



Habitat-builders complexity boosts associated fauna functional trait richness (*Zostera marina* meadows, Baltic Sea)

Emilia Jankowska^{*}, Maria Włodarska-Kowalczyk

Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland

ARTICLE INFO

Keywords:

Biodiversity indicators
Ecosystem engineers
Functional diversity
Eelgrass

ABSTRACT

Seagrass has been widely recognized as ecosystem engineers and habitat-builders increasing biodiversity and abundance of associated fauna. However, seagrass habitats are being degraded globally due to modification of coastline, terrestrial inputs, and climate change. While the effects of seagrass meadows vegetation density on associated macrofauna standing stocks and taxonomic richness have been widely investigated, the relationships with functional diversity aspects remain poorly understood. Here, we investigate if macrofauna standing stocks and richness indicators (both taxonomic and functional) are related to the habitat-builders presence and structural characteristics (density, biomass, diversity) in temperate *Zostera marina* Linnaeus, 1753 meadows (Baltic Sea). Relationships between faunal (density, biomass, species and functional trait composition and diversity), vegetation and sediment indicators were tested based on materials collected by scuba divers. Macrofauna density (ranging from 587.6 ± 188.2 to 4514.1 ± 977.8 ind. 0.1 m^{-2}), biomass (ranging from 43.1 ± 28.3 to 13.6 ± 30.8 g 0.1 m^{-2}) and species richness (ranging from 7 ± 1.4 to 20 ± 1.4) responded positively to seagrass presence regardless of meadows characteristics. Functional trait richness ranged from 203.7 ± 64.3 to 44.7 ± 41.1 and was enhanced only in presence of the greatest macrophyte diversity. Therefore, it is the diversity of meadows that boosts the functional richness of associated fauna. This implies that 1) monospecies seagrass meadows do not necessarily provide a higher number of functions than neighboring bare sediments in systems with low diversity such as Baltic Sea, 2) both taxonomic and functional indicators should be used to describe macrofauna communities. This result is an important message for conservation planning for systems with low diversity, as restoration of at least a few macrophytes species not only the dominant seagrass species could be considered to secure greater taxonomic and functional richness.

1. Introduction.

The effects of diversity on the functioning of biological systems are one of the major questions of the present-day ecology (Cardinale et al., 2006). A positive relationship between biodiversity and ecosystem functioning has been reported, but mechanisms behind the observed patterns remain poorly studied (Balvanera et al., 2006; Nordström et al., 2010; Rooney and McCann, 2012; Sokołowski et al., 2012). This relation can be explored by investigating taxonomic and functional trait diversity of assemblages (Hooper et al., 2005). A functional trait has been defined as “a component of an organism’s phenotype that determines its effect on processes and its response to environmental factors” (Reiss et al., 2009) and may be expressed with the use of categories such as mobility, size, feeding type, etc. Several indicators measuring richness, evenness, and divergence of functional traits distribution in multispecies

assemblages has been proposed to estimate different aspects of functional diversity (Schleuter et al., 2010; Villéger et al., 2008). The functional trait-based approach enables us to make comparisons between localities representing different regional species pools and different habitats (Villéger et al., 2008). Moreover, using a functional diversity approach allows to link benthic communities to various ecosystem processes such as production, oxygen consumption, and organic matter transformation (Violle et al., 2007). Therefore, it might provide information about community dynamics and processes rather than only the community structure that is provided by the taxonomic-based approach.

Seagrass meadows are among the most diverse and productive coastal ecosystems in the world (Hemminga and Duarte, 2000). Seagrass plants play the role of ecosystem engineers as they modify the water flow regimes and sedimentation of particles (Bos et al., 2007), provide habitat (Green and Short, 2003), and food (Jankowska et al., 2018) for

^{*} Corresponding author.

E-mail address: ejankowska.ocean@gmail.pl (E. Jankowska).

<https://doi.org/10.1016/j.ecolind.2022.109512>

Received 22 May 2022; Received in revised form 26 September 2022; Accepted 27 September 2022

Available online 29 September 2022

1470-160X/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

many organisms. Many studies have detected a positive effect of meadows on associated fauna species diversity and abundance (e.g. (Fredriksen et al., 2010; Gartner et al., 2013; Jankowska et al., 2014; Włodarska-Kowalczyk et al., 2014)). However less is known about the vegetation effects on faunal functional diversity and traits expression. Trait-based approach applied on to Baltic Sea zoobenthic communities associated with seagrass meadows showed that the invertebrate functional structure was affected by both presence of vegetation and its heterogeneity (Törnroos, 2014). A big-scale inventory of the Baltic Sea coastal zoobenthos reported that salinity gradient-related species richness decline is not necessarily accompanied by the parallel reduction in the measured functional diversity (Törnroos et al., 2015). It proved that, despite the common notion, patterns in taxonomic diversity are not always reflected in the similar variability of functional trait diversity. Therefore, it remains intriguing to explore which of the seagrass meadows' vegetation characteristics are crucial for structuring associated macrofaunal communities and its functions, the biomass/volume of the vegetation, or its diversity/complexity.

The ecosystem engineering effects are dependent on the engineer species abundance with possible threshold values, however, these relationships are rarely described and quantified in the natural marine systems (Harley and O'Riley, 2011; Jones et al., 1997). It has been proven that the interactions between ecosystem engineers and the dependent biota can run according to a non-linear model and a higher concentration of engineering species does not necessarily imply a stronger impact on the ecosystem (Harley and O'Riley, 2011). In the Baltic Sea seagrass meadows, the effects of vegetation cover on faunal species richness, diversity, and composition persisted throughout the year, but the magnitude of these effects varied seasonally and followed changes in macrophyte cover (Włodarska-Kowalczyk et al., 2014). However, in this seasonal study, the abundance and diversity of macrophytes changed similarly and so it was not possible to disentangle the

effects of these two on the faunal characteristics. In the present study, we visit three localities that differ in either abundance or complexity of the vegetation and explore the effects of these features on the indicators of macrofaunal community structure. We hypothesize the faunal standing stocks (density and biomass) are linked to habitat building macrophytes standing stocks (density and biomass), and faunal diversity is structured by the vegetation complexity defined as a diversity of macrophytes. We investigate two aspects of macrofauna biodiversity – taxonomic through species richness and functional through functional traits richness. Low functional richness indicates that part of the resource pool potentially available to the community remains unused and thus productivity of the community may be reduced regardless of the high resource abundance (Villéger et al., 2008). Higher functional traits diversity may translate into the higher productivity of the communities (Petchey et al., 2004), capacity to buffer against environmental fluctuations, and the potential to resist invasive species (Dukes, 2001). Therefore it is important to study both species and functional trait diversity.

2. Materials and methods

2.1. Study area

The research was conducted in Puck Bay (southern Baltic Sea, Fig. 1). The Puck Bay is a large part of the gulf separated from the open sea by the Hel Peninsula and can be further divided into shallow, inner (3 m on average), and deeper, outer (average depth of 20 m) part by the Ryf Mew sandbank. It is also an outstanding natural area that hosts one of the highest richness of benthic assemblages among the Polish Exclusive Economic Zone (Węśławski et al., 2009). The coastal zone off Sopot-Gdynia agglomeration neighboring the Puck Bay is less protected from the open sea influence; it also contains valuable areas planned for marine reserves (Smola et al., 2014). *Zostera marina* meadows occur along

