ORIGINAL RESEARCH ARTICLE

Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon

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Abstract   The role of reeds in the functioning of ecosystems and their significance for zoobenthos in the coastal lagoons is poorly understood. We hypothesise that next to the spatial zonal differentiation of abiotic factors in the apparently homogeneous habitat of reeds, benthic macroinvertebrate fauna is also unevenly distributed, and differs in taxonomic and functional diversity, as well as density and biomass across the reed stand. The research was carried out in the Vistula Lagoon (southern Baltic) along three designated sectors arranged parallel to the shoreline and differing in distance from the shore and depth. Mean density of reed stems in the analysed stand was within the range of values reported from different American and European wetlands. Regardless of the location within the reeds and the season, the fauna was dominated by detritivorous Tubificinae and larvae of Chironomidae. The highest diversity, density, and biomass of fauna were found in the middle littoral zone, and the lowest in the outer zone adjacent to the open water. The presented data support our hypothesis predicting the existence of a spatial variation pattern in the composition and distribution of macroinvertebrates in response to the changing zonal habitat conditions within the reed stand.
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1. Introduction

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Common reed, *Phragmites australis* (Cav.) Trin. ex Steud, is believed to be one of the most widespread riparian plants in a wide range of wetland habitats worldwide. Although the common reed is considered a freshwater species (Ostendorp, 1993), it is well adapted to brackish water conditions (Karstens et al., 2019; Lissner and Schierup, 1997). The plant is considered native to Europe. Beyond the continent, it is often treated as an invasive species (Swearingen and Saltonstall, 2012). There-

fore, depending on where the reed occurs, its environmental significance and role in wetland vegetation communities may be perceived differently (Gabriel and Bodensteiner, 2011). European literature emphasises the multiple ecosystem functions and services of reeds (Karstens et al., 2019; Mancinelli et al., 2005; Okun and Mehner, 2005; Pawlikowski and Kornijów, 2019). They constitute feeding and breeding places, shape habitat conditions, and determine sediment and water quality for animals and other plants. They also play a role in matter circulation, damp wave energy, and stabilise bottom sediments and banks. In countries where the reed has emerged as an invasive species, particularly in disturbed habitats, its rapid rate of colonisation and tendency to replace other plant and animal species is often considered a nuisance, negatively affecting local biodiversity (Gabriel and Bodensteiner, 2011; Warren et al., 2001). In both cases, however, although for a different reason, it is important to know the role of reeds in the functioning of ecosystems and their significance as a habitat for other organisms. As pointed out by Ostendorp (1993), the latter issue is barely investigated. This is especially true of benthic macroinvertebrates living in sediments overgrown by reeds. One of the reasons could be methodological difficulties in sampling bottom sediments among the tangle of roots and rhizomes (Moss, 1998). The most frequently used methods of sampling include sweeping by hand nets, or collecting a littoral section together with sediments and macrophytes by means of e.g. Surber, Wisconsin, Macan, or Ekman box-samplers (Arnold and Ormerod, 1997; Fell et al., 1998; James et al., 1998; Jayawardana et al., 2006; Jayawardana and Westbrooke, 2010; Miler et al., 2018; Olson et al., 1995; Sychra et al., 2010). Various types of traps are also sometimes used (Fell et al., 1998; Oertli, 1995; Raichel et al., 2003). While such studies provide valuable insight into the general diversity of macroinvertebrates within a stand, they do not reflect the real distribution and quantitative proportions between various invertebrate communities with their distinctive feeding behaviour and diet, such as sediment-living, plant-associated, and free-swimming animals (Moss, 1998). Consequently, such data offer little information on the relationships and drivers that potentially structure truly benthic communities, i.e. those inhabiting bottom sediments. Moreover, the use of different sampling approaches makes it difficult to compare results and draw general conclusions.

Only several papers employ quantitative methods that take into account selective sampling of sediments and, importantly, sampling to a known depth (Cardinale et al., 1998; Kornijów and Gulati, 1992; Okun and Mehner, 2005; Yozzo and Osgood, 2013). These publications focus on benthic invertebrates in reed beds of lakes or rivers. Coastal wetlands have not yet been subject to similar research. The purpose of this work is to fill this gap, and to find a pattern in the distribution of benthic macroinvertebrates within the reed stand.

