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ORIGINAL ARTICLE

Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data

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Abstract In the Helsinki Commission Red List project 2009–2012, taxonomic and distributional data of benthic (macro) invertebrates were compiled by the present authors in a comprehensive checklist of the Baltic Sea fauna. Based on the most recent and comprehensive data, this paper presents the diversity patterns observed among benthic invertebrates in the Baltic Sea. As expected, the total number of species per sub-region generally declined along the salinity gradient from the Danish Straits to the northern Baltic Sea. This relationship is well known from the Baltic Sea and has resulted in a general assumption of an exponentially positive relationship between species richness and salinity for marine species, and a negative relationship for freshwater species. In 1934, Remane produced a diagram to describe the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient. Our results clearly indicated the validity of this theory for the macrozoobenthic diversity pattern within the Baltic Sea. Categorisation of sub-regions according to species composition showed both separation and grouping of some sub-regions and a strong alignment of similarity patterns of zoobenthic species composition along the salinity gradient.

Keywords Baltic Sea · Species diversity · Macrozoobenthos · Inventory · Checklist

Introduction

The patterns of biodiversity in the Baltic Sea follow many ecological gradients, with salinity appearing to be the most prominent. The salinity changes from almost marine conditions in the Kattegat to almost limnic conditions in the northern parts of the Bothnian Bay and the eastern parts of the Gulf of Finland. The Baltic Sea is also a very dynamic water body, strongly affected by both natural and anthropogenic processes. Some species may disappear locally, e.g. due to eutrophication, oxygen depletion, pollution, etc.,

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whereas new non-indigenous species arrive and may become established in the Baltic Sea (e.g. Leppäkoski and Olenin 2001; Leppäkoski et al. 2002; Bonsdorff 2006). An inventory of data on benthic invertebrates was compiled within the HELCOM (Helsinki Commission) Red List project in 2009–2012 by the authors of this paper, resulting in a comprehensive and updated checklist of macroscopic zoobenthic species of the Baltic Sea (http://www.helcom.fi/stc/files/Projects/RedList/BSEP130.pdf). The work of continuing updates is also included (status: June 2013).

The aim of this study was to analyse the data of the checklist in order to: (1) discern biodiversity patterns of macrozoobenthos in the Baltic Sea and (2) clarify the relationships between salinity and species richness of different salinity preferences (marine and freshwater) and origin (native and non-indigenous species). The similarity patterns of macrozoobenthic species composition between sub-regions and along the salinity gradient were also analysed.

Materials and methods

Data sources

The HELCOM Benthic Invertebrate Checklist is based on the data of Gerlach (2000), Zettler and Röhner (2004), Zettler et al. (2008), Ojaveer et al. (2010) and Zettler (2011), including more than 1,400 species altogether. During the HELCOM Red List work, new data for more than 600 species were added, obtained from literature, national marine databases and unpublished sources by the present authors. The timeframe of data sets included ranges from the early nineteenth century to the current date (June 2013). This means that the data may not necessarily reflect the current state of the Baltic Sea macrofauna distribution patterns but rather the records of species (distribution potential) observed per sub-region.

Data processing

The collected data represent the presence/absence of data at species level on a spatial scale of sub-regions (see below). Not all species that have ever been observed in the Baltic Sea were listed. It only includes those which are believed to form sustainable populations in brackish water with minimum salinity of 0.5 PSU. Furthermore, only those records which are geographically located within the Baltic Sea itself have been included. Nearby freshwater lakes and ponds, rocky pools and rivers have been included. Species with a very low number of records were checked, and uncertain observations were consequently excluded.

Non-metric multidimensional scaling (NMDS) based on a Bray–Curtis dissimilarity matrix was used to examine differences in species composition at the sub-regional level. The distances between sub-regions on the ordination plot show the similarities of zoobenthic community compositions between sub-regions: A smaller distance reflects higher similarity and vice versa. NMDS ordinations were employed in the package "vegan" (Oksanen et al. 2012) for the statistical software R version 2.15.1 (The R Foundation for Statistical Computing 2012). The average salinity value of sub-regions was fitted to the categorisation using the routine *envfit* of the package "vegan". The fitting of salinity the gradient was based on a regression between scores of categorisation axes and salinity: the vector (arrow in the plot) points to the direction where the change in salinity values most strongly correlates with the scores of the first two ordination axes (i.e. change in community composition). In the function *envfit*, the strength of the relationship (R^2) between categorisation of species composition and salinity was derived from multiple regression: the salinity values of all sub-basins were regressed against the respective scores of the first two ordination axes (Oksanen et al. 2012). The statistical significance of the relationship was assessed using a permutation test with 9,999 permutations.

