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Physical drivers of epi- and infauna communities related to dominating macrophytes in shallow bays in the Northern Baltic Sea

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ABSTRACT

Shallow coastal bays with dense aquatic phytobenthic communities are important but vulnerable habitats and nursery areas for fish and invertebrates in the Baltic Sea. These habitats are under increasing anthropogenic stress, and understanding their dynamics is a prerequisite for management and conservation. In this study, we examined the effects of isolation of the bay from the sea, water and sediment characteristics, and macrophyte species on the invertebrate communities. In each bay, both epifauna and infauna were sampled in pairs of monospecific patches of dominating habitat-forming macrophytes (*Stuckenia pectinata*, *Chara tomentosa* and *Ceratophyllum demersum*). We found that the invertebrate community was mainly affected by bay isolation, which correlated with other environmental variables, and thus likely drives many processes in the bays. Further, the epifauna community responded to both the median grainsize and geometric standard deviation across both the isolation gradient (*S. pectinata* alone) and in the *S. pectinata* - *C. demersum* macrophyte pair, whereas the median grainsize affected the epifauna in the *S. pectinata* - *C. tomentosa* macrophyte pair. The infauna community responded to either the median grainsize or the geometric standard deviation across the isolation gradient and in both macrophyte pairs. Only minor differences between the dominating macrophyte species were seen regarding invertebrate abundance, taxon richness and diversity, although the more structurally complex *C. demersum* supported the highest epifauna diversity and lowest infauna abundance. However, at local, within bay scale, epifauna communities varied between most pairs of macrophyte species, suggesting that habitat-forming macrophytes have important roles in structuring local invertebrate community patterns. This study emphasizes the complexity of biotic and abiotic interactions within and among shallow coastal bays, and the challenges with studying and comparing processes in these unique ecosystems.

1. Introduction

Shallow coastal lagoons (hereafter bays) are enclosed sea areas, separated from the sea by a barrier, and connected to it by one or more inlets (Phleger, 1969). Similar to estuaries and other shallow environments, these bays are one of the most productive ecosystems in the world (Boynton et al., 1996). Due to morphometric characteristics, organic material accumulates in the bays, and temperature differences may be large especially during spring (Snickars et al., 2009). Shallow bays are naturally nutrient rich, have a photic sediment and host rooted vegetation (Lee and Olsen, 1985).

In the northern Baltic Sea, the morphology of the archipelagos is constantly changing through isostatic land uplift and shoreline displacement. Bays with a threshold at the inlet transition through different stages of isolation, and over time, open bays are cut off from the

sea and form lakes, marshes or land, which takes approximately 500–700 years (Munsterhjelm, 1997; Hansen, 2013). These environments, play an important role as nurseries and habitats for coastal fish and invertebrates and by harboring several threatened and unique species of aquatic macrophytes (Appelgren and Mattila, 2005; Hansen et al., 2008; Snickars et al., 2009).

During the last 50 years, shallow Baltic Sea bays have been exposed to increasing levels of anthropogenic stressors such as nutrient loading, mechanical disturbance caused by coastal construction and dredging, increased boat traffic (Schubert and Blindow, 2003; Munsterhjelm, 2005; Sagerman et al., 2019) as well as fishing (e.g. Bergström et al., 2016; Olsson, 2019). Due to the ecological importance of these habitats, they are also included in the EU Habitats Directive and classified as habitats of special importance (Coastal lagoons 1150) (EC, 2007) and needs to be carefully managed.

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The biotic communities of these bays are largely affected by an isolation gradient, which relative role seems to vary depending on organism groups. This has been reported for submerged macrophytes (e.g. Appelgren and Mattila, 2005; Munsterhjelm, 1997), phytoplankton (Scheinin and Mattila, 2010) and benthic invertebrates (Hansen et al., 2008, 2011, 2011). The vegetation of open bays with high water exchange are characterized by species of marine origin, such as the brown algae *Fucus vesiculosus* and the vascular plant *Ruppia cirrhosa*, but also by species of freshwater origin such as *Potamogeton perfoliatus*. As the isolation of a bay increases, the vegetation shifts and becomes dominated by vascular freshwater plants like *Stuckenia pectinata*, *Myriophyllum* spp. and *Ceratophyllum demersum*. In isolated bays, the vegetation is characterized by an increased cover of *Najas marina* and stoneworts such as *Chara tomentosa* (Munsterhjelm, 1997; Appelgren and Mattila, 2005; Hansen et al., 2012). The community structure of fish and zooplankton also varies in bays with level of isolation. Sheltered bays with higher nutrient levels support less plankton diversity compared to more open bays (Scheinin and Mattila, 2010). The fish community, especially juveniles, in sheltered bays are dominated by perch (*Perca fluviatilis*) and cyprinids, whereas the three-spined stickleback (*Gasterosteus aculeatus*) is more common in open bays (Snickars et al., 2009).

Only a few studies have examined invertebrate communities related to a bay isolation gradient and macrophyte composition in shallow Baltic Sea bays (e.g. Wallström et al., 2000; Hansen et al., 2008, 2010; 2012). Open bays have generally been dominated by gastropods, bivalves, and crustaceans, and sheltered bays by a few insect taxa (Hansen et al., 2008). The taxon richness of the submerged flora in the bays, have also been found to have a greater positive effect on the invertebrate biomass and taxon richness than the structural complexity of the macrophyte species itself (Hansen et al., 2008). Both epi- and infauna have important roles, e.g. in trophic interactions (Eriksson et al., 2009), nutrient recycling and as periphyton grazers (Merritt and Cummins, 2006; Norling et al., 2007). However, the knowledge on the distribution of the epi- and infauna communities in shallow Baltic Sea bays with

varying levels of isolation, is still largely lacking.

This study aims to test the relationship between the macro-invertebrate community and physical and biotic drivers in shallow Baltic Sea bays. This was done through a holistic approach where both the epi- and infauna communities were analyzed across a gradient in bay's isolation from the sea. The macroinvertebrate community composition, abundance, taxon richness and diversity were analyzed in relation to isolation, water quality, sediment properties and macrophyte species. This was made to study the ecology in shallow Baltic Sea bays and further, to offer base line information of these important environments for managers.

2. Materials and methods

2.1. Study area

The non-tidal Baltic Sea is characterized by both latitudinal and longitudinal salinity, nutrient (Rinne et al., 2011) and temperature gradients, with water levels fluctuating according to wind and air pressure (± 1 m) (Novotny et al., 2006). The sea is also subject to an isostatic land-uplift ranging from 1 mm/year in the southern part of the Baltic Proper to 11 mm/year in the northern part of the Bothnian Bay (Vestøl et al., 2019), being around 4–6 mm in our study area. The study area is also affected by eutrophication due to decades of excess nutrient input (Rönnberg and Bonsdorff, 2004; Andersen et al., 2017).

This study was conducted during July and August 2017 in six land-uplift bays throughout the Åland Islands, a vast archipelago between the Baltic Proper and the Bothnian Sea in the northern Baltic Sea (Fig. 1). The studied bays were chosen along a gradient of isolation, which further affects physical properties such as the temperature, salinity, nutrient load (Bonsdorff et al., 2003) and turbidity (Veneranta et al., 2011).