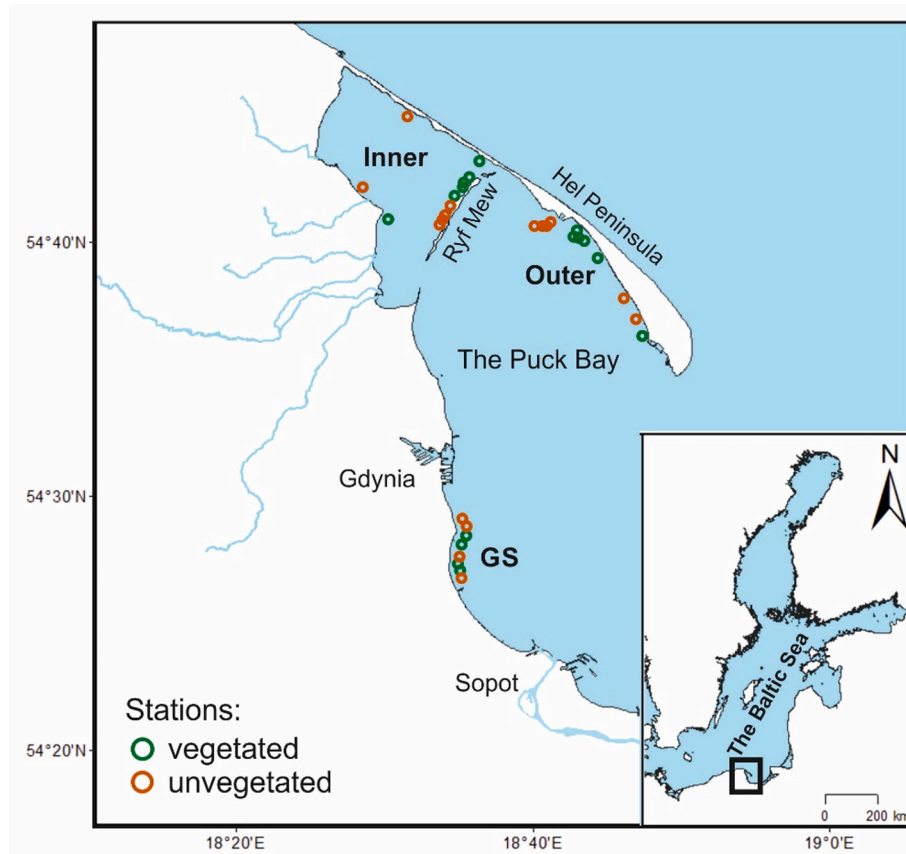


Fig. 1. Study area and the sampling points.

the Puck Bay coastline, with variable spatial coverage and vegetation density (for a detailed description see (Jankowska et al., 2016)). Historical occurrence of *Zostera* meadows shows dramatic changes with extensive meadows covering most of the Puck Bay before 1950 and a significant reduction in areal coverage (to 16.0 ha) observed in 1987 (Kruk-Dowigallo, 1991). Such degradation was most probably driven by eutrophication and replacement by filamentous algae (Kruk-Dowigallo, 1991). At present, natural recovery is observed, with 320 ha of eelgrass meadows cover estimated only for the inner Puck Bay in 2009 (Weslawski et al., 2013) and new locations of vegetation presence observed within the last years (E. Jankowska, personal observations, 2012–2014). The salinity measured during the sampling ranged from 7.67 PSU in the Inner bay, 7.94 PSU in the GS site, to 8.0 PSU in the Outer bay.

2.2. Sampling and laboratory analysis

Sampling took place in summer (peak season of vegetation development in the Puck Bay (Jankowska et al., 2014)), July 2012 and 2013, at 96 sampling points located in three sites: Inner (inner Puck Bay, 36 stations, depths from 1.5 to 2.0 m, Fig. 1), Outer (outer Puck Bay, 36 stations, 1.5 m, Fig. 1), and GS (off Sopot-Gdynia agglomeration, 24 stations, 3.0 m, Fig. 1). In each site half of the stations were located on the vegetated bottom and the other half on bare sands. Vegetated stations were placed in the central parts of the meadows, and bare sand stations were placed at least 50 m away from the nearest meadow's edge.

A set of samples collected by SCUBA divers at each station included a sample for macrophytes and macrofauna (upper 10 cm, 15 cm diameter core) and three sediment samples (2 cm diameter core) – for grain size (upper 10 cm), particulate organic carbon (POC) and total nitrogen (TN) contents, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (upper 2 cm) and photosynthetic pigments content (upper 2 cm). Macrofauna and macrophytes samples were sieved through 0.5 mm mesh and fixed in 4 % formaldehyde. The sediment samples for photosynthetic pigment analyses were frozen at -80°C , the other sediment samples at -20°C . In the laboratory, chlorophyll *a* (chl_a) and pheopigment concentrations were assessed with the spectrophotometric method (Evans and O'Reilly, 1982). POC, TN, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ in sediments were analyzed using an Elemental Analyzer Flash EA 1112 Series combined with an Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). To determine the grain-size composition, sediment samples were dried (48 h, 60°C) and sieved through mesh sizes at thirteen 0.5 phi intervals (Folk and Ward, 1957). All macrofaunal individuals were identified to the lowest possible taxonomic level (WoRMS Editorial Board, 2022), counted, and weighed.

2.3. Data analysis

Biological traits were assigned to species or higher taxonomic levels (if assignment to species was not possible) following (Törnroos, 2014) based on available online traits database for the northern Baltic Sea macrozoobenthos (Törnroos and Bonsdorff, 2012). As a broad set of traits as possible was compiled for this study to describe the overall trait diversity of the communities. Seven trait categories with 34 sub-categories were used (Appendix Table S1). For each subcategory, species were scored using a presence/absence scale (Törnroos and Bonsdorff, 2012). An abundance weighted trait scores matrix (the stations vs trait matrix) was built by multiplying each species abundance value at a station point with the trait score of the species. The scores were then summed over all species at the station and this matrix was further used for analysis as functional traits richness data. Additionally, the overall frequency occurrence of traits was calculated for each site (Site: Inner, Outer, GS) and habitat (Hab: vegetated, unvegetated). Macrofauna species richness, defined as the number of taxa at a station (S), and macrofauna functional richness (FRic) measured as the multifunctional volume used by the macrofauna species occurring at a station and traits

assigned to species (Villéger et al., 2008) were assessed for all stations. The indices FRic was obtained using the function “dbFD” of the library “FD” for R-Project (Laliberté et al., 2014) following the criteria of (Villéger et al., 2008).

To explore the patterns of similarities in macrobenthic species and traits composition among stations, Bray-Curtis similarities were calculated for square root transformed data of species density and biomass and untransformed data of functional traits composition. The two-way PERMANOVA model, to test the effects of two factors (Site and Hab) was applied to the similarity matrices, with post-hoc tests performed when applicable. To visualize multivariate variability along two axes that best discriminated groups of samples defined by habitats and sites a Canonical analysis of principal coordinates plot (CAP) was constructed for species density (composition), species biomass (composition), and functional traits richness. Spearman rank correlation vectors of species abundances, biomass, and functional traits richness with 2 canonical axes were overlaid on the CAP plots.

Differences in macrozoobenthic univariate characteristics (abundance, biomass, S, FRic) between two habitats and among three sites were tested using the two-way PERMANOVA model based on a similarity matrix created from the Euclidean distances among samples. When significant effects in the main tests were detected, pairwise post-hoc tests were applied. Spearman correlation was applied to test the pairwise relationships between density, biomass, S and FRic. The ratio of differences in S and FRic between vegetated and unvegetated habitats at three stations was calculated by dividing mean values at vegetated by the mean values at unvegetated sites. All the analysis was done using PRIMER 7 Version 7.0.13 with PERMANOVA + 1 add package (Anderson et al., 2008).

The environmental predictors of macrobenthic standing stocks and diversity were explored using the Distance-based Linear Models (DISTLM) procedure in PERMANOVA+ (Anderson et al., 2008). The original data set of explanatory variables included 13 quantitative environmental variables: descriptors of organic matter content ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, POC, TN, POC/TN), photosynthetic pigments (chl_a, CPE – chloroplastic pigment equivalent, i.e., the concentration of all photosynthetic pigments, including pheopigments, %chl_a – the percentage of chl_a in CPE, chl_a/POC), and the granulometric characteristics of sediments (mean grain size, sorting, fine sand and medium sand fractions) and two categorical variables (Hab and Site as defined above). Quantitative variables were tested preliminarily for collinearity using the Draftsman plot and the Spearman correlation matrix, which left six quantitative variables for further analysis (POC, POC/ TN, CPE, mean grain size, medium sand, sorting). The forward selection procedure was used to determine the best combination of predictor variables (Anderson et al., 2008).