The structure and processes in lagoon environments are primarily maintained by physical forces, including wave action that can be mediated by dense patches of emergent macrophytes such as reeds (Karstens et al., 2019; Kornijów, 2018; Pawlikowski and Kornijów, 2019; Perez-Ruzafa et al., 2011; Viaroli et al., 1996). This can lead to

a spatial gradient of organic matter content in the sediments, and through the consumption of oxygen in decaying processes, also of water oxygenation. The research on abiotic factors in the reeds of the Vistula Lagoon in fact showed low oxygenation of water in the near-shore zone compared to the middle and peripheral part of the patch, adjacent to the open water zone. On the one hand, that was most likely due to the horizontal distribution of sediment organic matter, and on the other hand due to a different rate of water exchange with the pelagic zone (Pawlikowski and Kornijów, 2019). Similar horizontal zonation of oxygen conditions, and other physical and chemical properties of water or sediment, such as pH or salinity within stands of emergent vegetation, were found in various aquatic ecosystems. This suggests the universal character of the phenomenon (Dvorak, 1970; Howard-Williams and Lenton, 1975; Kłosowski, 1992; Suzuki et al., 1995). However, there are exceptions, e.g. water throughout the stand of emergent vegetation in Lake Huron was typically supersaturated with dissolved oxygen, and there was never any evidence of anoxia (Cardinale et al., 1997).

It can be assumed that due to the spatial zonal differentiation of abiotic factors in the apparently homogeneous habitat of reeds, also benthic macroinvertebrate fauna is not evenly distributed, and differs across the reed stand in terms of taxonomy and functional diversity, as well as density and biomass. In order to verify this hypothesis, we carried out seasonal research in the Vistula Lagoon — one of the most important and well-known ecosystems in the southern Baltic coast with extensive reed beds (Karstens et al., 2019).

2. Material and methods

2.1. Study site

The Vistula Lagoon is a brackish coastal lagoon adjacent to the Gulf of Gdansk of the Baltic Sea. The lagoon has a surface area of 838 km^2, including 328 km^2 on the Polish side of the border. The Vistula Lagoon is shallow, with a depth not exceeding 5.2 m in the Russian, and 4 m in the Polish part. The hydrological dynamics of the waters of the lagoon are determined by the inflow of freshwater masses from its extensive catchment area, mixed with salty water inflowing from the Gulf of Gdańsk through the Baltiysk Strait. Salinity varies from 0 to 6.5 PSU. No tides occur, although wind action causes daily water level fluctuations reaching 1 m. The concentrations of total nitrogen and phosphorus in water are high, reaching 1.1—4.4 mg dm^{-3} and 0.06—0.19 mg dm^{-3}, respectively. The most frequently recorded water transparency, measured as Secchi disc depth, fluctuates around 40 cm (Kornijów, 2018). Bottom sediments are primarily composed of silt and sand (Zachowicz, 1985). The lagoon is very productive, with advanced eutrophic processes (Kownacka et al., 2020). It is influenced by both maritime and continental climates, with ice cover persisting for several days in mild winters, and from December until March in the coldest years (Herman, 2018).

The research was conducted in a reed patch with a length of 200 m and width of approximately 60 m (54.33360°N, 19.54700°E), located approximately 2 km north-east of the
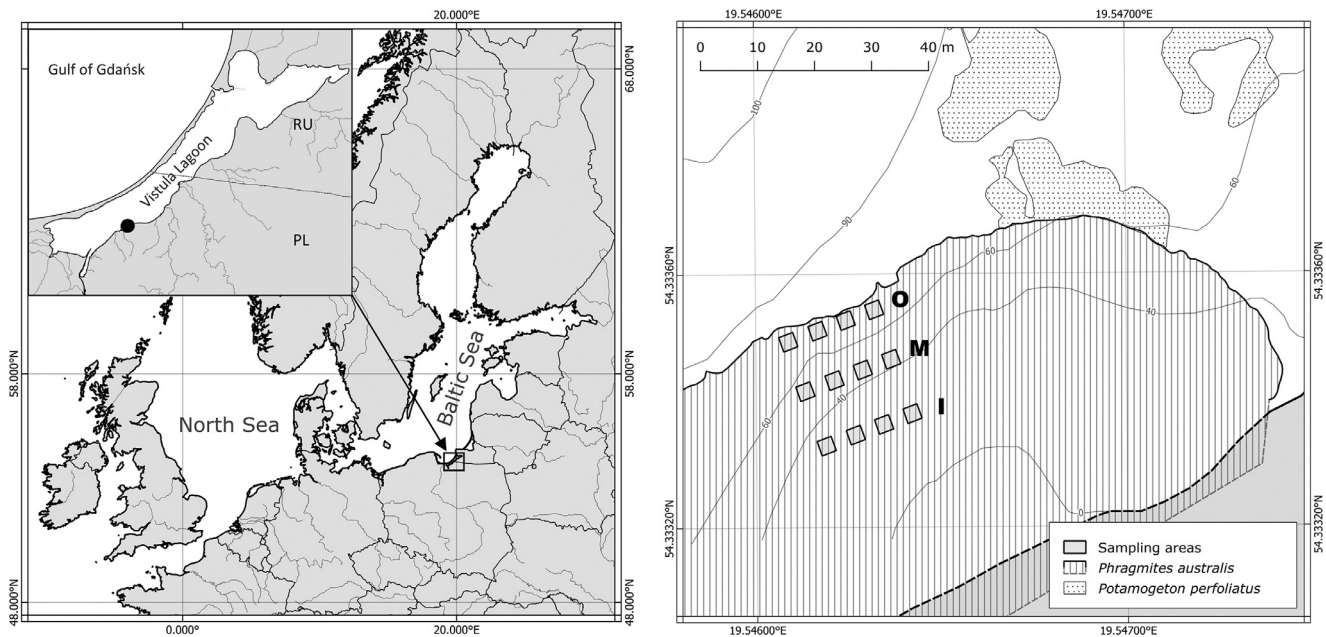
Figure 1 Location of the study area on the map of Northern Europe (left side, marked with a dot). On the right side — detailed map of the analysed reed stand in the Vistula Lagoon. Note that the coastline was drawn conventionally — its range varied as the water level changed. Depths are expressed in centimetres. I — inner zone, M — middle zone, O — outer zone. GIS layers sources for the map of Northern Europe: Europe coastline and rivers: Natural Earth (2020); Country borderlines: NOAA GSHHG (2014); Polish coastline: SIPAM (2020) simplified; Rivers of Vistula Lagoon catchment: OpenStreetMap (2021) modified; Coastline of the Russian part of the Vistula Lagoon: digitized scanned map from Domnin and Chubarenko (2008).

