |
| 4         | Marenzelleria, Oligochaeta, Diptera, Cyanophthalma obscura, Pisidium sp., Sphaerium corneum | 57      | 269      | 4 (79)                          | 660                                    | 22                                | 1.4                   | <75   | 11.3 (6.2–20.9)        | Mud                      |
| 5         | Bylgides sarsi | 53      | 286      | 2 (34)                          | 34                                     | 1                                 | 62.0                  | 48–158 | 20.9 (15.5–30.6)       | Mud                      |
| 6         | Capitella | 37      | 56       | 18 (203)                        | 1150                                   | 25                                | 1.2                   | 5–19  | 28.8 (21.7–33.6)       | Sand                     |
| 7         | Nucula nitidosa, Rhodine gracilior, Owenia fusiformis, Virgularia mirabilis, Thyasira flexuosa | 29      | 151      | 43 (413)                        | 2399                                   | 430                               | 4.4                   | 12–24 | 24.1 (19.4–30.8)       | Mud                      |
| 8         | Tellina tenuis, Ophelia borealis, Haustorius arenarius, Ensis | 25      | 28       | 26 (212)                        | 3017                                   | 67                                | 0.7                   | <16   | 7.3 (4.1–14.9)         | Sand                     |
| 9         | Amphibalanus improvisus, NS Idotea | 23      | 50       | 8 (60)                          | 2788                                   | 356                               | 0.1                   | <58   | 20.7 (14–27.2)         | Gravelly to sand         |
| 10        | Mytilus, Asterias rubens, Carcinus maenas, Parvicardium pinnulatum, Balanus crenatus, Corbula gibba, Alitta succinea | 21      | 59       | 38 (276)                        | 3979                                   | 466                               | 0.5                   | <21   | 27.7 (20.9–31.9)       | Gravelly to sand         |
| 11        | Phoronis, Lanice conchigea, Arctica islandica, Tellina fabula, Echinocardium cordatum, Nucula sulcata, Macoma calcarea | 19      | 21       | 43 (212)                        | 2733                                   | 1041                              | 2.4                   | <27   | 22.7 (17.9–28.6)       | Sand                     |
| 12        | Cerastoderma edule, Nassarius, Pygospio elegans, Scoloplos armiger, Aricidea serrata, Spio gonioccephala | 18      | 157      | 17 (239)                        | 909                                    | 27                                | 0.1                   | <24   | 27.4 (19.7–33.2)       | Sand                     |
| 13        | Alitta virens, Ampelisca, Dipolydora coeca, Phyllodoce groenlandica, Nephtys, Spiophanes bombyx, Aporrhais pespelecani | 16      | 24       | 34 (226)                        | 2585                                   | 110                               | 1.8                   | <17   | 33.2 (28–34.7)         | Sand to mud              |
| 14        | Brissopsis lyrifera, Amphiura, Thracia convexa, Scoletoma fragilis, Hyala vitrea, Lipobranchius jeffreysi | 15      | 182      | 49 (364)                        | 1662                                   | 141                               | 5.4                   | 13–49 | 26.9 (23.2–34.7)       | Mud                      |
| 15        | Diplomicrus glauces, Pholoe baltica, Abra nitida, Nemertea, Eudorella emarginata, Parvicardium minimum | 12      | 242      | 42 (358)                        | 1847                                   | 144                               | 0.3                   | <68   | 29 (18.8–31.1)         | Mud                      |
| 16        | Branchiostoma lanceolatum, Dosinia lupinus, Euspira nitida, Modiolus modiolus, Chamelea striatula | 12      | 102      | 25 (256)                        | 1045                                   | 806                               | 0.7                   | 9–18  | 5.6 (3.2–9.8)          | Sand                     |
| 17        | Odonata, Theodoxus fluviatilis, Radix baltica, Coleoptera, Gammaridae, Bithynia tentaculata, Asellus aquaticus | 11      | 33       | 5 (26)                          | 2072                                   | 34                                | 0.3                   | 5–90  | 20.1 (0.5–34.5)        | Gravelly to sand         |
| 18        | other | 128     | 255      | 18 (557)                        | 1412                                   | 89                                | 10.1                  | 3–37  |                        |                          |
Figure 6. Seventeen major communities with characteristic species according to hierarchical clustering (based on point data aggregated to 5 km grid cells), SIMPER, and Indicator species analysis based on biomass data. Crosses indicate sampled cells with no benthic infauna recorded (mainly Polis h dataset). Light grey and dark grey areas mask out the deep water hypoxic and anoxic oxygen conditions, correspondingly (winters 2014 and 2015, after Aranda’s monitoring cruise, SYKE)—when oxygen depletion takes place these areas usually lack macrofauna. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.
solved by grouping difficult taxa to higher taxonomic levels. An exception and a crucial shortcoming of our study was the presence of both Chironomidae and Diptera in data matrices used for clustering, although it would be correct to aggregate all the corresponding records under Diptera. In the Finnish data, most chironomids are identified to species level, whereas in Estonian data, both individuals...
Table 4. Confusion matrix for the Random Forest of abundance-based classes (classes 1–10 are communities 1–10, class 11—“other” communities, class 12—cells with only no macrofauna records, respectively).