The effects of macrophyte vegetation characteristics on macrobenthic standing stocks and diversity at stations in seagrass meadows were explored using DISTLM tests. The original data set included 6 quantitative variables: total macrophyte biomass, seagrass above-ground biomass, total seagrass biomass, seagrass shoot density, macroalgal biomass, and macrophytes diversity (number of macrophytes species). These variables were tested preliminarily for collinearity using the Draftsman plot and the Spearman correlation matrix and total macrophyte biomass and seagrass above-ground biomass were excluded from further analysis. The similarity matrix created from the Euclidean distances among samples was used for macrozoobenthic univariate characteristics (abundance, biomass, S, FRic) while Bray-Curtis similarities of double-root transformed data (species abundances and biomass) or none transformed data (functional trait composition). The forward selection procedure was used to determine the best combination of predictor variables.

3. Results

3.1. Environmental and macrophyte characteristics

The lowest seagrass shoot density and seagrass biomass was recorded at the Outer while the highest was recorded at the GS site (Table 1). Nine macrophyte taxa were present in the studied sites: *Pylaiella littoralis* (Linnaeus) Kjellman 1872 (Ectocarpales), *Ceramium* sp. Roth 1797, *Polysiphonia* sp. Greville 1823 (Ceramiales), and *Z. marina*, *Ruppia maritima* Linnaeus 1753, *Zanichella palustris* Linnaeus 1753, *Chara* sp. Linnaeus 1753, *Potamogeton perfoliatus* L., *Myriophyllum* sp. L. (Angiospermae).

The macrophyte number of species at Outer was 2.3 on average (± 1.0 SD) compared to only 0.4 (± 0.5) at GS and 1.6 (± 1.5 , Table 1) at Inner. All nine taxa were present at Inner and Outer, while only four (*Z. marina*, *P. littoralis*, *Ceramium* sp., and *Polysiphonia* sp.) were noted at GS. The POC content in the sediments varied from 0.03 ± 0.02 % (unvegetated (unveg) Outer) to 0.14 ± 0.03 % (vegetated (veg) GS, Table 1). The chl_a content in the sediments ranged from 4.0 ± 2.7 $\mu\text{g g}^{-1}$ (unveg Outer) to 10.0 ± 3.4 $\mu\text{g g}^{-1}$ (veg GS, Table 1). Higher values of POC, $\delta^{15}\text{N}$, chl_a, pheo, and CPE were documented in the veg sediments compared to the bare sands. Only chl_a% was higher in the unveg bottom.

3.2. Benthic macrofauna characteristics

The lowest mean abundance was recorded at the GS site unveg habitat (587.6 ± 188.2 ind. 0.1 m^{-2}), whereas the highest mean abundance was observed at the Outer site in the veg one (4514.1 ± 977.8 ind. 0.1 m^{-2} , Fig. 2). There were significant differences in macrobenthic abundance between habitats (PERMANOVA, $P > 0.001$, Table 2) but not among sites.

A similar pattern was noted for macrofaunal biomass at Inner and Outer sites, with a mean of 43.1 ± 28.3 g 0.1 m^{-2} in veg while only 13.6 ± 30.8 g 0.1 m^{-2} in unveg habitat. However, at the GS site, the total biomass was slightly higher in unveg than veg habitat.

Species richness per sample (S) was higher in veg than unveg habitat for all three sites, with the highest ratio of the veg/unveg mean at the Outer site (2.7, compared to 1.7 at GS and 1.4 at Inner). S differed significantly among sites and habitats with significant interaction of those two factors (PERMANOVA, $P > 0.001$, Table 2). The two-way PERMANOVA pseudoF values indicated that Hab had a much stronger effect on S than did the Site factor (Table 2).

There was no effect of Site or Hab, but a significant effect of SiteHab

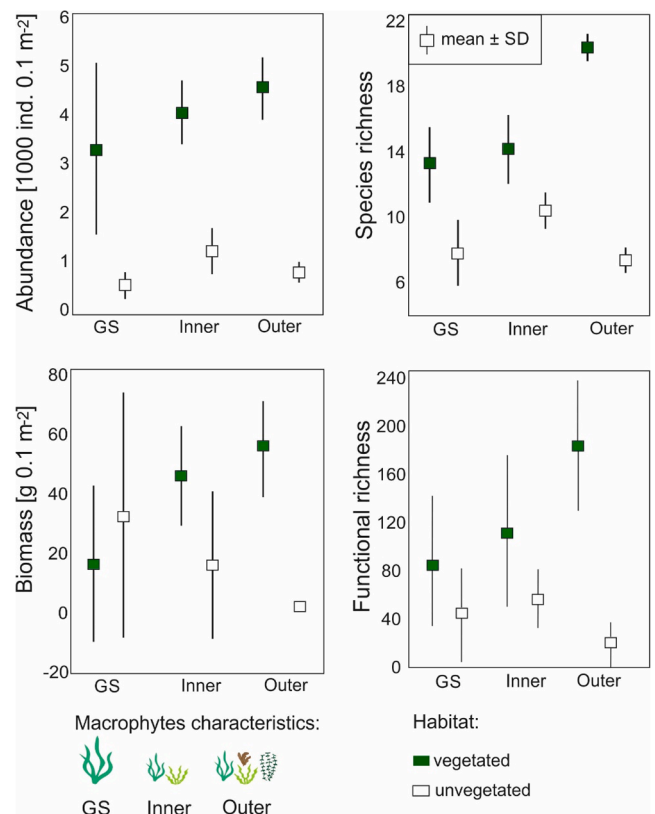


Fig. 2. Macrozoobenthic community univariate characteristics recorded in two habitats (vegetated, unvegetated) at three sites (GS, Inner, Outer). Mean and standard deviations values are presented. Symbols below the plots indicate the macrophyte biomass and diversity at the three sites.

interaction on the functional richness (FRic, PERMANOVA, Table 2). Post hoc analysis identified that significant differences between habitats in FRic were noted only at the Outer site. Indeed, the highest FRic was observed at the veg Outer site (203.7 ± 64.3) with also the highest veg/unveg mean ratio (13.0, Fig. 2). The lowest mean functional richness was recorded at the GS site on the unveg habitat (44.7 ± 41.1). Macrofaunal FRic was significantly correlated with density (Spearman correlation $r = 0.97$, $p < 0.05$) and S (Spearman correlation $r = 0.91$, $p < 0.05$), but not with biomass ($p > 0.05$).

Table 1

Sediment and seagrass meadows characteristics in two habitats (veg - vegetated, unveg - unvegetated) at three studies sites (GS, Inner, Outer). Means and standard deviations (SD) are presented.

	GS				Inner				Outer			
	veg		unveg		veg		unveg		veg		unveg	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
POC [%]	0.14	0.11	0.06	0.03	0.11	0.08	0.05	0.02	0.08	0.03	0.03	0.01
PON [%]	0.02	0.01	0.01	0.01	0.03	0.02	0.02	0.05	0.02	0.01	0.01	0.00
$\delta^{13}\text{C}$ [‰]	19.29	8.87	18.05	1.70	20.14	1.44	18.27	1.83	19.12	1.07	18.21	4.61
$\delta^{15}\text{N}$ [‰]	4.88	2.35	2.55	2.01	3.56	0.84	1.85	0.63	3.69	0.90	2.51	2.00
POC/PON	6.78	4.54	4.99	1.65	6.43	13.40	4.38	1.96	3.19	0.71	4.03	2.34
pheo	48.72	38.65	15.51	4.54	27.64	18.60	9.84	4.54	33.17	41.11	7.20	7.05
chl _a	46.03	16.04	32.32	9.11	44.41	12.25	21.34	6.38	27.47	12.08	18.83	12.79
chl _a /POC	423.35	210.91	543.97	236.57	510.96	237.41	418.88	142.59	437.25	315.14	684.70	353.06
chl _a %	53.48	12.22	67.30	5.99	64.08	7.74	68.89	7.04	54.10	13.41	74.07	5.73
CPE	94.75	52.60	47.84	12.15	72.05	29.84	31.18	9.91	60.64	49.84	26.03	19.60
fine sand [%]	0.29	0.18	0.44	0.30	0.26	0.11	0.57	0.34	0.32	0.11	0.09	0.02
mean grain size [ϕ]	2.39	0.48	1.88	0.56	2.01	0.42	2.02	0.37	1.68	0.17	1.50	0.07
seagrass shoot density [shoot m^{-1}]	84.93	29.96	–	–	53.16	23.95	–	–	46.87	18.30	–	–
macrophytes diversity [nr of species]	0.40	0.51	–	–	1.60	1.50	–	–	2.33	1.00	–	–
total macrophyte biomass [g dwt m^{-1}]	24.01	12.70	–	–	13.39	4.63	–	–	15.25	4.34	–	–
seagrass above-ground biomass [g dwt m^{-1}]	12.75	8.89	–	–	7.36	4.69	–	–	8.70	4.83	–	–

Table 2

Two-way PERMANOVA tests for differences in the macrobenthic community multivariate and univariate characteristics among sites (Site) and habitats (Hab). Tests were performed on Bray-Curtis similarity matrices for square root (species density and biomass), untransformed (functional traits) multivariate data, and Euclidean distances matrices for univariate data (abundance, biomass, richness (S), functional trait richness (FRic)). PsF - PERMANOVA pseudoF statistics. Significant effects: * $P < 0.05$, ** $P < 0.001$. Significant post-hoc effects ($P < 0.01$) are listed.