A Spearman rank order correlation analysis was used to test relationships between the number of species and salinity and between the numbers and proportions of species with different salinity preferences.

Division into sub-regions

As the Baltic Sea is not a uniform water body throughout its extent, the area was divided into sub-regions according to geomorphological and hydrological characteristics (Fig. 1). The benthic invertebrate checklist provides presence/absence data for these sub-regions as well as for 13 smaller areas such as lagoons, estuaries and bays (Fig. 2). The latter were added because the number of species found in shallow coastal waters can be very high compared to open, deeper waters, and the species found here may differ in salinity preference (freshwater or marine).

Results

Based on the data compiled in the HELCOM checklist and its update, 2,035 macrozoobenthic species are currently known to live in the Baltic Sea. The checklist includes both distributional and taxonomic data on these species, information on the origin of species (marine or freshwater), information on non-indigenous species, most common synonyms, a minimum of one valid taxon code in

Fig. 1 Baltic Sea sub-regions that were used as a basis for the compilation of distribution data for the checklists

taxonomic databases or other taxonomic reference, as well as a minimum of one reference confirming the occurrence—historic and/or present—of the species in the sub-regions of the Baltic Sea.

A summary of the main data processed for inter-sub-region analysis can be found in Table 1; 1,423 marine species and 612 fresh and/or brackish water species were identified. Fifty-one species were classified as non-indigenous species.

Taxonomic structure

Figure 3 shows the distribution of species among different higher taxonomic groups. Overall, Polychaeta contributes with the highest number of species (355). With one exception (*Hypania invalida*, which we identified as a freshwater species), all polychaetes in the checklist are of marine origin. Amphipods and gastropods rank second and third in diversity with 187 and 160 marine species, respectively. For these groups, freshwater species are also found (16 and 40 species, respectively). Diptera is the group represented by most freshwater species, amounting to 180 species. Several taxonomic groups only have one species occurring in the Baltic Sea, e.g. Aphanoneura, Arguloidea, Echiurida and Leptostraca.

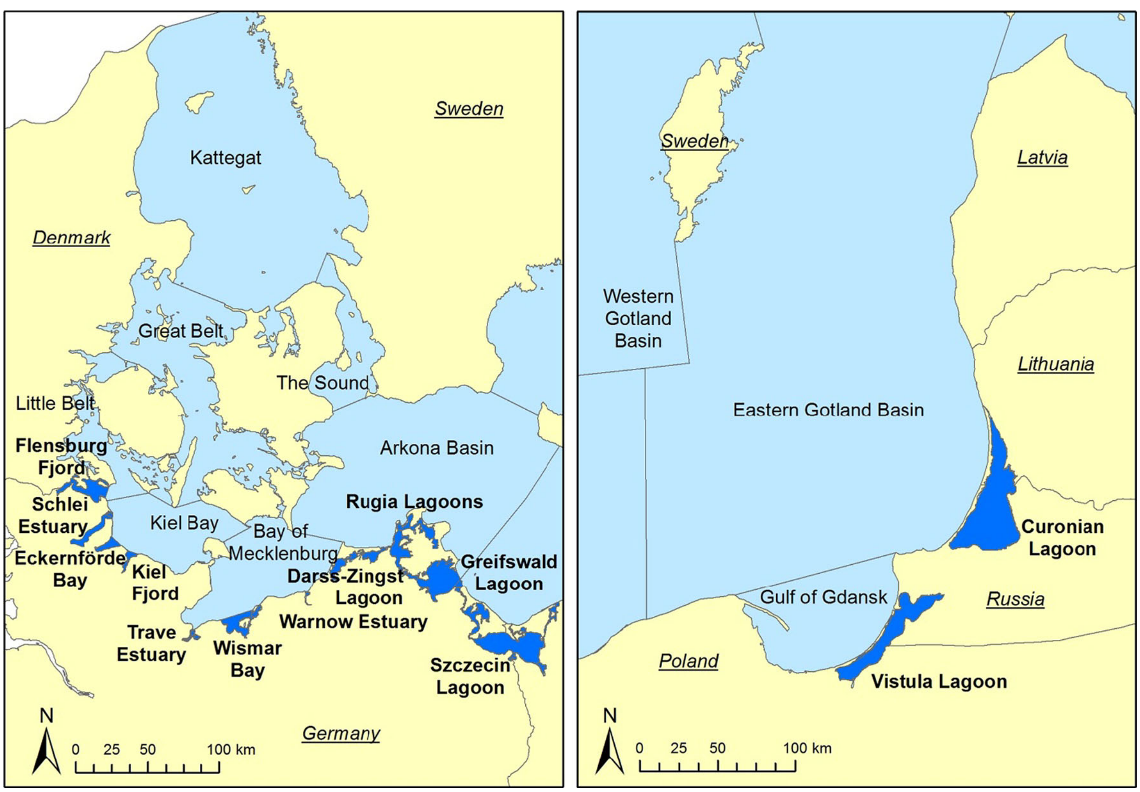

Fig. 2 Additional sub-regions used for the benthic invertebrate checklist

Table 1 The total number of species, number of freshwater and marine species, number of non-indigenous species, mean salinity and in each sub-region and its area (km^2) (in alphabetical order)