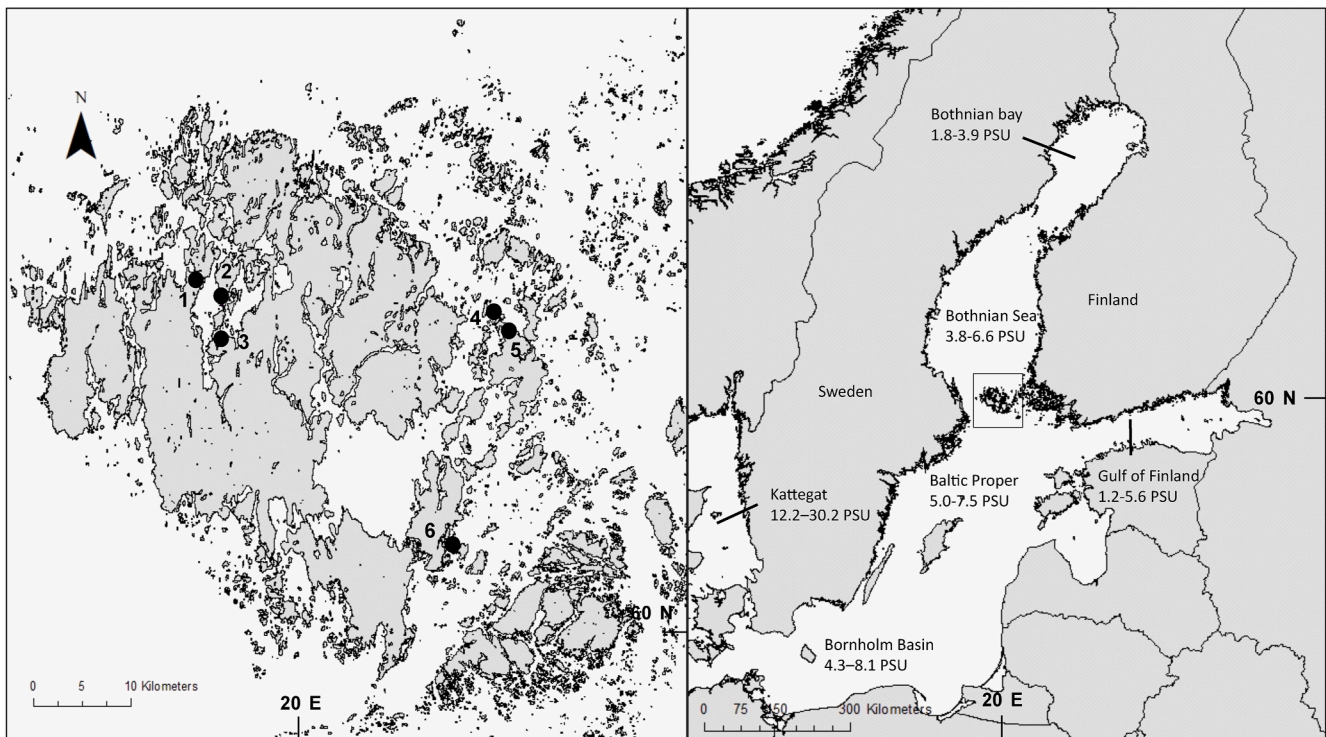


Fig. 1. Location of the studied bays in the Åland Islands, the Northern Baltic Sea, in decreasing order of isolation 1–6 (left) Position of the Åland Islands and the average salinity per basin (right) (Andersen et al., 2017).

2.2. Field sampling

The vegetation and water depth in the bays were mapped during June and July 2017, by snorkeling along transects according to the method used in Snickars et al. (2009) to find suitable sites for sampling invertebrates. Only sites where one macrophyte species clearly dominated (monospecific patches) were chosen (>70% coverage of one species, similarly to Hansen et al., 2011). Three macrophyte species, *C. tomentosa*, *S. pectinata*, and *C. demersum*, were dominating in several of the bays and selected for this study.

2.3. Sampling of macrofauna

Five replicates of epifauna and infauna were sampled during late July and early August in each dominating macrophyte species present in each bay (maximum 2 dominant macrophyte species per bays were found) (Appendix A), at a depth between 0.6 and 1.7 m. Samples from different macrophyte species in the same bay were taken no more than 150 m apart. The epifauna was sampled in the middle of a 0.5 * 0.5 m square with >70% cover of the selected macrophyte species, using standard net bags (25 × 30 cm, 250 µm mesh) that were put over the macrophyte, enclosed and lifted to the surface. Each sample consisted of a single shoot with a length of 25 cm (±3 cm). The net bag samples were stored in seawater during transportation to the lab, where the epifauna was sorted. The macroscopic epiphyte cover (e.g. filamentous algae) on the macrophyte samples was so low, or non-existent, that it was excluded in this study. The infauna was sampled from a corresponding macrophyte site from the top 10 cm of the sediment with a small 6.8 cm Ø corer, to include potential effects of the associated macrophytes and their root systems. The sediment was sieved through a 0.5 mm mesh in the field and remaining invertebrates and detritus (>0.5 mm) were preserved in 70% ethanol. The macroinvertebrate samples were sorted to species/taxa level and counted under a microscope.

2.4. Water quality and sediment

The water quality parameters were measured by taking water samples at 1 m depth at three sites in each bay (inner, middle and outer part) in June and August 2017. The samples were analyzed for turbidity (NTU), total phosphorous (µg/l) and chlorophyll *a* (µg/l) (Grasshoff and Kremling, 1983) and the mean values per bay were calculated. To study the grain size of the sediment where the macrophyte species occurred, five replicates were sampled near (5 cm) each macrophyte species per bay, at the same sites where the fauna was sampled, using a 100 ml syringe, which was pressed 10 cm into the sediment. The sediment samples were dried, and organic material was dissolved in a 6% hydrogen peroxide solution for 72 h. The samples were separated through a range of sieves using the Wentworth scale (4 mm, 2 mm, 500 µm, 250 µm, 125 µm and 63 µm), dried for 48 h at 60 °C. The dry weight was obtained for each fraction and the median grain size (D50) and the geometric standard deviation as a measure of grain size evenness were calculated (Blott and Pye, 2001).

2.5. Bay isolation gradient

The bay isolation was calculated according to the site scores of the first axis of a principal component analysis (PCA; 'Vegan' package in the software R (version 3.6.1), Oksanen et al., 2009) of wave exposure and water exchange (Ea) (Hansen et al., 2012).

The water exchange between the bay and the outside sea area was calculated as openness (Ea) (Snickars et al., 2009), as there is a close relationship between openness and water exchange (Persson et al., 1994). Ea was calculated using the formula: $Ea = 100 * At/a$ where *At* is the cross-section area (mean depth * width, measured along a transect) at the threshold of the inlet to the bay, and *a* is the water surface area of the bay (Persson et al., 1994). The wave-exposure was estimated using

the WaveImpact 1.0 model where fetch is calculated by determining the refraction/diffraction for 25 * 25-m grids covering the study area. Wave exposure values were obtained by multiplying the mean wind speed of 16 directions over a 5-yr period by the adjusted fetch of the corresponding direction. Exposure was calculated as the mean wave-exposure of all 25 * 25 grids in a bay (Isæus, 2004; Sundblad et al., 2014).

2.6. Statistical analyses

Taxon richness and Shannon-Wiener diversity were calculated using the "specnumber" and "diversity" functions in the software R (version 3.6.1). The difference in total abundance, taxon richness and Shannon-Wiener diversity between pairs of macrophyte species in bays were both species occur, were analyzed by performing Mann-Whitney U tests by using the "wilcox.test" function in the software R (version 3.6.1).