		Species composition (density)	Species composition (biomass)	Functional traits	Abundance	Biomass	S	FRic
Source	df	PsF	PsF	PsF	PsF	PsF	PsF	PsF
Site	2	21,7**	13,8**	0,8	2,3	0,05	10,7**	0,2
Hab	1	47,3**	26,5**	4,1	124,6**	9,5*	159,6**	4,9
SitexHab	2	16,8**	12,1**	16,0**	1,9	1,0	30,1**	14,1**
Res	54							
Post hoc Site		GS ≠ Inner ≠ Outer	GS ≠ Inner ≠ Outer	–	–	–	GS ≠ Outer, Inner ≠ Outer	–
Post hoc SitexHab		GSveg ≠ GSuveg Inveg ≠ Inuveg Oveg ≠ Ouveg	GSveg ≠ GSuveg Inveg ≠ Inuveg Oveg ≠ Ouveg	GSveg = GSuveg Inuveg Oveg ≠ Ouveg	–	–	GSveg ≠ GSuveg Inuveg, Oveg ≠ Inuveg, Oveg ≠ Ouveg	GSveg = GSuveg; Inveg = Inuveg; Oveg ≠ Ouveg

3.3. Benthic assemblages

The CAP ordinations of species density and species biomass show that groups defined by habitat and site could be easily discriminated except for overlapping points representing veg GS and unveg Inner (density) and veg and unveg GS (biomass, Fig. 3).

The species vectors on both CAP plots indicated a correlation of *Bathyporeia pilosa* Lindström 1855 to unveg habitat (indeed, it was present only in the unveg habitat at the Inner and Outer sites) and correlation of *Hydrobia* spp. W. Hartmann 1821, *Jaera* spp. Leach 1814, *Theodoxus fluviatilis* Montfort 1810, few species of *Gammarus* Fabricius 1775 and *Mytilus edulis* Linnaeus 1758 to veg habitat (indeed they were present only in the seagrass beds (*Jaera* spp., *T. fluviatilis*, *Gammarus* spp.) or their abundance was much higher there than in unveg habitat (*Hydrobia* spp., *M. edulis*)). Additionally, vectors on the species density

plot indicated that *Macoma balthica* was correlated with unveg habitat in GS site and indeed, for this site *M. balthica* Linnaeus 1758 density was higher in this habitat.

On the CAP plot of functional traits, points representing veg Outer site were separated from those representing veg habitat in two other sites and those representing unveg habitat (Fig. 3). Vectors indicated many trait categories correlated with Outer veg habitat along the axis of difference between the two habitats (Fig. 3). Indeed, all these trait subcategories were present in the Outer veg habitat (total sum of traits occurrence for all samples – 187) while the communities at other habitats and sites consisted of a lower number of traits subcategories (GS veg – 116, unveg – 124; Inner veg – 135, unveg – 118; Outer unveg – 88, see Appendix Table S2).

PERMANOVA identified significant effects (at $P < 0.001$) of Site, Hab, and SitexHab interaction on composition in terms of species

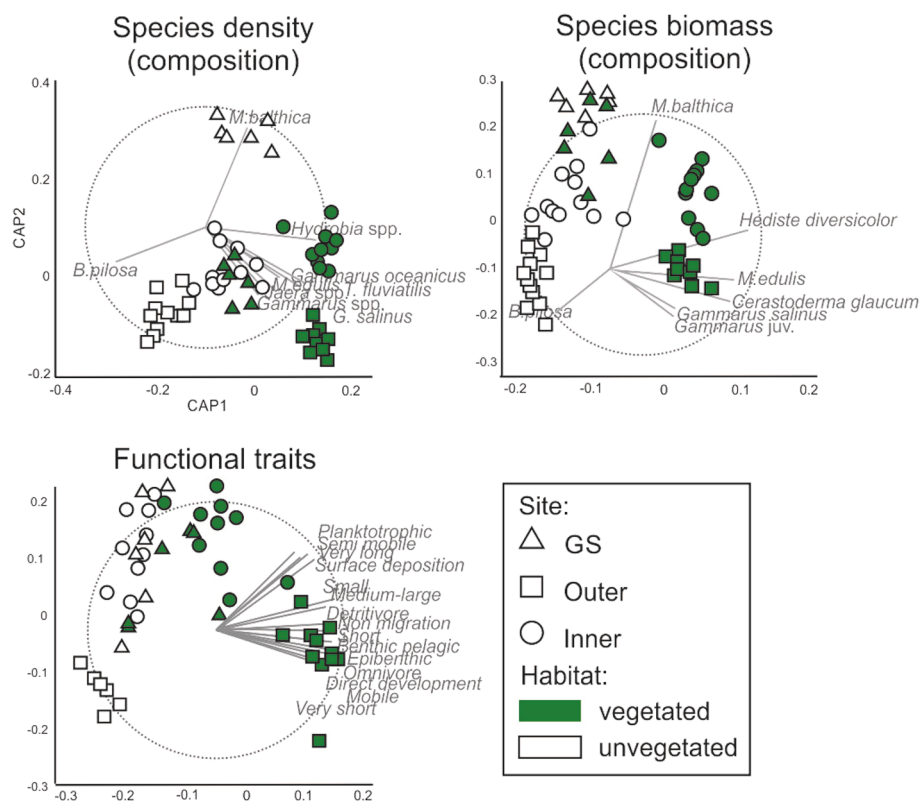


Fig. 3. CAP ordination of Bray-Curtis similarities of (square-root transformed) species density, species biomass, and (untransformed) functional traits in stations. Symbols and colors represent sites and habitats. Vectors indicate the taxa or traits best correlated with the ordination coordinates ($r > 0.7$). Vector length corresponds to the correlation values.

densities and biomass (Table 2). Habitat had the strongest effect as indicated by the highest pseudo-F (Table 2). Pairwise comparisons documented significant differences between habitats for each site.

The interaction Site×Habit was the only significant effect in PERMANOVA (at $P < 0.01$) performed on functional trait composition data (Table 2). Post-hoc pairwise comparisons of samples collected from two habitats performed separately for each site documented significant effects only at the Outer site.

Ten out of identified 35 traits subcategories occurred with frequency $> 2.5\%$ at all studied sites and habitats: medium, short, direct development, infauna top and epibenthic, detritivore, mobile, non-migratory, no transport, or diffusive mixing (see Appendix Table S2). As indicated by PERMANOVA and CAP the functional traits subcategories differed between habitats only at the Outer site. At the Outer site, there were 8 traits categories recorded only in the veg habitat: small, medium-large, very long, planktotrophic, benthic/pelagic, parasite, sessile. Also, at the Outer site, there was a higher frequency of epibenthic (higher by 1.9), herbivore (2.6), and no transporting sediment (3.0) traits in the veg habitat (see Appendix Table S2). On the other hand, in the unveg habitat, there was a higher frequency of very short living (higher by 3.0), infauna top (3.7), and detritivore (2.1) trait categories (see Appendix Table S2).