municipality of Tolkmicko at the southern shore of the lagoon (Figure 1). No local changes resulting from human activity such as shoreline alteration were recorded which could potentially interfere with the obtained results (Brauns et al., 2007; Miler et al., 2013). Growth of the macrophytes was seasonal, with regeneration from rhizomes after winter ice-scour. Seasonal changes in reed density involved a gradual increase in the number of stems during the vegetative season, lasting from April until October. The highest and spatially relatively even values of reed density (132—158 stems m^{-2}) in the analysed patch were observed in late summer (Pawlikowski and Kornijów, 2019).

Measurements of physico-chemical properties conducted in 2011 revealed no trends in salinity across the stand (Pawlikowski and Kornijów, 2019). Water oxygenation at the time was generally lower in the near-shore area than in the periphery adjacent to open water. The opposite pattern was observed for water temperature. Water level fluctuations were characterized by high dynamics, with an amplitude of approximately 40 cm (Pawlikowski and Kornijów, 2019).

2.2. Field survey and laboratory analyses

The study was conducted in spring (April), summer (August), and autumn (October) 2011. The width of the analysed reed stand exceeded 60 m, but the sampling area covered a much smaller strip (approx. 30 m wide) due to the shallow depth in the near-shore area and strong water fluctuations. Samples from the reed stand were collected along three designated sectors arranged parallel to the shoreline, at a distance of around 10 m from one another, differing in depth and distance from the shore, depending on geographic dis-

tribution and changing water level: inner (depth 0—40 cm, distance from the shore of approximately 30—40 m), middle (depth 40—60 cm, distance from the shore of 40—50 m), and outer (depth 60—90 cm, distance from the shore of 50—60 m) (Figure 1).

Four sampling locations, each of approximately 9 m^2 and spaced 3 m from one another, were established in each sector, referred to as zones. In each sampling location, 3 pooled sediment cores were collected by means of a transparent acrylic tube (length 1.5 m; diameter 4.4 cm) closed from the top with a stopper. In our opinion, the sampler used is appropriate not only for the sampling of sedentary invertebrates, but also for mobile gammarids, and even free-living mysids in turbid lagoon water (Linkowski et al., 2021). The tube was pushed into the bottom to a depth of 25 cm. No fauna occurred deeper in the sediment, as suggested by studies on the vertical distribution of macroinvertebrates in sediments (Pawlikowski and Kornijów, 2022). A total of 36 samples consisting of 108 sediment cores were collected on all sampling occasions. Each sample was washed separately through a net with 0.3 mm mesh size, and transported to the laboratory in plastic containers with no water. We chose such fine mesh to provide accurate community and population estimates given the relatively small size of macro-invertebrates living in estuarine and lagoon ecosystems (Schlacher and Wooldridge, 1996). Invertebrates were sorted live by hand on a white tray filled with water, and preserved with 4% formaldehyde solution. Oligochaeta were treated with Amman's lactophenol solution, and Chironomidae larvae with Faure liquid, and identified to the lowest possible taxon according to Timm (1999) and Andersen et al. (2013), respectively. The nomenclature of Naididae was adopted after

WoRMS (2021). Macrobenthic taxa were assigned to trophic groups based on food preferences documented in the literature (Armitage et al., 1995; Pellan et al. 2016; Savage, 1982; Vaughn, 1982). Categorisation of macroinvertebrates into groups allows a better understanding of the processes of the material cycle and ecosystem function (Cummins, 1973).