The covariation of the environmental variables were analyzed by Spearman ranked correlation. To avoid collinearity, total phosphorous was selected as single water parameter, as it is the limiting factor for Baltic Sea coastal primary production (Andersson et al., 1996). The community composition of the epifauna and infauna between two pairs of macrophyte species in bays where both co-occur and within *S. pectinata* over the isolation gradient, was analyzed by Bray-Curtis dissimilarity matrices of the abundance, and was visualized in a 2-dimensional ordination space by non-metric multidimensional scaling (NMDS). The NMDS was done using the function "metaMDS". The NMDS was run until solutions with minimal stress were obtained (Oksanen et al., 2009). The "metaMDS" function autotransformed (square root) the epifauna community data prior to calculating the Bray-Curtis dissimilarity matrix, while no transformations were applied to the infauna community. The influence of the environmental variables on the invertebrate community composition were analyzed by covariate type I PERMANOVA on both the epi- and infauna within *S. pectinata* and within the two pairs of co-occurring macrophyte species (*S. pectinata* - *C. tomentosa* and *S. pectinata* - *C. demersum*). The environmental variables included in the models were isolation, total phosphorous, geometric standard deviation and D50 (median sediment grain size). In the *S. pectinata* and *C. demersum* pair, the levels of isolation and total phosphorous coincided, so total phosphorous was excluded from the model as isolation was the causal factor, driving the nutrient levels.

To analyze how the two invertebrate communities were affected by the isolation gradient, permutational analysis of variance (PERMANOVA, Anderson et al., 2008) was used with bays grouped according to the isolation scores. As the macrophyte species *S. pectinata* occurred in five bays, the analysis was conducted based on epi- and infauna associated to this macrophyte. To analyze the role of different macrophyte species, a PERMANOVA was used on the two invertebrate communities between pairs of co-occurring dominating macrophyte species within the bays. 999 permutations with residuals under reduced model and type I (sequential) sums of squares were used in the PERMANOVA with the "adonis" function. The homogeneity of dispersion between macrophyte species per bay was tested with PERMDISP, using the "betadisper" function. The F-value was calculated by dispersion from the median and the p-value was obtained through 999 permutations. The "metaMDS", "adonis" and "betadisper" functions are part of the "vegan" package in the software R (version 3.6.1).

A similarity percentage (SIMPER) analysis (Clarke and Gorley, 2006) was used to analyze, which epi- and infauna species/taxa contributed to the variation between different macrophyte species. The SIMPER analysis was done using PRIMER7 +.

3. Results

The level of bay isolation was strongly correlated with chlorophyll-*a* and turbidity, where the open bays generally had lower phosphorous and chlorophyll-*a* and turbidity values (Table 1, Appendix B), indicating that isolation drives the variation of many water parameters. The

Table 1

Spearman rank correlation coefficients (upper part) and p-values (lower part) for the isolation, water quality parameters and sediment properties (Geometric st. dev. and D50) (>0.05 p-value in bold). Data is presented in [Appendix B](#).

	Isolation	Tot.P	Chlorophyll <i>a</i>	Turbidity	Geometric.st.dev	D50
Isolation		0.79	0.86	0.63	−0.23	0.02
Tot.P	<0.001		0.83	0.69	0.07	−0.29
Chlorophyll <i>a</i>	<0.001	<0.001		0.72	−0.06	−0.24
Turbidity	<0.001	<0.001	<0.001		0.53	−0.23
Geometric.st.dev	0.091	0.594	0.689	<0.001		−0.29
D50	0.868	0.032	0.073	0.089	0.031	

sediment geometric standard deviation also correlated with turbidity.

In total, 43 invertebrate species/taxa were found in the bays, 29 were epifauna species/taxa and 31 were infauna species/taxa ([Appendix C and D](#)). Of these species, 17 species/taxa (39.5%) occurred as both epi- and infauna.

Between the epifauna abundance, species richness and Shannon-Wiener diversity among the pairs of macrophyte species, the diversity between *S. pectinata* and *C. demersum* was the only measure with a significant difference, with *C. demersum* supporting the higher diversity ([Fig. 2](#)). The infauna species richness and diversity showed no significant difference between the macrophyte pairs. The infauna abundance between *S. pectinata* and *C. demersum* was significantly different with

S. pectinata supporting the higher abundance ([Fig. 2](#)).

The most common species/taxa among both epi- and infauna in the bays were the insect larvae i.e. chironomids, followed by the gastropod *Potamopyrgus antipodarum*. Other gastropods, like *Ecrebia ventrosa* and *Bithynia tentaculata*, the bivalve *Cerastoderma glaucum* and the isopod *Idotea chelipes* also contributed to the epifauna communities, while mainly other gastropods, the polychaetes *Hediste diversicolor* and *Marzelleria* sp. as well as the bivalve *Limecola balthica* contributed to the infauna communities ([Appendix C, D and E](#)).

The NMDS of the epi- and infauna communities within *S. pectinata* over a gradient of isolation showed a clear trajectory for both communities with the isolated bays placed in the lower-left and the most open