|   | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | class.error |
|---|---|---|---|---|---|---|---|---|---|----|----|----|------------|
| 1 | 1033 | 59 | 1 | 22 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0769 |
| 2 | 75 | 328 | 22 | 7 | 1 | 4 | 0 | 0 | 1 | 1 | 1 | 0 | 0.2545 |
| 3 | 0 | 16 | 155 | 1 | 9 | 0 | 1 | 3 | 0 | 1 | 0 | 0 | 0.1667 |
| 4 | 41 | 6 | 8 | 146 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0.2913 |
| 5 | 0 | 10 | 0 | 63 | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0.2125 |
| 6 | 20 | 12 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.9714 |
| 7 | 0 | 1 | 2 | 0 | 10 | 0 | 21 | 0 | 0 | 0 | 2 | 0 | 0.4167 |
| 8 | 0 | 0 | 5 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 0 | 0 | 0.75 |
| 9 | 0 | 4 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0.8333 |
| 10 | 0 | 2 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11 | 12 | 6 | 16 | 2 | 4 | 0 | 4 | 2 | 4 | 0 | 0 | 0 | 1 |
| 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 |

OOB estimate of error rate: 19.8%
Cohen’s k coefficient: 0.90

Note Random Forest fails to predict classes 6, 9, 10, and 11 based on available predictors.
Model note: 2703cellsAvAbu_7_SpatJoin_for_Sed_kl_check: factor(community) ~ iowtopo_bs + tempulf + speedUlf + saltmean_L + factor(factor(sedkor), levels = c("1", "2", "3", "4", "5")) + saltstd3.

It is important to highlight that our community analysis results are not directly comparable with HELCOM HUB classification of biotopes. The HELCOM HUB developed particularly for the Baltic Sea is a hierarchical classification structured into six levels, whereby the first three habitat levels are defined by abiotic factors such as the presence of photic zone and substrate type. These habitat levels then constrain levels 4–6 that describe biotope. The treatment of Diptera as a uniform taxonomic unit would result in the shift of branching between the stations of these two communities.

To provide a solid statistical estimation, we included data with different sampling and laboratory methods, or stations not necessarily fully representative for the respective subareas. As already pointed out by Carman and Cederwall (2001), this approach can sometimes lead to under- or overestimates of total biomass for different subregions. Differences in gear and mesh size within the joint dataset (Table 1) can cause concerns about the validity of the classification. For example, no standard 1 mm sieved data are available for the Russian part of the Gulf of Finland and for Estonian waters. Instead of excluding these regions, we chose to include the data based on 0.25 or 0.4 mm sieves. The risk of misleading estimate due to this methodological difference while comparing between sites was reduced by (i) considering only macrobenthic species, and (ii) the use of data transformation before the community analysis to reduce variance inflation. The total biomass values depend mainly on a few large species. The findings of Elmgren (1978) supported the point that within regions of relatively high macrofauna biomass, meiofauna are likely to have less importance for the total biomass.

Densities of individual species vary greatly seasonally but also between years. Due to these fluctuations, only rough estimates (with significant error bars) can be made for the benthos biomass of the whole Baltic Sea and its individual subregions. For some regions and depth strata, the total macrofauna wet weight estimated in this study is in good agreement with Carman and Cederwall (2001), e.g. for the zone 70–120 m in Bothnian Bay and the Quark region. Our estimate for the 30–70 m strata of the same region is at least one order of magnitude higher than reported by Carman and Cederwall. Similar numbers hold for the Baltic Proper. Additionally, total biomass calculated for the deepest part of the region calculated in this study was two orders of magnitude larger (Table 6).