3.4. Relationship between environmental, macrophyte and biological data

DISTLM marginal tests confirmed the significant effects of seven environmental variables on species density and functional traits composition (Habitat, POC, CPE, POC/TN, mean grain size, sorting, medium sand) and ten variables on the species biomass (Habitat, Site, medium sand, sorting, POC, CPE, POC/TN, $\delta^{13}\text{C}$, chl a /POC, mean grain size) that together explained 52 % (abundance), 55 % (biomass) and 51 % (functional traits) of the total variation (Table 3, Appendix Table S3). In all three models, habitat explained a major part of variation (30 % in species abundance, 23 % in species biomass, 41 % in functional traits). However, only four variables were significant in sequential tests for species abundance (Habitat, CPE, mean grain size, and medium sand), five variables for species biomass (Habitat, Site, mean grain size, CPE, medium sand), and only two for functional traits (Habitat, CPE).

When only samples collected on the vegetated bottom were considered, four macrophyte biometrics variables were included in the best-fitting models for DISTLM marginal tests (total seagrass biomass, seagrass shoot density, macroalgal biomass, and macrophytes diversity)

Table 3

DISTLM tests for fitting environmental variables to macrofauna multivariate characteristics (species abundance, species biomass, functional traits) in both habitats and vegetation characteristics only in vegetated habitat. Only sequential tests and significant variables are presented; for all results see Appendix S3, S4. PsF - PERMANOVA pseudo statistics, Var% - a percentage of explained variation. Significant effects: * $P < 0.05$, ** $P < 0.001$.

<i>Both habitats</i>			<i>Only vegetated habitat</i>		
<i>Species abundance</i>					
	Ps-F	Var%		Ps-F	Var%
habitat	25.5**	30	total seagrass biomass	5.0**	15
CPE	9.1**	10	macrophytes diversity	4.4**	12
mean grain size	4.7**	5	macroalgae biomass	2.8*	7
medium sand	3.8**	4			
<i>Species biomass</i>					
habitat	22.9**	28.0	macrophytes diversity	7.6**	21
site	9.2**	10.0	total seagrass biomass	3.7**	10
mean grain size	4.9**	5.0			
<i>Functional traits</i>					
habitat	39.9**	41	macrophytes diversity	5.3**	16
CPE	4.5**	4			

together explaining 35 % (species abundance), 36 % (species biomass) and 21 % (functional traits) of the variation (Table 3, Table S4). Three of the variables (total seagrass biomass, macrophytes diversity, macrophytes biomass) were significant in the sequential tests for species abundance, two variables (macrophytes diversity, total seagrass biomass) were significant in the species biomass model while only macrophytes diversity was significant in the functional traits model.

DISTLM marginal tests confirmed significant effects of one environmental variable (sorting) for macrofauna density and S, two variables (POC/TN, Site) on biomass, two variables (CPE, site) on FRic - together explaining 39, 60, 32, and 47 % of the total variation in density, biomass, S, and FRic, respectively (Table 4, Appendix Table S3). Sorting had a significant effect in sequential tests for species density and S, while Site for biomass and FRic (Table 4, Appendix Table S3).

Four seagrass meadows characteristics (shoot density, total seagrass biomass, macroalgae biomass, macrophytes diversity) were significant for macrobenthic univariate characteristics on veg bottom, together explaining 15, 19, 22, and 41 % of the total variation in FRic, S, abundance, and biomass, respectively (Table 4, Appendix Table S4). In sequential tests, only total seagrass biomass was significant for macrofauna density, biomass, and S (explaining 16, 32, and 14 % of the variation, respectively), while only macrophyte diversity was significant for FRic (explaining 12 % of the variation, Table 4).

4. Discussion

Opposite to our expectations, the two aspects of faunal diversity (taxonomic, and functional indicators) responded differently to the habitat-builders (macrophytes) presence and complexity. Macrofauna species richness was higher in all meadows regardless of the vegetation characteristics whereas functional richness was only enhanced for the meadow with the highest macrophyte diversity. It is the complexity of meadows (not just their presence) that boosts the functional richness of associated faunal communities. It suggests that in the systems with low diversity such as the Puck Bay, the monospecies seagrass meadows do not necessarily provide a high number of functions. Therefore, in the similar systems, restoration of at least a few macrophytes species together with the dominant seagrass could be beneficial as might promote higher taxonomic and functional richness.

4.1. Vegetation effects on faunal abundance, biomass, and species richness.

The effect of seagrass presence on macrofauna communities may

Table 4

Results of DISTLM results for fitting environmental variables to macrofauna univariate characteristics (abundance, biomass, species richness, functional richness) in both habitats and vegetation characteristics only in vegetated habitat. Only sequential tests and significant variables are presented; for all results see Appendix S3, S4. PsF - PERMANOVA pseudo statistics, Var% - a percentage of explained variation. Significant effects: * $P < 0.05$, ** $P < 0.001$.

<i>Both habitats</i>			<i>Only vegetated habitat</i>		
<i>Abundance</i>					
	Ps-F	Var%		Ps-F	Var%
sorting	7.1**	22	total seagrass biomass	5.4*	16
<i>Biomass</i>					
site	25.9**	51	total seagrass biomass	13.4**	32
<i>Species richness</i>					
sorting	7.0**	21	total seagrass biomass	4.6*	14
<i>Functional richness</i>					
site	16.3**	39	macrophyte diversity	3.8*	12

vary depending on the seagrass species, development and size of the meadows, as well as the environmental settings at a given location (Boström and Bonsdorff, 1997). Vegetation has been shown to increase faunal density and diversity in several in situ observations and experimental surveys (Gartner et al., 2013; Sirota and Hovel, 2006; Stoner and Graham Lewis, 1985). In some cases, especially in *Posidonia oceanica* (Linnaeus) Delile 1813 (one of the largest seagrass species meadows), positive effects of macrophytes were dependent on seagrass density, biomass, and leaf length (Urre et al., 2013). For *Zostera* seagrass species, these positive effects were less evident, often dependent on a threshold level of seagrass density (Jankowska et al., 2014). Such non-linear relationships have been described for engineering species effects by (Harley and O'Riley, 2011). The present study confirmed the positive effect of seagrass presence on macrofauna standing stocks indicators (abundance, biomass) and richness, with the strongest effect noted for the Outer site (Fig. 2). The three study sites are shaped by different hydrodynamic conditions (GS - the most exposed, Inner - sheltered) and different vegetation characteristics (GS - the highest seagrass density and meadow biomass, Outer - the most diverse meadow, Table 1). In the seasonal study conducted at the Outer and Inner sites, seagrass effects on faunal species richness, diversity, and composition persisted throughout the year, but the magnitude of these effects varied seasonally mirroring the seasonal changes in macrophyte cover – with the lowest macrophyte biomass, diversity and the weakest effects on the fauna in winter (Włodarska-Kowalczyk et al., 2014). The present study was conducted in the summer, in three meadows differing considerably in seagrass density and diversity, but the effects on macrofauna were noted regardless of the meadows' features. Habitat (presence or absence of vegetation) was the variable that explained most of the variation in both macrofauna density and biomass. Considering only vegetated sites, total seagrass biomass and macrophytes diversity and biomass were responsible for most of the variation in taxonomic composition and species diversity, similarly to the previously conducted seasonal study (Włodarska-Kowalczyk et al., 2014). Similar effects of plant vegetation were reported in both terrestrial and aquatic environments suggesting that the relationship between plant diversity and faunal abundance or species diversity is weak (Parker et al., 2001; Symstad et al., 2000). For instance, seagrass meadows' diversity accounted for only about 13 % of the variance of the macrofauna communities' diversity in temperate *Z. marina* meadows in the Chesapeake Bay (Parker et al., 2001). A simple species-area relationship has been discovered in temperate *Z. marina* beds highlighting that the structural complexity of seagrass was not responsible for the increase of macrofauna diversity, only the presence and spatial coverage of plants (Attrill, Strong, and Rowden, 2000). The presence of seagrass meadows usually increases the pool of food resources with enhanced microphytobenthos and organic matter content thus attracting consumers (Fredriksen et al., 2010; Jankowska et al., 2018; Lundquist et al., 2018). Also in the current study, significantly higher amounts of POC, chlorophyll *a*, and CPE were noted in all vegetated compared to neighboring unvegetated sites (Table 1, Jankowska et al., 2016).