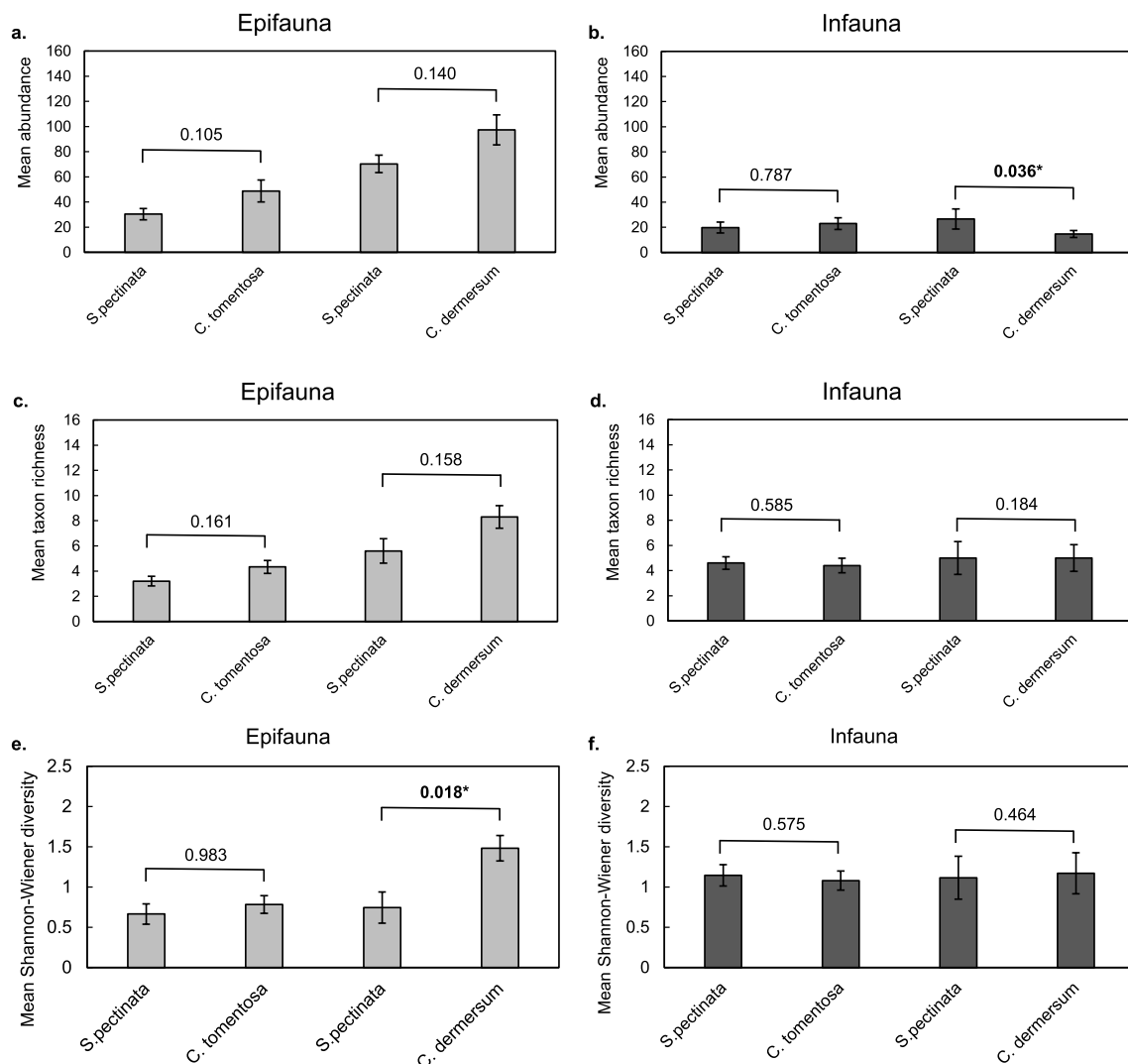


Fig. 2. Comparison of the epi- and infauna (a & b) mean abundance and SE, (c & d) mean species/taxon richness and SE and (e & f) Shannon-Wiener diversity and SE of the macrophyte species *S. pectinata* – *C. tomentosa* (Bay 1,3 & 5) and *S. pectinata* – *C. demersum* (Bay 4 & 6) with Mann-Whitney U p-values ($p < 0.05$ = in bold*).

bays placed in the upper-left corners of the plot (Fig. 3 a & b).

The NMDS of the epifauna community within *S. pectinata* and *C. tomentosa* showed clustering of the *C. tomentosa* community in the central and right part of the plot while the *S. pectinata* community was more dispersed (Fig. 3c). The infauna community within *S. pectinata* and *C. tomentosa* appeared to be equally dispersed over the plot (Fig. 3d). Both the epi- and infauna communities grouped well within the *S. pectinata* and *C. demersum* environments (Fig. 3e and f).

According to the covariate PERMANOVA (Table 2), isolation was the

primary variable with the largest effect on both the epi- and infauna communities within *S. pectinata*, and between the macrophyte pairs, with the exception of epifauna within *S. pectinata* and *C. tomentosa* pair. The total phosphorous affected both epi- and infauna of the *S. pectinata* and *C. tomentosa* pair (total phosphorous was excluded from the *S. pectinata* and *C. tomentosa* pair as it contains two levels, which coincided with the values of the isolation score from the same bays). The sediment properties had an effect on both the single macrophyte species (*S. pectinata*), as well as the macrophyte species pairs, except for

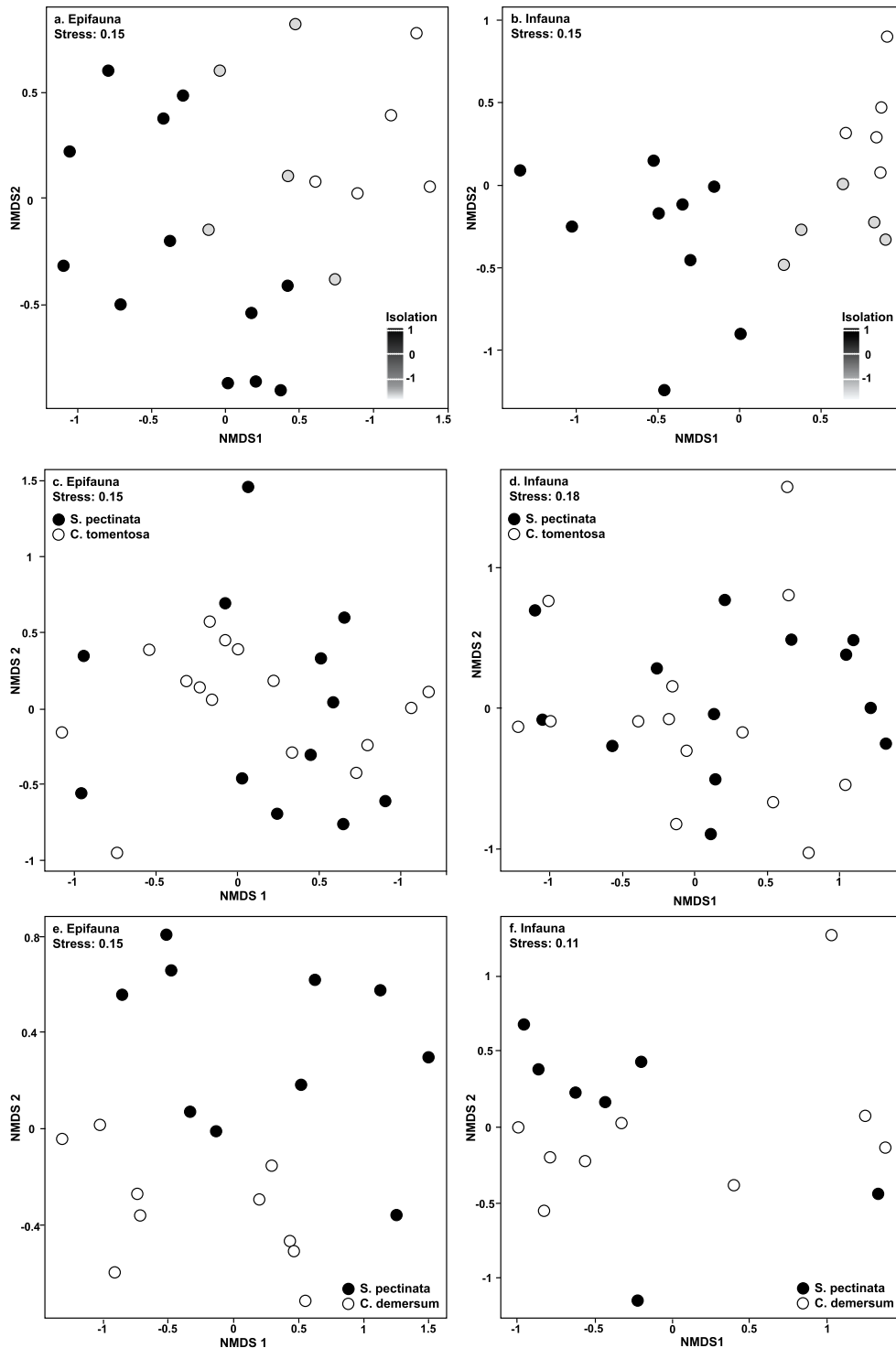


Fig. 3. NMDS ordination based on Bray-Curtis dissimilarity of the epi- and infauna (a & b) within *S. pectinata* over the isolation gradient (Bay 1, 3, 4, 5 & 6), (c & d) within *S. pectinata* and *C. tomentosa* (Bay 1, 3 & 5) and (e & f) within *S. pectinata* and *C. demersum* (Bay 4 & 6).

Table 2

Covariate PERMANOVA (R^2) and p - values ($p < 0.05$ in bold) of the tested variables for both the epifauna and infauna communities. (N.a. stands for non-applicable where covariates could not be included in the same model).