Spatial modelling and mapping
Many recent case studies that report spatial mapping of benthic fauna were focused either on some distinct regions (Glogzin and Zettler, 2008; Gogina et al., 2010) or relating the distribution of biodiversity or single species to three physical predictors. These are sediment properties and two main environmental variables for brackish-water systems, salinity and oxygen supply (Ojaveer et al., 2010; Zettler et al., 2014). The presented analysis was using averages of all the available sampling events for faunal abundance and biomass over a 5 × 5 km grid which includes the integration of the temporal variation over the available data (Figure 1). The use of large grid cells also provides a smoothing effect on certain scales of the predicted major benthic macrofaunal communities over the Baltic Sea. This can be seen as a trade-off between capturing the most important large-scale patterns in their distribution while omitting the fine-scale structures phenomena.
To generate full coverage prediction maps based on classified point data, we have used the Random Forest method, chosen due to its best predictive performance achieved in most of the comparative studies (Collin et al., 2011; Reiss et al., 2011; Šiaulys and Bučas, 2012). Despite an overall good performance, this method has limitations. For example, Marenzelleria community 4

Figure 8. Distribution of interpolated total wet weight biomass, derived using ordinary kriging interpolation of available biomass data averaged per 5 × 5 km grid cell. Transparent light grey and dark grey areas mask out the deep water hypoxic and anoxic oxygen conditions. Note that at the areas where biomass data are lacking interpolation artefacts are evident, for instance, values at the shallow parts of the Eastern Gotland Basin at the west coast off Latvia are presumably too low. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.
in the biomass-based classification is not well captured by the Random Forest model (see error rate in Table 5). Important predictors that drive and explain the distribution patterns of this community, such as oxygen concentrations, are not included in this study. Moreover, we did not investigate interspecific interactions. The size of modelled classes strongly influences the resulting model, favouring the performance for the largest class at the cost of the smaller one. This is in agreement with the findings of Diesing et al. (2014) that

Table 5. Confusion matrix for the Random Forest of biomass-based classes (classes 1–17 are communities 1–17, class 18—“other”, respectively).

|     | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | class.error |
|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-------------|
| 1   | 747| 44 | 3  | 5  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0.0697     |
| 2   | 80 | 434| 7  | 0  | 3  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 4  | 0.1796    |
| 3   | 0  | 5  | 128| 0  | 0  | 0  | 4  | 0  | 0  | 0  | 0  | 0  | 0  | 16 | 0  | 0.1847    |
| 4   | 35 | 0  | 5  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0.878     |
| 5   | 16 | 0  | 1  | 36 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0.3208    |
| 6   | 0  | 6  | 5  | 0  | 3  | 3  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 4  | 0.8462    |
| 7   | 0  | 1  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0.4483    |
| 8   | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 1  | 0  | 0  | 0  | 0  | 2  | 0  | 1  | 0  | 0.91       |
| 9   | 5  | 14| 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1          |
| 10  | 0  | 3  | 7  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0.5        |
| 11  | 0  | 0  | 1  | 0  | 1  | 3  | 0  | 0  | 0  | 7  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0.6111     |
| 12  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 0.875      |
| 13  | 0  | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 2  | 0  | 7  | 0  | 0  | 0  | 2          |
| 14  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 10 | 0  | 0  | 0  | 0  | 3  | 0.3333     |
| 15  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 3  | 0.875      |
| 16  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 10 | 0  | 0  | 0  | 0  | 7  | 2  | 0  | 0.4167     |
| 17  | 0  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1          |
| 18  | 8  | 19 | 18 | 0  | 2  | 9  | 3  | 0  | 1  | 2  | 1  | 2  | 1  | 0  | 1  | 0  | 33 | 0.67       |

OOB estimate of error rate: 23.1%
Cohen’s κ coefficient: 0.89

Note that Random Forest fails to predict classes 4, 6, 8–10, 12, 17, and 18 based on available predictors.

Model note: FWHcl381slog_2:sedcr~factor(cHclFW381s) ~ iowtopo_bs + tempulf + speedUlf + saltmean_L + factor(factor(sedcr), levels = c("1", "2", "3", "4", "5") + saltstd3 + speedstd3 + tempstd3).