Sub-basin/sub-region	Species number	Freshwater species	Marine species	Neozoan species	Mean salinity	Area km^2
Åland Sea	71	30	41	4	6	4,433
Archipelago Sea	130	73	57	10	6	11,076
Arkona Basin	304	25	279	13	9.85	15,555
Bay of Mecklenburg	440	19	421	16	18	4,423
Bornholm Basin	165	17	148	14	7.6	41,138
Bothnian Bay	135	108	27	7	3.1	33,224
Bothnian Sea	147	101	46	11	5.5	63,650
Curonian Lagoon	252	225	27	19	0.5	1,555
Darss-Zingst Lagoon	120	57	63	11	4.92	166
Eastern Gotland Basin	106	19	87	8	7.2	73,449
Eckernfde Bay	247	2	245	6	15	68
Flensburg Fjord	214	1	213	4	15	250
Great Belt	345	11	334	6	21	7,765
Greifswald Lagoon	121	33	88	12	5.8	501
Gulf of Finland	482	410	72	27	4.6	29,901
Gulf of Gdansk	127	54	73	14	7	5,076
Gulf of Riga	122	66	56	11	5.2	18,795
Kattegat	1,161	7	1,154	7	25	22,102
Kiel Bay	508	5	503	7	20	3,266
Kiel Fjord	227	6	221	6	15	40
Little Belt	411	12	399	6	21	2,701
Northern Baltic Proper	84	22	62	9	6.5	41,113
Rugia Lagoons	115	25	90	10	5.1	360
Schlei Estuary	166	54	112	8	9.8	132
Szczecin Lagoon	260	206	54	24	1	874
The Quark	105	65	40	7	4	4,509
The Sound	668	9	659	7	22	2,278
Trave Estuary	119	12	107	9	8.7	41
Vistula Lagoon	127	92	35	23	1	773
Warnow Estuary	144	51	93	16	8.9	12
Western Gotland Basin	69	12	57	5	6.7	27,876
Wismar Bay	211	16	195	12	11.33	198
Total	2,035	612	1,423	51		417,302

The NMDS ordination of the sub-regions according to species composition together with the fitting of a salinity gradient to the categorisation clearly showed: (1) the separation and grouping of some sub-regions and (2) salinity-dependent pattern of similarities between sub-regions in the whole Baltic scale (Fig. 4). Salinity was significantly correlated ($p < 0.001$) with the categorisation axes.

Spatial patterns of macrozoobenthic diversity

The number of species found in each sub-region is shown in Figs. 5 and 6. Not surprisingly, the Kattegat hosted the highest number of macrozoobenthic species within the Baltic Sea, with 1,161 species, of which 1,154 are of marine origin (Fig. 5, 6, 7). The Gulf of Finland, on the other hand, hosted the highest number of freshwater species (410) and only 72 marine species. With the exception of the Gulf of Finland, species diversity was generally higher in the south-western area of the Baltic Sea than in the north-eastern area.

A continuous decline in the percentage of marine species in relation to overall species numbers was observed from the west to the east (Fig. 6c). In contrast, the occurrence of freshwater species was highest in the Gulf of Finland, followed by some smaller coastal areas (e.g. Curonian Lagoon, Szczecin Lagoon), Bothnian Bay and Bothnian Sea. This trend in species composition and diversity followed the salinity gradient. With decreasing