Environmental variable	<i>S. pectinata</i>		<i>S. pectinata</i> - <i>C. tomentosa</i>		<i>S. pectinata</i> - <i>C. demersum</i>	
	R^2	p-value	R^2	p-value	R^2	p-value
Epifauna						
Isolation	0.272	0.001	0.067	0.035	0.551	0.001
Total phosphorous	0.025	0.161	0.127	0.002	n.a.	n.a.
Geometric st. dev.	0.189	0.001	0.015	0.620	0.084	0.009
D50	0.211	0.001	0.211	0.001	0.09	0.011
Infauna						
Isolation	0.316	0.001	0.129	0.002	0.447	0.001
Total phosphorous	0.026	0.426	0.066	0.034	n.a.	n.a.
Geometric st. dev.	0.143	0.002	0.037	0.218	0.039	0.279
D50	0.049	0.104	0.062	0.043	0.105	0.020

geometric standard deviation that did not affect the epifauna comparing *S. pectinata* and *C. tomentosa*. The median grain size (D50) had small effects on the infauna community with both macrophyte species pairs, whereas Geometric standard deviation only influenced the single macrophyte species *S. pectinata* group.

The SIMPER analysis revealed that among the macrophyte species pairs, the infauna community had a higher degree of dissimilarity than the epifauna. The species, which contribute most to the dissimilarity, were similar in both epi- and infauna. However, chironomids had a larger effect on the dissimilarity within the epifauna community, compared to the infauna community. The dissimilarity between the infauna of *S. pectinata* and *C. demersum* was relatively high, yet the contribution of the single species was low, indicating many species with rather large contribution to the dissimilarity.

According to the PERMANOVA, the isolation gradient had a significant effect on both the epi- and infauna communities within *S. pectinata* ($R^2 = 0.212$ and 0.316 respectively) (Table 3). According to the within bay, pairwise PERMANOVA, the epifauna community was significantly different between macrophyte species in all bays except from one (bay 3). The infauna community was significantly different in only the most exposed bays for both macrophyte species pairs (bay 4 for *S. pectinata* and *C. tomentosa*, and bay 6 for *S. pectinata* and *C. demersum*). The PERMDISP showed significant differences in dispersion between the epifauna within *S. pectinata* and *C. tomentosa*. No differences in dispersion were found within the infauna community (Table 3).

4. Discussion

4.1. Response to isolation

This study shows the complex dynamics in shallow Baltic Sea bays and how the environment affects the invertebrate communities (both in- and epifauna) across an isolation gradient and between dominating macrophyte species among and within bays. The results demonstrate that isolation is the main factor driving the variation in both epi- and infauna communities. In addition, when comparing both communities in the *S. pectinata* and *C. tomentosa*, isolation was found to induce differences, although the sediment properties were found to have a stronger effect on the community pattern. This is most likely due to the narrow range of isolation of the bays where these two macrophytes were found in this study. The level of isolation affects the invertebrate community, either directly or indirectly, by driving the variation in other variables. Isolated bays that have reduced water exchange, which has a negative effect on the abundance of filter-feeding macroinvertebrates (Lenihan et al., 1996; Wildish and Kristmanson, 2005) and likely explains the low abundance of bivalves in the isolated bays in this study. Another effect of decreased isolation is an increase in salinity, since direct precipitation

and land run-off are less influential, which decreases the abundance of freshwater-associated macroinvertebrates e.g. insects, and increases species and taxa with a marine origin (Hansen et al., 2008). Further, this may explain the high abundance of chironomids and their high contribution to within bay similarity in all but the open bay.

4.2. Response to macrophyte species

A large part (>39%) of the invertebrates occurs as both epifauna among the sediment and root systems of the macrophytes, and as epifauna among the above ground structure of the macrophyte. The epifauna diversity only differed between the macrophyte species *S. pectinata* and *C. demersum*. These findings are in not entirely in accordance with results by Hansen et al. (2011) who showed that the most structurally complex macrophyte species, *Myriophyllum spicatum*, supported the highest abundance, the charophyte *Chara baltica* the lowest, and *S. pectinata* supporting epifauna abundances between the two other species. Even though the abundance differs little between the macrophyte species in this study, the results from the NMDS show that there are larger differences between the community composition of *S. pectinata* and *C. demersum*, compared to *S. pectinata* and *C. tomentosa*.

Although no large-scale differences between epi- and infauna communities in different macrophyte species were observed, there were variations between the macrophyte species at local, within bay scale, with the epifauna community being significantly different for all pairs of macrophytes in all bays, except in one. On the other hand, the infauna community differed between macrophyte species only in the most exposed bay. This implies that the epifauna community responds more strongly to local scale variations in environmental variables. This may be due to varying predation pressure (Donadi et al., 2017), or differences in macrophyte assemblages, which affect the epifauna abundance (Hansen et al., 2008). In this study, *C. demersum* seems to offer more shelter and suitable substrate to epifauna, compared to the less structurally complex *S. pectinata*, which is in line with Hansen et al. (2011). *C. demersum* also has the highest degree of fractional diversity, which has been found to support higher diversity and species abundance due to increased habitat availability, e.g. niches (Jeffries, 1993; Kovalenko et al., 2012).

The effects of the macrophyte species on the infauna taxon richness is less clear. However, the most structurally complex, but rootless *C. demersum* supported lower infauna abundance in comparison to *S. pectinata*. The infauna taxon richness and diversity was unaffected by the macrophyte species, indicating that the infauna diversity is not that dependent on the above sediment vegetation in Baltic Sea bays. In *Z. marina* meadows, the above ground properties (e.g. leaf number per shoot, shoot density) had an indirect effect on the infauna community structure, possibly through increased deposition of organic matter (food resources) or reduced predator efficiency (shelter), while the macrophyte root structure was found to have little effect (Webster et al., 1998). The complete absence of a root system in *C. demersum*, compared to the other two studied rooted macrophyte species, may have caused the low infauna abundance.

4.3. Response to nutrient levels

Total phosphorous (as representative variable for water quality) did not have a large effect on the invertebrate communities. It only had a significant effect on the epi- and infauna of the *S. pectinata* and *C. tomentosa* pairs in bays with the highest and lowest total phosphorous values, respectively. Higher degrees of isolation generally causes a decrease in water circulation (Hansen et al., 2008; Snickars et al., 2009) and an increase in freshwater and nutrient loading. In this study, this is seen as positive correlations between isolation, and total phosphorous, chlorophyll-a and turbidity. In other vegetated habitats e.g. in seagrass meadows, nutrient levels may have a strong positive effect on the biomass and abundance of grazing marine macroinvertebrates (Baden

Table 3

Comparisons of the Bray-Curtis similarity of epi- and infauna communities between and within levels of isolation and dominating pairs of macrophyte species in the bays. The between group dissimilarity, within group similarity and single invertebrate species/taxon contributing most to the average dissimilarity between the groups, derived from the SIMPER are listed in the center column. R^2 from the PERMANOVA and within bay PERMANOVA as well as F value for PERMDISP with associated p-values of invertebrate communities between isolation groups across *Stuckenia pectinata* (bays 1, 3–6) and pairs of dominating macrophyte species are listed in the right columns. Significant differences ($p < 0.05$) in bold, non-applicable (n.a.) in bay 2 as only one macrophyte species was sampled in this bay three samples from *C. demersum* with no fauna present were excluded from the analyses).