Table 6. Storage of macrofauna wet weight in tonnes × 10⁴ in different subareas (HELCOM division) and depth strata of the Baltic Sea (derived using ordinary kriging interpolation of total biomass averaged per 5 km grid cell) and for selected regions comparison to numbers for these subareas and depth strata published in Carman and Cederwall (2001).

| HELCOM subbasin | 0–30 m | 30–70 m | 70–120 m | >120 m | Sum   |
|-----------------|--------|---------|----------|--------|-------|
| 1. Bothnian Bay | 11.2   | 6.9     | 2.6      | 20.8   |
| 2. The Quark    | 7.4    | 0.2     |          | 7.6    |
| Sum for 1 and 2 | 18.6   | 7.1     | 2.6      | 28.4   |
| Factor          | 3.2    | 12.5    | 1.1      | 3.3    |
| 3. Bothnian Sea | 226.3  | 165.2   | 78.4     | 484.1  |
| Factor          | 14.0   | 15.0    | 6.0      | 42.2   |
| 4. Aland Sea    | 1118.0 | 11.5    |          | 1129.4 |
| Sum for 3, 4, and 5 | 1358.2 | 191.6   | 84.5     | 1655.7 |
| Factor          | 9.4    | 1.3     | 2.2      | 2.1    |
| 6. Gulf of Finland | 75.3    | 30.9    | 7.5      | 113.7  |
| Factor          | 0.7    | 0.3     | 6.2      | 9.5    |
| 7. Arkona Basin | 150.6  | 48.9    |          | 199.5  |
| 8. Bay of Mecklenburg | 125.2 |        |          | 125.2  |
| 9. Bornholm Basin | 93.7    | 97.3    | 11.8     | 202.8  |
| 10. Eastern Gotland Basin | 54.0 | 76.0    | 45.2     | 180.9  |
| 11. Kiel Bay    | 148.9  |         |          | 148.9  |
| 12. Northern Baltic Proper | 179.1 | 130.1   | 51.5     | 374.5  |
| 13. Western Gotland Basin | 52.0 | 43.0    | 46.7     | 148.7  |
| Sum for 7–13    | 803.4  | 395.4   | 155.2    | 1380.5 |
| Factor          | 0.8    | 1.1     | 14.1     | 1325.  |
| Great Belt      | 71.9   | 1.9     |          | 73.7   |
| Gulf of Gdański | 19.7    | 22.4    | 15.7     | 57.8   |
| Gulf of Riga    | 77.4   | 34.7    |          | 112.1  |
| Kattegat       | 336.5  | 59.5    | 2.4      | 398.4  |
| Little Belt     | 20.2   | 0.1     |          | 20.4   |
| The Sound       | 28.0   |         |          | 28.0   |
| Overall sum     | 2809.4 | 743.6   | 267.8    | 479.8  | 3868.7 |

That is, Factor shown in italics is the ratio between current storage and corresponding estimate reported in Carman and Cederwall (2001).
misclassifications are mainly associated with uncommon (rarely sampled) classes. Apart from an unbalanced design and lack of available well-suited predictors, the low model skill for such class as “other” in our study is caused by very high natural variability. Rather than classifying models as correct or incorrect, they should be viewed as useful starting points for different applications (Reiss et al., 2011). The presented community maps are general overviews and many local details including temporal variability of benthic fauna are masked out in our representation. Due to a coarse approach however, these maps must be used with caution.

The relevance of the presented maps and their temporal validity is also limited by the regional variability of benthic communities. In some regions, the community structure is stable over time, whereas in other areas, higher fluctuations or even regime shifts due to species invasions are recorded (e.g. Gogina et al. (2014) in the southern Baltic Sea; Maximov (2011), Maximov et al. (2014) for the eastern Gulf of Finland; Kauppi et al. (2015) for the major part of the Baltic Sea area). The variable environment of the Baltic Sea (especially oxygen and temperature conditions) is another reason of temporal changes in benthic communities (Laine, 2003; Rousi et al., 2013).