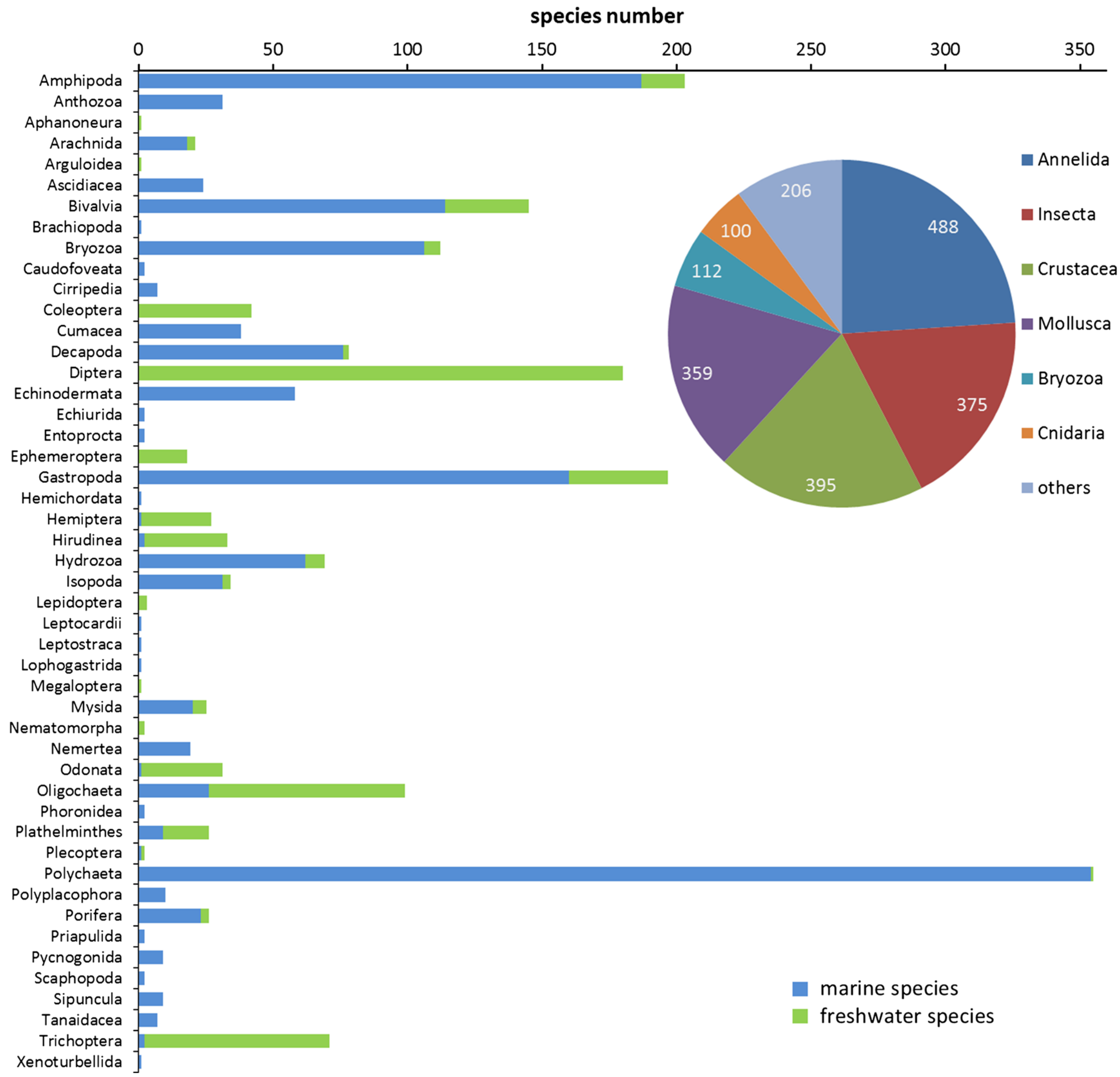

Fig. 3 Number of species per higher taxonomical group in the Baltic Sea for marine/freshwater species, respectively (*columns*), and the species richest groups, partly merged (*pie chart*)

salinity, the number of marine species declined, whereas the number of species from inland water bodies increased (Figs. 7, 8).

The sub-regions with the lowest total numbers of species were the Western Gotland Basin (69), Åland Sea (71), the northern Baltic Proper (84) and the Quark (105) (Figs. 5, 7). Numbers of freshwater and marine species were almost equal in the Gulf of Riga (66/56), Darss-Zingst Lagoon (57/63) and Åland Sea (30/41) (Fig. 7).

Non-indigenous species

The highest numbers of non-indigenous species were found in the Gulf of Finland (27), the Szczecin Lagoon (24) and the Vistula Lagoon (23) (Fig. 6d). Less than 10 non-indigenous species were found in the Bothnian Bay, in the central basins and in the majority of the western sub-regions. About 33 % of non-indigenous species originate from marine waters, and about 67 % of non-indigenous species originate from inland waters. Among non-indigenous species from inland waters, 48 % originate from the Ponto-Caspian region, whereas 19 % are of fully freshwater origin. The proportion of non-indigenous species is negatively correlated with salinity and the total number of species and positively correlated with the number of fresh/inland water species (Table 2).