Epifauna			SIMPER					PERMANOVA		PERMDISP		PERMANOVA (within bays)		
Factor	Group 1	Group 2	Between group dissimilarity	Within group 1 similarity	Within group 2 similarity	Species	Average dissimilarity	R ²	p-value	F-value	p-value	Bays	R ²	p-value
Isolation	n.a.	n.a.	n.a.	n.a.	n.a.		n.a.	0.212	0.001	1.423	0.263	1, 3 - 6	n.a.	n.a.
Macrophyte species	<i>S. pectinata</i>	<i>C. tomentosa</i>	54.84	39.81	54.21	Chironomidea sp.	26.99	0.059	0.155	5.625	0.025	1	0.618	0.003
	n = 15 Bay 1,3,5	n = 15 Bay 1,3,5				<i>P. antipodarum</i>	15.07					3	0.125	0.292
Macrophyte species	<i>S. pectinata</i>	<i>C. demersum</i>	72.29	35.19	32.45	<i>T. fluviatus</i>	2.98					5	0.508	0.010
	n = 10 Bay 4,6	n = 10 Bay 4, 6				Chironomidea sp.	22.79	0.097	0.146	0.004	0.953	4	0.401	0.018
						<i>C. glaucum</i>	14.91					6	0.385	0.008
						<i>R. peregra</i>	6.05							
Infauna			SIMPER					PERMANOVA		PERMDISP		PERMANOVA (within bays)		
Factor	Group 1	Group 2	Between group dissimilarity	Within group 1 similarity	Within group 2 similarity	Species	Average dissimilarity	R ²	p-value	F-value	p-value	Bays	R ²	p-value
Isolation	n.a.	n.a.	n.a.	n.a.	n.a.		n.a.	0.316	0.001	0.242	0.331	1, 3 - 6	n.a.	n.a.
Macrophyte species	<i>S. pectinata</i>	<i>C. tomentosa</i>	67.01	35.33	29.96	Chironomidea sp.	20.31	0.027	0.575	0.594	0.447	1	0.135	0.253
	n = 15 Bay 1,3,5	n = 15 Bay 1,3,5				<i>B. tentaculata</i>	12.79					3	0.124	0.315
Macrophyte species	<i>S. pectinata</i>	<i>C. demersum</i>	80.75	16.93	29.66	<i>P. antipodarum</i>	11.31					5	0.240	0.007
	n = 10 Bay 4,6	n = 7 Bay 4, 6				Chironomidea sp.	6.54	0.086	0.215	0.631	0.439	4	0.117	0.762
						<i>C. glaucum</i>	5.14					6	0.421	0.005
						<i>P. antipodarum</i>	4.72							

et al., 2010; York et al., 2012). In *F. vesiculosus* belts, increased nutrient levels and the subsequent increase in filamentous algae have been linked to increased abundance of invertebrates (Kraufvelin and Salovius, 2004; Råberg and Kautsky, 2007). Apart from changes in abundance and taxon richness, increased nutrients can also cause an increase in gastropods and bivalves, as well as a decrease in crustacean abundance (Korpinen et al., 2010).

4.4. Response to sediment properties

Both the median sediment grainsize (D50) and the sediment evenness (geometric standard deviation) affected both the epi- and infauna communities. Although grainsize is a poor correlate for the infauna community composition due to variability in animal–sediment relationships (Snelgrove and Butman, 1994), the accumulation of organic matter could increase the food availability for species such as detritivores (Hansen et al., 2008) and may have a negative effect on infauna like filter-feeding bivalves (MacIsaac and Rocha, 1995; Iglesias et al., 1996). This explains the high abundance of chironomids and low abundance of bivalves in the isolated more bays. Fine sediments have increased retention of particulate organic matter, which benefit deposit-feeders like chironomids, although it may also decrease the nutritional value due to increased amounts of inorganic material (Nuttall and Bielby, 1973; Jones et al., 2012). Finally, the macrophyte species composition and their variation in structural complexity could cause reduced flow velocity around the macrophytes, which increases sedimentation rates and reduces the rate of resuspension (Madsen et al., 2001). However, differences in sediment grainsize may also have affected the presence of macrophyte species, since *S. pectinata* prefers silty substrates, whereas *C. demersum* prefers fine muddy substrates (Koch, 2001), similarly to *C. tomentosa* (Selig et al., 2007).

5. Conclusion

A large part (>39%) of the invertebrates occur both in sediments and among vegetation, demonstrating that many of the invertebrates in shallow bays have a broad tolerance to different environments. The epi- and infauna communities in shallow Baltic Sea bays are largely driven

by level of isolation and mainly affected by similar environmental factors. Variation in isolation causes differences in the functional and taxonomic groups of invertebrates, with open bays supporting filter feeders and isolated bays hosting detritivores. The structuring role of dominating macrophyte species is mainly acting at local scales, especially in epifauna communities, whereas the role is more subtle at larger scale as the isolation drives community patterns among bays. To summarize, these complex and diverse systems host a large number of invertebrates that are governed mainly by isolation as well as locally by macrophyte species composition.

Author statement

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Declaration of competing interest

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

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Appendix A. Macrophyte species sampled per bay

Number	Bay name	Chara tomentosa		Stuckenia pectinata		Ceratophyllum demersum	
		Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna
1	Mjärdvik	5	5	5	5		
2	Gloet	5	5				
3	Notgrundsgloet	5	5	5	5		
4	Andholmssund			5	5	5	5
5	Hamnfladan	5	5	5	5		
6	Norrfladan			5	5	5	5

Appendix B. Mean (SE) values of the environmental variables in the studied bays. D50 refers to sediment median grain size and geometric standard deviation (Geom. St. dev)

Bay	Isolation (dimensionless)	Total P (µg/l)	Chlorophyll-a (µg/l)	Turbidity (NTU)	D50 (mm)	Geom st.dev. (mm)
1	1.013	32.8 (1.4)	6.2 (0.5)	1.7 (0.1)	0.18 (0.01)	2.21 (0.07)
2	0.884	30.8 (4.0)	6.9 (1.0)	1.7 (0.3)	0.10 (0.00)	2.01 (0.03)
3	0.782	41.4 (4.5)	6.4 (0.3)	2.9 (0.3)	0.03 (0.01)	3.96 (0.37)
4	0.736	27.0 (4.0)	3.6 (0.5)	0.9 (0.1)	0.08 (0.00)	2.04 (0.03)
5	−1.439	23.5 (2.8)	3.3 (0.5)	1.5 (0.4)	0.32 (0.09)	2.98 (0.14)
6	−1.977	24.3 (2.4)	2.8 (0.4)	1.4 (0.1)	0.13 (0.03)	2.64 (0.17)

Appendix C. Epifauna and Infauna mean abundance per dm³ per bay. Standard deviation in brackets. All species from different macrophyte species within bays are pooled