While the strong positive effects of vegetation have been noted for macrofauna abundance, density, and richness, the relationship to macrofauna biomass was less straightforward as the biomass was even slightly higher in unvegetated habitat at the GS site (Fig. 3). This was shaped by the high abundance of large bivalves of *Macoma balthica* and *Mya arenaria* Linnaeus 1758 at the GS unvegetated site. On the contrary, the vegetated GS site lacked the typical species of gastropods broadly present at the other vegetated sites (such as *Theodoxus fluviatilis* and *Radix labiate* Rossmässler 1835). Similarly, the seasonal study conducted in the same area noted higher densities of *Macoma balthica* on the bare sand (Włodarska-Kowalczyk et al., 2014). The equivocal response of epifauna and infauna to seagrass presence and structure has been already noted with epifauna being more attracted by the seagrass habitat as complex seagrass structures provide more substrate and shelter (Leopardas, Uy, and Nakaoka, 2014). It suggests that in specific habitats of the Baltic Sea, bivalves seem to favor unvegetated sediments

and that was tested in a settlement experiment in the Finnish archipelago (Boström et al., 2010). *Z. marina* vegetation was proven to inhibit the settlement of the larvae of the bivalves *M. balthica* and *Cerastoderma glaucum* Bruguière 1789, also the post-settlement transportation of bivalves by resuspension events and secondary settlements of larger individuals were much more common on bare sands and in smaller seagrass patches than within continuous *Z. marina* vegetation (Boström et al., 2010).

4.2. Vegetation effects on faunal functional trait richness.

It has been already identified that relationships between functional and species richness depend on the number of complementary niches (Díaz and Cabido, 2001; Tilman, 1997), the presence of ecological engineers (Lawton and Jones, 1995), and keystone species (Bond, 1993). Seagrasses have been widely recognized as ecosystem engineers and habitat-builders increasing biodiversity and abundance of associated fauna (Green and Short, 2003). Ecosystem engineer effects of populations can depend and vary with the quantitative characteristics such as the density of the engineering organism (Harley and O'Riley, 2011; Jones et al., 1994; Lawton and Jones, 1995). While the relationship of seagrass meadows vegetation density and macrofauna taxonomic composition and diversity has been widely investigated, the functional diversity aspects remain poorly understood as is its interrelation to habitat-builders features. A big-scale functional traits inventory of the Baltic Sea revealed that despite the taxon richness dropping drastically along the salinity gradient, the functioning (indicated by functional trait diversity) varied more subtly and with a threshold in salinity below which no response of functionality could be noted (Törnroos et al., 2015). Within all the three study sites, seagrass meadows' presence alone caused an increase in macrofauna species richness and density compared to the bare bottom (Fig. 2). In contrast, for the functional richness and several traits expressed by the benthic community, the presence of a meadow had no effect, until its complexity reached a certain level at the Outer site (diversity of at least 3 macrophyte species). The FRic measure has no a priori relationship with species richness (Villéger et al., 2008) however, in most studies, functional diversity and richness tend to increase with increasing species richness (Hooper et al., 2005; Petchey and Gaston, 2002; Wiedmann et al., 2014; Włodarska-Kowalczyk et al., 2019; Zhong et al., 2020). In the present study, within the vegetated habitat, functional richness was best correlated to macrophyte diversity, while species diversity was shaped rather by the habitat-builders abundance. A recent inventory of macrofauna diversity across a seascape gradient of eleven seagrass meadows differing in the number, composition, and density of plant species from the Baltic Sea concluded that macrofauna benefits from the natural occurrence of drifting algae trapped in the aboveground structures of the meadows (Rodil et al., 2021). The experimental study of primary (eelgrass), and secondary (pen clams) foundation species in the North Carolina, US coast demonstrated that secondary foundation species are important drivers of local biodiversity in marine ecosystems and that functioning may more likely be enhanced in scenarios where secondary foundation species specifically increase the diversity of key functional groups such as epiphyte grazers (Stacy Zhang and Silliman, 2019). Likely, seagrass meadows with higher diversity of associated macrophytes species offer more food sources for grazers such as amphipods, isopods, and gastropods that mostly feed on epiphytes growing on the surface of the larger plants and algae (Jankowska et al., 2018). Therefore, enhanced macrophytes and macroalgal diversity might favor a wider range of specialized invertebrate consumers. In the present study, some macrofauna species are noted only at the vegetated Outer site, including the grazers: *Jaera* sp., *Radix labiate*, and three *Gammarus* species. The enhancement of POC and chlorophyll-*a* concentration (common descriptors of food availability for benthic fauna), was noted at vegetated habitat at all three sites (Table 1, Jankowska et al., 2016) while the highest pool of associated macrophyte species was presented at the

Outer site supporting the greater number of grazers species and greater functional diversity. This effect can be linked to higher access of epiphytes. The greater macrophyte diversity of seagrass meadows may not only widen a pool of available food sources but also create better shelter or nursery ground for some fish or invertebrate species. Indeed, as shown by a global *meta*-analysis assessing the seagrass nursery role, dominant seagrass species morphology seemed to be less important for nursery functionality than the coexistence of different habitat-forming species (McDevitt-Irwin et al., 2016). Therefore, the highest macrofaunal functional richness noted at the vegetated Outer site might also come from the fact that a higher number of associated macrophytes offer more shelter opportunities for macrofauna individuals of different ages, sizes, and lifestyle preferences.

There are different sets of species inhabiting vegetated and unvegetated habitats at the Inner and GS site, and even though there are fewer species at the unvegetated habitats from the traits and functional richness perspective, the seagrass, and bare sands communities encompass a similar set of functions. On the other side, the macrofauna communities of the vegetated Outer site had all traits subcategories that were noted within this study as well as presented the highest frequency of traits occurrence. And when comparing vegetated and unvegetated habitat at Outer site, the functional traits subcategories that occurred only within macrofauna communities at vegetated habitat are within six out of total eight trait categories noted in this study (very long longevity, planktonic larvae, benthic-pelagic environmental position, feeding type of parasite, and mobility sessile as well as small and large body sizes). Body size is a central trait of an organism, linked to biological rates of respiration, growth, reproduction, mortality and is often used as an indicator that both captures and simplifies biological information for interacting taxa in assemblages, providing metrics to describe community structure, function, and response to environmental change (Brown et al., 2004; Górka and Włodarska-Kowalczyk, 2017; Mazurkiewicz et al., 2020; Woodward et al., 2005). Functional richness indicates resources use, thus productivity of the communities (Petchey et al., 2004), capacity to buffer against environmental fluctuations, and the potential to resist invasive species (Dukes, 2001). At the vegetated Outer site, functional richness was the highest, and all five body size ranges (from small to large) were noted contrary to the other sites where only three (from small-medium to medium-large) were present. Therefore, both higher functional richness and the number of body size subcategories for vegetated Outer sites indicate that the productivity, resistance, and stability within this habitat might be the highest.

Short geological history and low salinity of the Baltic Sea induce its taxonomic impoverishment, and it is still debated to what extent the low taxonomic diversity influences the functioning of the Baltic Sea system as compared to the open sea, highly diverse systems Nordström i in. (2010). The present study shows that the Southern Baltic Sea seagrass meadows communities are characterized by relatively high functional richness (FRic from 203.7 ± 64.3 to 44.7 ± 41.1), comparable to other diverse, fully saline systems such as Arctic fjords (FRic from 32.3 ± 33.8 to 430.8 ± 84.9 , (Włodarska-Kowalczyk et al., 2019)), or the coast of Brazil (FRic below 200, (Gusmao et al., 2016)). In contrast, the species richness noted in the studied region (from 7 ± 1.4 to 20 ± 1.4 , Outer unvegetated and vegetated respectively) lay in the low end in a range of values recorded in other temperate seagrass communities (from 22 to 115 in the Danish coast, Josefson & Hansen, 2004) and was much lower than tropical seagrass communities (e.g. 149 in Indonesian multispecific seagrass beds, Lin et al., 2018). Thus, our data confirm, that despite the taxonomic diversity impoverishment, the Baltic Sea seagrass systems sustain as high functional richness the other (species-rich) systems, supporting the theory of non-linear relation between taxonomic and functional richness. Moreover, our study shows that the species and functional trait richness relationship can be very complex, and these two indicators of faunal diversity may respond differently to changes in environmental conditions.