Comparison with historical data
In his work from the beginning of the last century, Petersen (1913) mapped the benthic macrofauna communities of the western Baltic Sea and Swedish west coast, delineating a Brissopsis lyrifera community in the Kattegat and an Echinocardium cordatum community along the Danish coast southwest of Læsø. Macoma communities are mostly reported further south to the Great Belt and the Sound down to Rügen. In our study, these areas match our biomass-based community 14 (B. lyrifera, Amphiura spp., Tracia convexa, Scolecomona fragilis, Hyala vetrea, Lipobranchus Jeffreyssii), community 11 (Phoroniis spp., Lanice conchilega, A. islandica, Te. fulba, Ec. cor- datum, Nucula sulcata, Ma. calcarea) and community 2 (He. diversicolor, My. arenaria, Hydrobiidae, C. glaucum), correspondingly. As for abundance-based communities, these were community 5 (Amphiura spp., Ab. nitida, G. oculata, E. tenuis, T. flexuosa, N. nitidosus, D. glaucus), community 7 (Phoroniis spp., T. fulba, Th. phascolina, O. borealis, S. bombex, B. lanceolatum, Sp. arndti), and community 2 (Hydrobiidae, P. elegans, C. glaucum), respectively. In Petersen (1918), an Ab. alba community occurs around the Island of Funen down to deepest parts of the Femarnbelt and the Bay of Mecklenburg. This roughly overlapped with our biomass-based community 3 (Diastylis, Astarte, My. truncata, Dendrodoa grossularia, Ab. alba, L. koreni, Trochochaeta multisetas, Lineus ruber) and community 6 (Capitella spp.), possibly indicating the latter to be a degraded variation of the former one. Naturally, communities’ distribution largely deviates, and it is important to outline that this not only mirrors distributional changes over time, or depiction of different characteristic species. This highlights the large transitional nature of areas that cannot be captured by statistical methods employed in this study.

Comparing the penetration of some marine and brackish-water animals into the Baltic Sea reported in Zenkevitch (1963), our study shows that many species overlap (e.g. Gammarus spp.). Others indicate different distribution limits according to the recent data. For example, distribution limits for Mya penetrate more to the north, whereas Priapulus does not occur beyond the 55.5°N. Zenkevitch reports only 25 known polychaete species in the southern part of the Baltic Sea. In contrast, our data list over 90 polychaete species, which are found in the Bay of Mecklenburg alone. Moreover, by comparing our aggregated dataset with the data published by Jarvekulg (1979), we show the more northerly penetration of the Gastropoda Alderia modesta in the Bothnian Sea. Bivalvia Ma. calcarea has its easternmost record on the edge of Arkona Basin, i.e. absent in the inner parts, according to our data. These inconsistencies might be caused by shifts in the species distribution during the last 30 years. Moreover, our larger set of collected field data helped to detect species, which were overlooked in former times. Finally, the differences in taxonomic expertise can be responsible for the deviations.

Conclusions and outlook
The present standardized dataset represents an important baseline for the present state of the benthic macrofauna in the Baltic Sea. It can therefore be used for multiple analyses of benthic fauna distribution and its features and has been a unique opportunity to collate all benthic macrofauna data from the Baltic Sea region to finally create Baltic Sea benthic communities maps, targeted at the community level.

The results strive towards a Baltic wide picture, and of course when going more in to details, more groups and species would appear important. The work will continue with further refinement of presented results and description of finer community units in selected regions.

A different approach, in contrast to the presented study for spatially explicit mapping, is to model key species distributions separately, similar to Schiele et al. (2015), where communities can be derived by overlaying the expected averaged abundance and biomass and estimating the expected dominance. Moreover, smaller grid cell sizes might be considered (1 km, 1 nm, 2 km as in HELCOM), as well as 10 km (EEA reference grid) or even an adaptive grid. An estimation of the spatial variability within a grid cell should be addressed in future studies and should include temporal changes in local community structure. This study considered abundance and biomass-based communities separately, although incorporation of these two metrics into a single meaningful metric remains an open question.

This paper provides a baseline for future studies for better recognition of links between benthic fauna and ecosystem functioning. As an outlook based on the derived maps, the spatial distribution of specific macrozoobenthos functions (e.g. biodeposition and bio-turbation) can be estimated. This will help to better understand the possible effects of natural or human-induced changes in macrofauna communities in the hosting ecosystem.

Supplementary data
Supplementary material is available at the ICESJMS online version of the manuscript. Additionally, the data outputs are made accessible through http://gis.ices.dk/sfdev/ and http://geo.ices.dk/geonetwork/srv/en/ under “Benthic faunal communities in the Baltic Sea”.

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