Bay	1		2		3		4		5		6	
Epifauna/Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna
GASTROPODA												
<i>Alderia modesta</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)	0 (0)
<i>Bithynia tentaculata</i>	0.11 (0.07)	13.49 (4.83)	1.28 (1.02)	74.33 (48.92)	0 (0)	3.03 (1.26)	0.59 (0.41)	1.38 (0.94)	0.69 (0.32)	18.17 (12.02)	0.59 (0.36)	1.38 (0.62)
<i>Ecrobia ventrosa</i>	1.39 (0.66)	11.84 (4.93)	0 (0)	14.87 (7.16)	0.05 (0.05)	6.88 (3.34)	1.65 (0.75)	0.55 (0.55)	0.75 (0.63)	3.3 (2.12)	1.01 (0.36)	10.74 (2.54)
<i>Lymnea auriculata</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.55 (0.55)	0 (0)	0.83 (0.83)	0 (0)	0 (0)
<i>Lymnea stagnalis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.07 (0.95)	0 (0)	0.21 (0.16)	0 (0)
<i>Potamopyrgus antipodarum</i>	7.36 (2.43)	15.69 (3.67)	0.32 (0.32)	0.55 (0.55)	0.16 (0.16)	1.93 (1.09)	1.17 (0.58)	0.55 (0.37)	7.57 (2.81)	14.04 (3.7)	5.39 (1.43)	18.17 (3.63)
<i>Radix auricularia</i>	0 (0)	0 (0)	0.11 (0.11)	0 (0)	0 (0)	0 (0)	0.16 (0.11)	0 (0)	0.16 (0.08)	0 (0)	0 (0)	0 (0)
<i>Radix balthica</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.83 (0.59)	0 (0)	2.75 (1.92)	0 (0)	0.55 (0.55)
<i>Radix peregra</i>	0.37 (0.21)	0.55 (0.37)	0 (0)	0 (0)	0 (0)	0 (0)	5.44 (2.07)	0 (0)	0.48 (0.2)	0 (0)	0.27 (0.12)	0.83 (0.83)
<i>Tenellia adspersa</i>	0.05 (0.05)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.21 (0.12)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Theodoxus fluviatilis</i>	1.23 (0.44)	0.55 (0.37)	0 (0)	2.2 (1.03)	0.16 (0.08)	0.55 (0.55)	0.27 (0.14)	0 (0)	0.59 (0.22)	3.03 (1.12)	1.39 (0.55)	0.28 (0.28)
<i>Valvata cristata</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)
<i>Valvata macrostoma</i>	0 (0)	0 (0)	0 (0)	1.1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Valvata piscinalis</i>	0 (0)	0.55 (0.37)	0.11 (0.11)	2.2 (2.2)	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0.11 (0.07)	0 (0)
<i>Viviparus fasciatus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.55 (0.55)	0 (0)	0 (0)	0 (0)	0 (0)
BIVALVIA												
<i>Cerastoderma glaucum</i>	0 (0)	2.2 (1.35)	0 (0)	0 (0)	0 (0)	0 (0)	1.07 (0.46)	1.1 (1.1)	1.81 (0.55)	3.03 (1.19)	17.49 (4.08)	18.45 (5.21)
<i>Limecola balthica</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.75 (1.23)	3.15 (1.63)	13.77 (1.97)
<i>Mytilus edulis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.16 (0.11)	0.28 (0.28)
CRUSTACEA												
<i>Asellus aquaticus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)	0 (0)
<i>Corophium volutator</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	16.52 (6.59)
<i>Gammarus lacustris</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)	2.56 (0.97)	0 (0)
<i>Gammarus oceanicus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.21 (0.09)	0 (0)
<i>Gammarus pulex</i>	0 (0)	0.83 (0.59)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3.68 (1.32)	0.55 (0.37)
<i>Gammarus tigrinus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.53 (0.43)	1.1 (1.1)
<i>Idotea balthica</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0.28 (0.28)	0.11 (0.07)	0 (0)
<i>Idotea chelipes</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)	5.28 (1.41)	0.55 (0.55)
<i>Leptocheirus pilosus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.91 (0.57)	0 (0)
<i>Monoporeia affinis</i>	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)
<i>Neomysis integer</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)
POLYCHAETA												
<i>Hediste diversicolor</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.2 (0.99)	0 (0)	6.33 (1.54)
<i>Marenzelleria</i> sp.	0 (0)	0.83 (0.83)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
CLITELLATA												
<i>Helobdella stagnalis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.83 (0.59)
<i>Pisicicola geometra</i>	0.16 (0.08)	0.28 (0.28)	0 (0)	0 (0)	0.11 (0.11)	0 (0)	0.11 (0.07)	0 (0)	0.05 (0.05)	0 (0)	0.05 (0.05)	0 (0)

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(continued)

Bay	1		2		3		4		5		6	
Epifauna/Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna
INSECTA												
<i>Caena horaria</i>	0 (0)	0.55 (0.55)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Chironomidea</i> sp.	9.97 (1.61)	27.81 (8.13)	5.23 (0.78)	20.92 (3.95)	15.04 (2.77)	27.25 (7.55)	33.33 (4.26)	11.56 (3.76)	13.49 (4.09)	8.53 (4.21)	2.24 (0.59)	5.23 (1.33)
<i>Chironomus anthracinus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Corixa geoffroyi</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)	0 (0)	0 (0)
<i>Donacia simplex</i>	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Haliphus</i> sp.	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Heptagenia fuscogrisea</i>	0 (0)	0 (0)	0.11 (0.11)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Plectrocnemia conspersa</i>	0 (0)	0 (0)	0.64 (0.31)	0 (0)	0.05 (0.05)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Polycentropus flavomaculatus</i>	0 (0)	0.55 (0.55)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Sialis lutaria</i>	0 (0)	0.55 (0.37)	0 (0)	0 (0)	0.05 (0.05)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Taxon richness	8	15	7	7	9	8	10	9	14	14	21	18

Appendix D. Epifauna and Infauna mean abundance per dm³ per macrophyte species Standard deviation in brackets. All bays are pooled