5. Conclusion.

Only diverse meadows consisting of both dominant seagrass and various plant and macroalgal species forming complex habitats significantly promoted functional richness and the higher number of traits expressed by macrofauna communities in the Puck Bay. Having more traits present, the faunal communities of the meadows characterized by the high macrophyte diversity might represent higher plasticity and stability. Our results might have implications for the conservation and restoration of seagrass ecosystems in systems with low diversity such as the Baltic Sea. It is possible that restoration of seagrasses that includes the simultaneous planting of both seagrass and other plant and macroalgae species is likely to return greater taxonomic and functional richness in the low diversity systems. Moreover, studying both taxonomic and functional indicators of macrofauna communities is necessary to depict the whole picture of marine ecosystems.

CRediT authorship contribution statement

Emilia Jankowska: Conceptualization, Methodology, Software, Writing – original draft. **Maria Włodarska-Kowalczyk:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Maria Włodarska-Kowalczyk reports financial support was provided by Foundation for Baltic and East European studies.

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

Data availability

I have shared the link to raw data in the attached file. The raw data are provided online at DOI: 10.17632/2p5rngm4rk.2.

Acknowledgements

We would like to thank to Alicja Rozenbajger for helping in the laboratory analysis. Moreover, special thanks for help with the field works to Wojtek Moskal, Piotr Bałazy, Kuba Kowalczyk, Kajetan Deja, Anna Piwoni-Piórewicz, and Madalena Łacka-Wojciechowska. We acknowledge funding from the Foundation for Baltic and East European Studies (ClimScope, grant number: 21-GP-0005).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109512>.

References

- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd., Plymouth.
- Atrill, M.J., Strong, J.A., Rowden, A.A., 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23 (1), 114–121. <https://doi.org/10.1111/j.1600-0587.2000.tb00266.x>.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9 (10), 1146–1156. <https://doi.org/10.1111/j.1461-0248.2006.00963.x>.
- Bond, W.J., 1993. Keystone Species. In: Schulze, E., Mooney, H. (Eds.), *Biodiv. Springer-Verlag, Berlin*.
- Bos, A.R., Bouma, T.J., de Kort, G.L.J., van Katwijk, M.M., 2007. Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuar. Coast. Shelf Sci.* 74 (1–2), 344–438. <https://doi.org/10.1016/j.ecss.2007.04.006>.

- Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera Marina* (L.) beds in the Northern Baltic Sea. *J. Sea Res.* 37 (1), 153–166. [https://doi.org/10.1016/S1385-1101\(96\)00007-X](https://doi.org/10.1016/S1385-1101(96)00007-X).
- Boström, C., Törnroos, A., Bonsdorff, E., 2010. Invertebrate dispersal and habitat heterogeneity: expression of biological traits in a seagrass landscape. *J. Exp. Mar. Biol. Ecol.* 390 (2), 106–117. <https://doi.org/10.1016/j.jembe.2010.05.008>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. TOWARD A METABOLIC THEORY OF ECOLOGY. *Ecology* 85 (7), 1771–1789. <https://doi.org/10.1890/03-9000>.
- Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443 (7114), 989–992. <https://doi.org/10.1038/nature05202>.
- Díaz, S., Cabido, M., 2001. Vive La Différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16 (11), 646–655.
- Dukes, J.S., 2001. Biodiversity and invasibility in Grassland Microcosms. *Oecologia* 126 (4), 563–568. <https://doi.org/10.1007/s004420000549>.
- Evans, C.A., O'Reilly, J.E., 1982. A manual for the measurement of Chlorophyll A, net phytoplankton, and Nanoplankton: provisional copy for use on vessels participating in FIBEX. *BIOMASS Sci. Ser.* 9, 40.
- Folk, R.L., Ward, W.C., 1957. Brazos River Bar [Texas]; a study in the significance of grain size parameters. *J. Sediment. Res.* 27 (1), 3–26. <https://doi.org/10.1306/74d70646-2b21-11d7-8648000102c1865d>.
- Fredriksen, S., de Backer, A., Boström, C., Christie, H., 2010. Infauna from *Zostera Marina* L. meadows in Norway. Differences in vegetated and Unvegetated areas. *Mar. Biol. Res.* 6 (2), 189–200. <https://doi.org/10.1080/1745100903042461>.
- Gartner, A., Tuya, F., Lavery, P.S., McMahon, K., 2013. Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *J. Exp. Mar. Biol. Ecol.* 439, 143–151. <https://doi.org/10.1016/j.jembe.2012.11.009>.
- Górska, B., Włodarska-Kowalczyk, M., 2017. Food and disturbance effects on arctic benthic biomass and production size spectra. *Prog. Oceanogr.* 152, 50–61. <https://doi.org/10.1016/j.pcean.2017.02.005>.
- Green, E.P., Short, F.T. 2003. *World Atlas of Seagrasses*. Prepared b. Berkeley, USA: University of California Press.
- Gusmao, J.B., Brauko, K.M., Eriksson, B.K., Lana, P.C., 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. *Ecol. Ind.* 66, 65–75. <https://doi.org/10.1016/j.ecolind.2016.01.003>.
- Harley, C.D.G., O'Riley, J.L., 2011. Non-linear density-dependent effects of an intertidal ecosystem engineer. *Oecologia* 166 (2), 531–541. <https://doi.org/10.1007/s00442-010-1864-1>.
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75 (1), 3–35. <https://doi.org/10.1890/04-0922>.
- Jankowska, Emilia, Marleen De Troch, Loïc N. Michel, Gilles Lepoint, Maria Włodarska-Kowalczyk. 2018. 'Modification of benthic food web structure by recovering seagrass meadows, as revealed by trophic markers and mixing models'. *Ecol. Ind.* 90 (September 2017):28–37. doi: 10.1016/j.ecolind.2018.02.054.
- Jankowska, E., Włodarska-Kowalczyk, M., Kotwicki, L., Balazy, P., Kuliński, K., 2014. Seasonality in vegetation biometrics and its effects on sediment characteristics and Meiofauna in Baltic Seagrass Meadows. *Estuar. Coast. Shelf Sci.* 139, 159–170. <https://doi.org/10.1016/j.ecss.2014.01.003>.
- Jankowska, E., Michel, L.N., Zaborska, A., Włodarska-Kowalczyk, M., 2016. Sediment carbon sink in low-density temperate Eelgrass Meadows (Baltic Sea). *J. Geophys. Res. Biogeosci.* 121 (12), 2918–2934. <https://doi.org/10.1002/2016JG003424>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69 (3), 373. <https://doi.org/10.2307/3545850>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78 (7), 1946. <https://doi.org/10.2307/2265935>.
- Josefson, A.B., Hansen, J.L.S., 2004. Species richness of benthic Macrofauna in Danish Estuaries and coastal areas. *Glob. Ecol. Biogeogr.* 13 (3), 273–288. <https://doi.org/10.1111/j.1466-822X.2004.00091.x>.
- Kruk-Dowigallo, Lidia. 1991. 'Long Term Changes in the Structure of Underwater Meadows of the Puck Lagoon'. Pp. 77–85 in *Proceedings 11th Baltic Marine Biology Symposium Acta Ichthyologica et Piscatoria vol. 21*, edited by T. Radziejewska. Szczecin.
- Laliberte, E., Legendre, P., Shipley, B., Laliberte, M.E. 2014. *Package 'FD'. Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology*.
- Lawton, J.H., Jones, C.G., 1995. *Linking Species and Ecosystems: Organisms as Ecosystem Engineers*. In: Jones, C., Lawton, J. (Eds.), Linkin. Chapman & Hall, New York.
- Leopardas, V., Uy, W., Nakaoka, M., 2014. Benthic Macrofaunal assemblages in multispecific seagrass meadows of the southern Philippines: variation among vegetation dominated by different seagrass species. *J. Exp. Mar. Biol. Ecol.* 457, 71–80. <https://doi.org/10.1016/j.jembe.2014.04.006>.
- Lin, J., Huang, Y., Arbi, U.Y., Lin, H., Azkab, M.H., Wang, J., He, X., Mou, J., Liu, K., Zhang, S., 2018. An ecological survey of the abundance and diversity of benthic Macrofauna in Indonesian Multispecific Seagrass beds. *Acta Oceanol. Sin.* 37 (6), 82–89. <https://doi.org/10.1007/s13131-018-1181-9>.
- Lundquist, C.J., Jones, T.C., Parkes, S.M., Bulmer, R.H., 2018. Changes in benthic community structure and sediment characteristics after natural recolonisation of the Seagrass *Zostera Muellieri*. *Sci. Rep.* 8 (1), 13250. <https://doi.org/10.1038/s41598-018-31398-2>.
- Mazurkiewicz, M., Górska, B., Renaud, P.E., Włodarska-Kowalczyk, M., 2020. Latitudinal consistency of biomass size spectra - Benthic resilience despite environmental, taxonomic and functional trait variability. *Sci. Rep.* 10 (1), 4164. <https://doi.org/10.1038/s41598-020-60889-4>.
- McDevitt-Irwin, J.M., Iacarella, J.C., Baum, J.K., 2016. Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. *Mar. Ecol. Prog. Ser.* 557, 133–143. <https://doi.org/10.3354/meps11848>.
- Nordström, M.C., Lindblad, P., Aarnio, K., Bonsdorff, E., 2010. A neighbour is a neighbour? Consumer diversity, trophic function, and spatial variability in benthic food webs. *J. Exp. Mar. Biol. Ecol.* 391 (1–2), 101–111. <https://doi.org/10.1016/j.jembe.2010.06.015>.
- Parker, J.D., Emmett Duffy, J., Orth, R.J., 2001. Plant species diversity and composition: experimental effects on marine Epifaunal assemblages. *Mar. Ecol. Prog. Ser.* 224, 55–67. <https://doi.org/10.3354/meps224055>.
- Petchey, O.L., Gaston, K.J., 2002. Functional Diversity (FD), species richness and community composition. *Ecol. Lett.* 5 (3), 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>.
- Petchey, O.L., Hector, A., Gaston, K.J., 2004. How do different measures of functional diversity perform? *Ecology* 85, 847–857.
- Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24 (9), 505–514.
- Rodil, I.F., Lohrer, A.M., Attard, K.M., Hewitt, J.E., Thrush, S.F., Norkko, A., 2021. Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. *Biodivers. Conserv.* 30 (11), 3023–3043. <https://doi.org/10.1007/s10531-021-02234-3>.
- Rooney, N., McCann, K.S., 2012. Integrating food web diversity, structure and stability. *Trends Ecol. Evol.* 27 (1), 40–46.
- Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. *Ecol. Monogr.* 80 (3), 469–484. <https://doi.org/10.1890/08-2225.1>.
- Sirota, L., Hovel, K.A., 2006. Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the Epifaunal Community of San Diego Bay, California, USA. *Mar. Ecol. Prog. Ser.* 326, 115–131.
- Smola, Z., Węslawski, J.M., Kotwicki, L., Balazy, P., Andrzejewicz, E., Piwowarczyk, J. (Eds.), 2014. *Podmorski Ogród Gdyni. Planowany Morski Rezerwat Poradnik Użytkownika*. Institute of Oceanology Polish Academy of Sciences, Sopot.
- Sokolowski, A., Wolowicz, M., Asmus, H., Asmus, R., Carlier, A., Gasunaitė, Z., Grémare, A., Hummel, H., Lesutienė, J., Razinkovas, A., Renaud, P.E., Richard, P., Kedra, M., 2012. Is benthic food web structure related to diversity of marine Macrobenthic communities? *Estuar. Coast. Shelf Sci.* 108, 76–86. <https://doi.org/10.1016/j.ecss.2011.11.011>.
- Stacy Zhang, Y., Silliman, B.R., 2019. A facilitation cascade enhances local biodiversity in seagrass beds. *Diversity* 11 (3), 30. <https://doi.org/10.3390/D11030030>.
- Stoner, A.W., Graham Lewis, F., 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *J. Exp. Mar. Biol. Ecol.* 94 (1–3), 19–40. [https://doi.org/10.1016/0022-0981\(85\)90048-6](https://doi.org/10.1016/0022-0981(85)90048-6).
- Symstad, A.J., Siemann, E., Haarstad, J., 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. *Oikos* 89 (2), 243–253.
- Tilman, D., 1997. Distinguishing between the effects of species diversity and species composition. *Oikos* 80 (1), 185. <https://doi.org/10.2307/3546532>.
- Törnroos, A., 2014. *Interpreting Marine Benthic Ecosystem Functioning in Coastal Waters: Validating the Biological Trait Concept*. Åbo Akademi University.
- Törnroos, Anna, Bonsdorff, Erik, 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecological Applications: A Publication of the Ecological Society of America* 22 (8), 2221–2236. <https://doi.org/10.1890/11-2042.1>.
- Törnroos, A., Bonsdorff, E., Bremner, J., Blomqvist, M., Josefson, A.B., Garcia, C., Warzocha, J., 2015. Marine benthic ecological functioning over decreasing taxonomic richness. *J. Sea Res.* 98 (May), 49–56. <https://doi.org/10.1016/j.seares.2014.04.010>.
- Urta, J., Ramirez, Á.M., Marina, P., Salas, C., Gofas, S., Rueda, J.L., 2013. Highly diverse Molluscan Assemblages of Posidonia Oceanica Meadows in Northwestern Alboran Sea (W Mediterranean): seasonal dynamics and environmental drivers. *Estuar. Coast. Shelf Sci.* 117, 136–147. <https://doi.org/10.1016/j.ecss.2012.11.005>.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89 (8), 2290–2301. <https://doi.org/10.1890/07-1206.1>.
- Violle, C., Navas, M.L., Vile, D., et al., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Węslawski, J.M., Kryla-Straszewska, L., Piwowarczyk, J., Urbański, J., Warzocha, J., Kotwicki, L., Włodarska-Kowalczyk, M., Wiktor, J., 2013. Habitat modelling limitations - Puck Bay, Baltic Sea - A case study. *Oceanologia* 55 (1), 167–183. <https://doi.org/10.5697/oc.55-1.167>.
- Węslawski, J.M., Warzocha, J., Wiktor, J., Urbański, J., Bradtke, K., Kryla, L., Tatarek, A., Kotwicki, L., Piwowarczyk, J., 2009. Biological valorisation of the Southern Baltic Sea (Polish Exclusive Economic Zone). *Oceanologia* 51 (3), 415–435. <https://doi.org/10.5697/oc.51-3.415>.
- Wiedmann, Magnus Aune, Michaela Aschan, Grégoire Certain, Andrey Dolgov, Michael Greenacre, Edda Johannessen, Benjamin Planque, Raul Primicerio. 2014. 'Functional diversity of the barents sea fish community'. *Mar. Ecol. Prog. Ser.* 495, 205–218. doi: 10.3354/meps10558.
- Włodarska-Kowalczyk, M., Jankowska, E., Kotwicki, L., Balazy, P., 2014. Evidence of season-dependency in vegetation effects on Macrofauna in temperate seagrass

- meadows (Baltic Sea). PLoS One 9 (7). <https://doi.org/10.1371/journal.pone.0100788>.
- Włodarska-Kowalczyk, M., Aune, M., Michel, L.N., Zaborska, A., Legeżyńska, J., 2019. Is the trophic diversity of marine benthic consumers decoupled from taxonomic and functional trait diversity? Isotopic niches of arctic communities. *Limnol. Oceanogr.* 64 (5), 2140–2151. <https://doi.org/10.1002/lno.11174>.
- Woodward, G., Ebenman, B.o., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. *Trends Ecol. Evol.* 20 (7), 402–409.
- WoRMS Editorial Board (2022). World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 2022-08-31. doi:10.14284/170.
- Zhong, X., Qiu, B., Liu, X., 2020. Functional diversity patterns of Macrofauna in the adjacent waters of the Yangtze river estuary. *Mar. Pollut. Bull.* 154, 111032 <https://doi.org/10.1016/j.marpolbul.2020.111032>.