Discussion

Species composition and diversity in the Baltic Sea are influenced by the steep salinity gradient from SW to NE

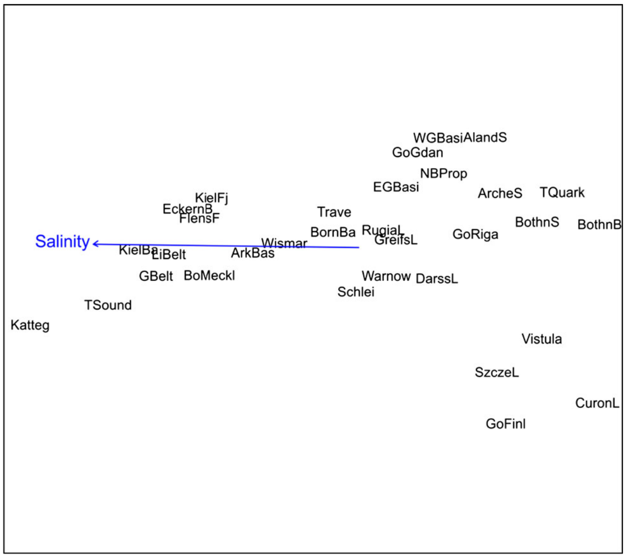

Fig. 4 NMDS ordination plot of the Baltic sub-regions based on the zoobenthic species composition. The average salinity value of sub-regions is fitted to the ordination

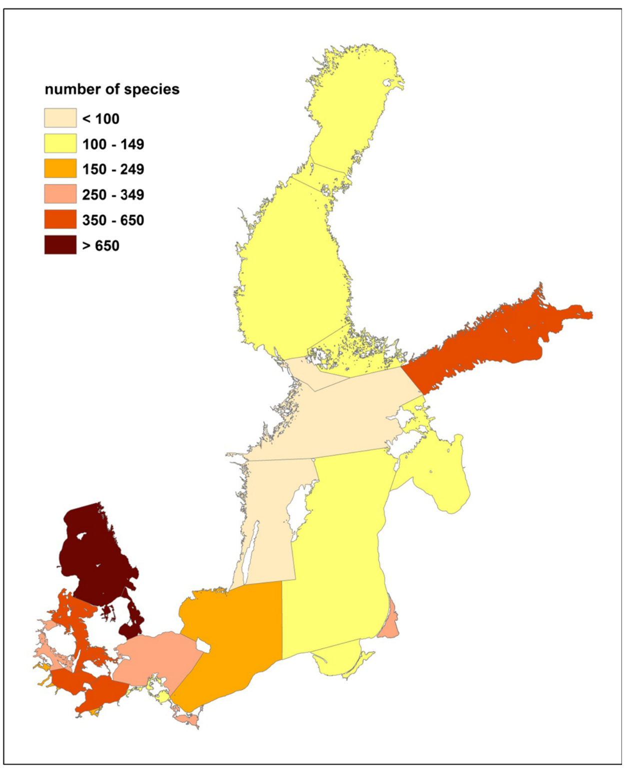

Fig. 5 Total numbers of macrozoobenthic species (marine and freshwater species) in the sub-regions of the Baltic Sea

(e.g. Bonsdorff 2006). This pattern can be clearly seen in our data. The categorisation of sub-regions according to species composition clearly revealed the separation and grouping of some sub-regions. The most distinct group was formed by the Vistula, Szczecin and Curonian Lagoons and the Gulf of Finland (Fig. 4). This separation in community composition is caused by the very low salinities in these sub-regions. At the other extreme of the salinity gradient, the species composition of the Sound and especially that of the Kattegat stood apart from the other sub-regions (Fig. 4). Spatial trends in species composition resulting from the salinity gradient were reflected in the respective amount of marine and freshwater species within the different sub-regions (Fig. 6a–c). The more saline western parts were dominated by marine species, whereas freshwater species dominated the eastern parts and coastal lagoons with brackish waters or more limnic conditions (Fig. 7). The influence of the salinity gradient created a pattern where the lowest numbers of species are found in the central Baltic Sea (Fig. 5). In this area, the prevailing oxygen depletion of deep and more saline water negatively affects benthic diversity (e.g. Laine et al. 1997).