Macrophyte species	C. Demersum		C. tomentosa		S. Pectinata	
Epifauna/Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna
GASTROPODA						
<i>Alderia modesta</i>	0 (0)	0 (0)	0 (0)	0.14 (0.14)	0 (0)	0 (0)
<i>Bithynia tentaculata</i>	0.27 (0.21)	2.2 (0.9)	0.61 (0.3)	32.07 (13.98)	0.45 (0.21)	3.3 (1.19)
<i>Ecrobia ventrosa</i>	2.4 (0.66)	3.85 (1.7)	0.4 (0.32)	9.64 (2.66)	0.66 (0.29)	7.05 (2.34)
<i>Lymnea auriculata</i>	0 (0)	0 (0)	0 (0)	0.41 (0.41)	0 (0)	0.22 (0.22)
<i>Lymnea stagnalis</i>	0 (0)	0 (0)	0.48 (0.48)	0 (0)	0.13 (0.08)	0 (0)
<i>Potamopyrgus antipodarum</i>	4 (1.38)	6.61 (2.73)	3.84 (1.58)	7.3 (2.18)	4.05 (1.22)	11.78 (2.61)
<i>Radix auricularia</i>	0.16 (0.11)	0 (0)	0.11 (0.05)	0 (0)	0 (0)	0 (0)
<i>Radix balthica</i>	0 (0)	0.83 (0.59)	0 (0)	1.38 (0.99)	0 (0)	0.22 (0.22)
<i>Radix peregra</i>	5.55 (2.04)	0 (0)	0.24 (0.11)	0.28 (0.19)	0.21 (0.09)	0.33 (0.33)
<i>Tenellia adspersa</i>	0.16 (0.11)	0 (0)	0 (0)	0 (0)	0.04 (0.03)	0 (0)
<i>Theodoxus fluviatilis</i>	0.16 (0.11)	0 (0)	0.69 (0.25)	1.38 (0.55)	0.83 (0.25)	1.1 (0.45)
<i>Valvata cristata</i>	0 (0)	0 (0)	0 (0)	0 (0)	0.02 (0.02)	0 (0)
<i>Valvata macrostoma</i>	0 (0)	0 (0)	0 (0)	0.28 (0.28)	0 (0)	0 (0)
<i>Valvata piscinalis</i>	0 (0)	0 (0)	0.03 (0.03)	0.96 (0.57)	0.04 (0.03)	0.11 (0.11)
<i>Viviparus fasciatus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.22 (0.22)
BIVALVIA						
<i>Cerastoderma glaucum</i>	5.92 (1.84)	4.68 (1.54)	0.83 (0.34)	1.38 (0.68)	5.12 (2.34)	6.94 (2.75)
<i>Limecola balthica</i>	3.15 (1.63)	6.33 (2.43)	0 (0)	0 (0)	0 (0)	4.07 (1.36)
<i>Mytilus edulis</i>	0.16 (0.11)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)
CRUSTACEA						
<i>Asellus aquaticus</i>	0 (0)	0 (0)	0 (0)	0.14 (0.14)	0 (0)	0 (0)
<i>Corophium volutator</i>	0.05 (0.05)	0.83 (0.59)	0 (0)	0 (0)	0 (0)	6.28 (3.06)
<i>Gammarus lacustris</i>	2.4 (1)	0 (0)	0.03 (0.03)	0 (0)	0.06 (0.06)	0 (0)
<i>Gammarus oceanicus</i>	0.11 (0.07)	0 (0)	0 (0)	0 (0)	0.04 (0.03)	0 (0)
<i>Gammarus pulex</i>	2.35 (1.15)	0.28 (0.28)	0 (0)	0.14 (0.14)	0.53 (0.43)	0.33 (0.24)
<i>Gammarus tigrinus</i>	0.53 (0.43)	1.1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Idotea balthica</i>	0.05 (0.05)	0 (0)	0 (0)	0.14 (0.14)	0.04 (0.03)	0 (0)
<i>Idotea chelipes</i>	4.48 (1.61)	0 (0)	0 (0)	0 (0)	0.34 (0.19)	0.22 (0.22)
<i>Leptocheirus pilosus</i>	0.91 (0.57)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Monoporeia affinis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.22 (0.15)
<i>Neomysis integer</i>	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	0 (0)
POLYCHAETA						
<i>Hediste diversicolor</i>	0 (0)	2.48 (0.87)	0 (0)	0 (0)	0 (0)	2.42 (0.89)
<i>Marenzelleria</i> sp.	0 (0)	0 (0)	0 (0)	0.14 (0.14)	0 (0)	0.33 (0.33)
CLITELLATA						
<i>Helobdella stagnalis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)
<i>Piscicola geometra</i>	0.05 (0.05)	0 (0)	0.08 (0.04)	0.14 (0.14)	0.11 (0.05)	0 (0)
INSECTA						
<i>Caena horaria</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)
<i>Chironomidea</i> sp.	0.05 (0.05)	0 (0)	0.08 (0.04)	0.14 (0.14)	0.11 (0.05)	0 (0)
<i>Chironomus anthracinus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)

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Macrophyte species	C. Demersum		C.tomentosa		S. Pectinata	
Epifauna/Infauna	Epifauna	Infauna	Epifauna	Infauna	Epifauna	Infauna
<i>Corixa geoffroyi</i>	0.05 (0.05)	0 (0)	0.08 (0.04)	0.14 (0.14)	0.11 (0.05)	0 (0)
<i>Donacia simplex</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)
<i>Haliphus</i> sp.	0.05 (0.05)	0 (0)	0.08 (0.04)	0.14 (0.14)	0.11 (0.05)	0 (0)
<i>Heptagenia fuscogrisea</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)
<i>Plectrocnemia conspersa</i>	0.05 (0.05)	0 (0)	0.08 (0.04)	0.14 (0.14)	0.11 (0.05)	0 (0)
<i>Polycentropus flavomaculatus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.24)
<i>Stalis luteria</i>	0 (0)	0 (0)	0.03 (0.03)	0.14 (0.14)	0 (0)	0.22 (0.15)
Taxon richness	20	14	18	18	18	22

Appendix E. Epifauna and infauna mean abundance and (SE) of most common species per dm³ and per bay 1–6 (species are ranked according to total abundance)

Epifauna							
Bay	Group	1	2	3	4	5	6
<i>Chironomidae</i> sp.	Insecta	9.97 (1.61)	5.23 (0.78)	15.04 (2.77)	13.49 (4.09)	33.33 (4.26)	2.24 (0.59)
<i>Potamopyrgus antipodarum</i>	Gastropoda	7.36 (2.43)	0.32 (0.32)	0.16 (0.16)	7.57 (2.81)	1.17 (0.58)	5.39 (1.43)
<i>Theodoxus fluviatilis</i>	Gastropoda	1.23 (0.44)	0 (0)	0.16 (0.08)	0.59 (0.22)	0.27 (0.14)	1.39 (0.55)
<i>Cerastoderma glaucum</i>	Bivalvia	0 (0)	0 (0)	0 (0)	1.81 (0.55)	1.07 (0.46)	17.49 (4.08)
<i>Ecrobia ventrosa</i>	Gastropoda	1.39 (0.66)	0 (0)	0.05 (0.05)	0.75 (0.63)	1.65 (0.75)	1.01 (0.36)
<i>Radix peregra</i>	Gastropoda	0.37 (0.21)	0 (0)	0 (0)	0.48 (0.20)	5.44 (2.07)	0.27 (0.12)
<i>Bithynia tentaculata</i>	Gastropoda	0.11 (0.07)	1.28 (1.02)	0 (0)	0.69 (0.32)	0.59 (0.41)	0.59 (0.36)
<i>Idotea chelipes</i>	Crustacea	0 (0)	0 (0)	0 (0)	0.05 (0.05)	0 (0)	5.28 (1.41)
Infauna							
Bay	Group	1	2	3	4	5	6
<i>Chironomidae</i> sp.	Insecta	27.81 (8.13)	20.92 (3.95)	27.25 (7.55)	8.53 (4.21)	11.56 (3.76)	5.23 (1.33)
<i>Potamopyrgus antipodarum</i>	Gastropoda	15.69 (3.67)	0.55 (0.55)	1.93 (1.09)	14.04 (3.70)	0.55 (0.37)	18.17 (3.63)
<i>Ecrobia ventrosa</i>	Gastropoda	11.84 (4.93)	14.87 (7.16)	6.88 (3.34)	3.30 (2.12)	0.55 (0.55)	10.74 (2.54)
<i>Bithynia tentaculata</i>	Gastropoda	13.49 (4.83)	74.33 (48.92)	3.03 (1.26)	18.17 (12.02)	1.38 (0.94)	1.38 (0.62)
<i>Cerastoderma glaucum</i>	Bivalvia	2.20 (1.35)	0 (0)	0 (0)	3.03 (1.19)	1.10 (1.10)	18.45 (5.21)
<i>Limicola balthica</i>	Bivalvia	0 (0)	0 (0)	0 (0)	2.75 (1.23)	0 (0)	13.77 (1.97)
<i>Hediste diversicolor</i>	Polychaeta	0 (0)	0 (0)	0 (0)	2.20 (0.99)	0 (0)	6.33 (1.54)
<i>Theodoxus fluviatilis</i>	Gastropoda	0.55 (0.37)	2.20 (1.03)	0.55 (0.55)	3.03 (1.12)	0 (0)	0.28 (0.28)

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