In the Baltic Sea, as in brackish water bodies in general, the salinity gradient is the predominant factor controlling the distribution patterns of organisms. In 1934, Remane developed a diagram which described the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient. Our results (see Fig. 8) clearly indicated the validity of this theory for the macrozoobenthic diversity pattern within the Baltic Sea. Although the theory of Remane has been discussed and disputed (see Whitfield et al. 2012 for review), we assume that it is true, at least for the Baltic Sea macrozoobenthic diversity pattern. It has been shown (Attrill 2002) that the major environmental factor influencing the distribution of organisms in tidal estuaries is the temporal variation in salinity (i.e. the extreme values), rather than tolerance of the mean salinity. In the Baltic Sea, however, the temporal variation is rather small due to the lack of tides. However, the variation in salinity is a concomitant effect in areas with salinity gradient (e.g. in local estuaries).

The general distribution pattern of benthic non-indigenous species in the Baltic Sea largely coincided with that of fresh and brackish water species. This may be due to the fact that a high proportion of alien species originates from inland waters. However, only a few alien species occur in the Bothnian Bay. This is because most alien species in the Baltic Sea originate from the warm-water Ponto-Caspian region. Ponto-Caspian fauna is especially rich in the lagoons and estuaries of the southern Baltic Sea. In the northern Baltic, their distribution is likely to be limited by low temperatures. The proportion of non-indigenous species was negatively correlated with the total benthic diversity. This result is in agreement with studies showing that areas with low native species richness are more susceptible to invasive species (e.g. Paavola et al. 2005). Additionally, major harbours are located in the sub-regions (and in close vicinity to these) with the highest number of

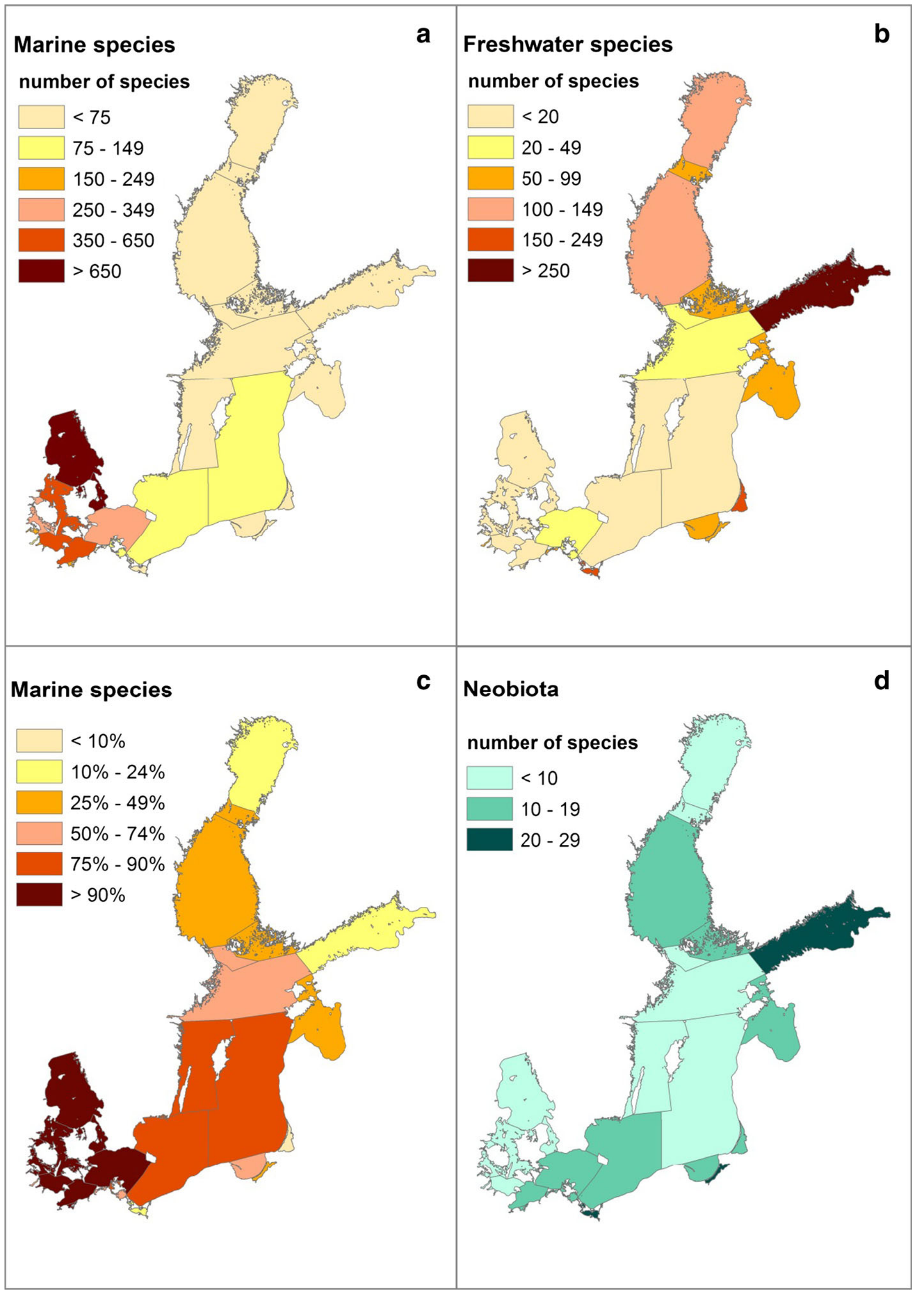

Fig. 6 Macrozoobenthic species in the sub-regions of the Baltic Sea: **a** number of marine species, **b** number of freshwater species, **c** percentage of marine species compared to overall species numbers of each sub-region, **d** number of non-indigenous species

non-indigenous macrobenthic species, e.g. St. Petersburg (Gulf of Finland), Szczecin and Świnoujście (Szczecin Lagoon), Kaliningrad and Gdańsk (Vistula Lagoon), Klaipeda (Curonian Lagoon) and Rostock (Warnow Estuary). These areas are often important for both sea-going and inland shipping—the main vectors for spreading non-indigenous aquatic invertebrates. Several of other human activities, e.g. aquaculture, live food trade and leisure activities, often concentrated in estuaries, offer additional pathways of alien species dispersal (e.g. Leppäkoski et al. 2002).

The number of species per sub-region declined from the south to the north (with the exception of the Gulf of Finland). This is a well-established pattern in the Baltic Sea and has led to a general assumption of an exponential relationship between the number of species and salinity (Fig. 8). The present study, however, differs from previous ones by a more intensive accounting of the freshwater fauna, and the view that the bottom fauna of the eastern Baltic Sea is species-poor may thus to some extent be disputed. In the easternmost areas of the Baltic Sea, benthic diversity increased due to the increase in the number of

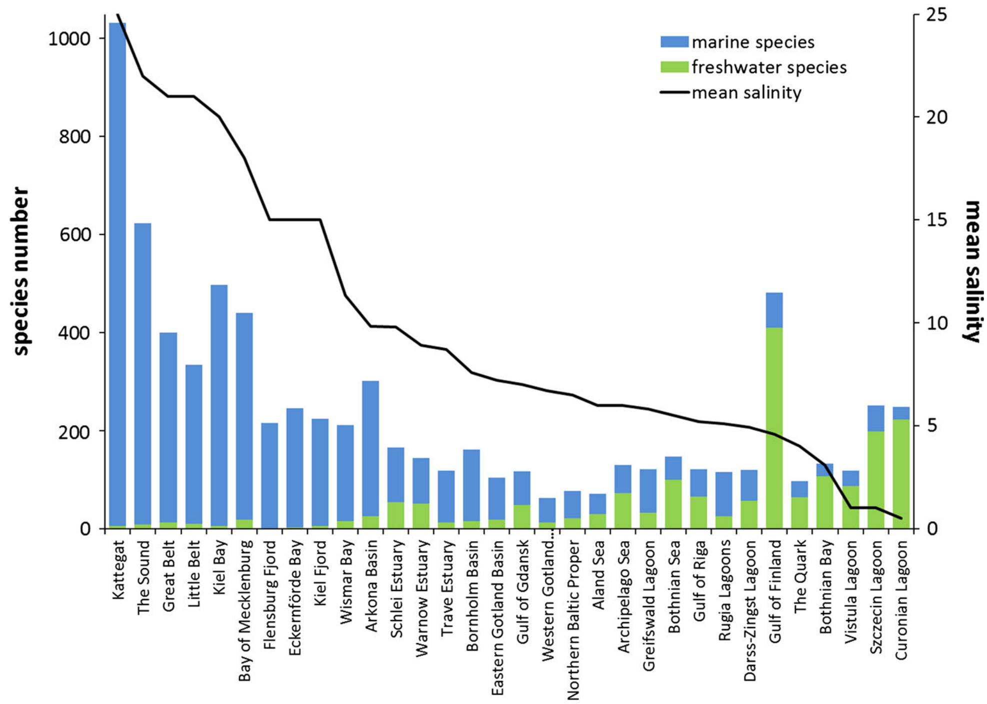

Fig. 7 Number of species in the Baltic Sea sub-regions ordered by the salinity gradient—marine/freshwater species, respectively. The mean salinity is indicated by a *curve*

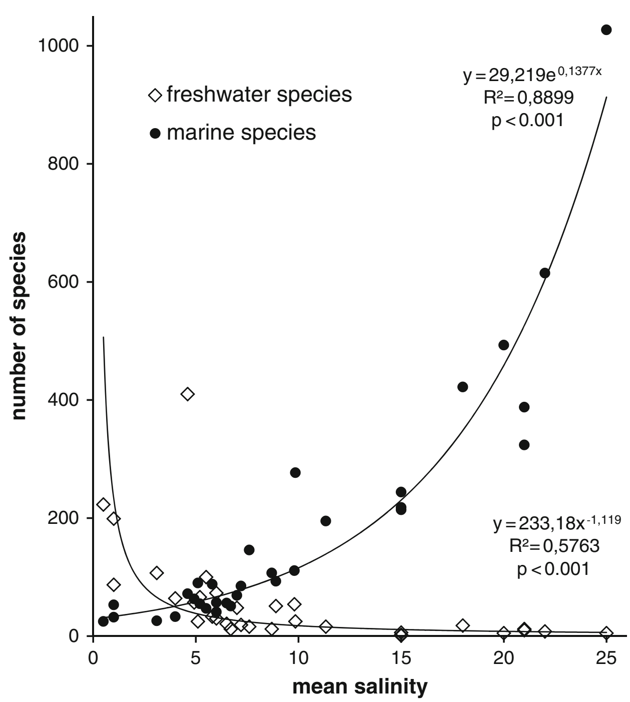

Fig. 8 Statistical test of the relationship between salinity and diversity of marine and freshwater species. The exponential and potential function gave the best fits ($R^2 = 0.89$ and 0.58, respectively). Each point represents one of the sub-regions

freshwater species. Therefore, the Gulf of Finland hosted as many species as the western parts of the Baltic Proper, due primarily to the vast estuary of the River Neva.

Although an equal sampling effort for marine biodiversity studies may never be achieved over large areas, and the taxonomical expertise and resolution may differ between sub-regions, we argue that sub-regional comparisons can still be made. The huge data sets and the long time frame of investigation minimise the effects mentioned above. Thus, the slightly lower number of freshwater species in the Quark area (Fig. 6) is most probably explained by the absence of estuaries in this sub-region and the relatively narrow salinity gradient as compared to both to the Bothnian Sea and the Bothnian Bay. Due to the large area of the Gulf of Finland and its high proportion of estuaries and fjordlike bays (e.g. Pojoviken Bay, Neva Estuary), the remarkably high number of freshwater species is explainable. In addition, the high number of some taxa (e.g. chironomid species) in some sub-regions may be caused by specially targeted studies involving experts on specific taxa.

In a previous study, an attempt was made to merge all the macrozoobenthos data around the Baltic Sea (Ojaveer et al. 2010). However, as we have learned during the present study, some areas, especially the highly saline area of the Kattegat and the areas with greater freshwater influence (e.g. Bothnian Bay and Gulf of Finland), were underrepresented by that previous inventory. The compilation of species checklists is a dynamic process and will never be fully completed. The HELCOM checklist of Baltic Sea macrozoobenthic species is the first ever to encompass the entire Baltic Sea and all macrozoobenthic species found therein, and it will function as an important knowledge base for management, administrative authorities as well as the scientific community.

Table 2 Spearman rank correlation matrix of macrozoobenthic diversity variables and salinity

	Mean salinity	Total *S*	Fresh/inland water *S*	Marine *S*	Non-indigenous *S*	Prop. of non-indigenous *S*	Prop. of fresh/inland water *S*	Prop. of marine *S*
Mean salinity	1	**0.53**	**−0.86**	**0.92**	**−0.46**	**−0.70**	**−0.92**	**0.92**
Total *S*	**0.53**	1	−0.26	**0.67**	0.12	**−0.71**	**−0.40**	**0.40**
Fresh/inland water *S*	**−0.86**	−0.26	1	**−0.78**	**0.62**	**0.56**	**0.97**	**−0.97**
Marine *S*	**0.92**	**0.67**	**−0.78**	1	−0.22	**−0.65**	**−0.88**	**0.88**
Non-indigenous *S*	**−0.46**	0.12	**0.62**	−0.22	1	**0.52**	**0.51**	**−0.51**
Proportion of non-indigenous *S*	**−0.70**	**−0.71**	**0.56**	**−0.65**	**0.52**	1	**0.61**	**−0.61**
Proportion of fresh/inland water *S*	**−0.92**	**−0.40**	**0.97**	**−0.88**	**0.51**	**0.61**	1	**−1**
Proportion of marine *S*	**0.92**	**0.40**	**−0.97**	**0.88**	**−0.51**	**−0.61**	**−1**	1

S number of species

Statistically significant ($p < 0.05$) correlations are marked in bold

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