Measurements of reed density were carried out in 10 random 0.5×0.5 m quadrats within each location, expressed as the number of shoots per square meter and averaged (Pawlikowski and Kornijów, 2019).

Granulometric analyses involved the collection of additional sediment cores with a length of 25 cm in each sampling location in August. The collected sediments were dried and manually ground in a mortar, and then sieved on a set of geological sieves with a mesh of 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm. The obtained data were processed with the application of GRADISTAT software version 8 (Blott and Pye, 2001). Organic matter content in sediment was determined by the direct method as a mass loss on ignition (LOI) at a temperature of 500°C for 24 hours.

Bathymetric measurements were performed by means of a ranging rod with an accuracy of 1 cm on 2014.09.04. Depth was measured in 154 points with geographic coordinates determined by means of a GPS receiver (Garmin GPSMAP 60CSx). The memory of the receiver also recorded the course of the shoreline (zero depth). The data matrix was loaded to Surfer 10 software in which a detailed bathymetric map of the studied water body was generated by means of the kriging method. The map was then visually processed by means of QGIS software (Figure 1).

Due to unequal variances or non-normal distribution, the following non-parametric statistics were applied:

— Kruskal-Wallis test (H) was applied for the determination of the effect of different locations within the reed patch on the density and biomass of fauna.
— Friedman test (Chi-Square) was applied for the determination of differences in the density and biomass of fauna between sampling occasions.

T-test was applied for the determination of differences in the density of fauna between 2011 and 2013. For this comparison, we used data from 2013 in zone M on the vertical distribution of macroinvertebrates in sediments (Pawlikowski and Kornijów, 2022), obtained in a similar way as in 2011. Statistical calculations were performed by means of Statistica 10 software (StatSoft, 2011).

3. Results

3.1. Zoobenthos

The material showed the presence of 31 taxa belonging to Chironomidae, Naididae, Hirudinea, Chrysomelidae, Amphipoda, Bivalvia, and Nematoda (Table 1). The highest diversity (24 taxa) was determined in the middle littoral zone, and lowest in the outer zone (16 taxa), adjacent to open water. Depending on the season, the diversity of fauna considerably changed in the middle and outer zones and was relatively stable in the inner zone (Figure 2).
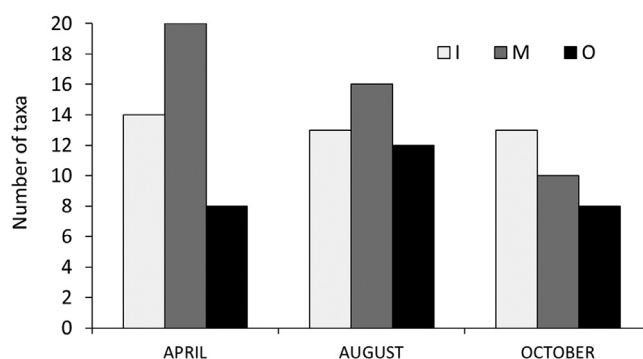

Figure 2 Number of zoobenthos taxa in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon.

The highest total density of fauna was reached in spring and summer in the middle zone (12 057−15 510 ind. m^{-2}), and lowest, irrespective of the season in the outer zone (4 165−4 658 ind. m^{-2}) (Kruskal-Wallis test H (n = 12) = 6.06 and 7.38; p = 0.04 and 0.02, respectively) (Figure 3). Differences in total density between the zones in autumn were at the threshold of significance (Kruskal-Wallis test H (n = 12) = 5.80; p = 0.06).

Biomass values in spring and autumn were the highest in the middle littoral zone (42−107 g ww m^{-2}), and lowest in the outer zone (8−10 g ww m^{-2}) (Kruskal-Wallis test H (n = 12) = 7.73 and 6.73; p = 0.02 and 0.03, respectively). In summer, differences in biomass between the zones were at the threshold of significance (Kruskal-Wallis test H (n = 12) = 5.54; p = 0.06) (Figure 3).

In terms of percent share, irrespective of the location within the reed stand (with the exception of the middle and outer zone in April), Tubificinae usually dominated (46−79%), and among them particularly *Limnodrilus hoffmeisteri* (Figure 4, Table 1). The second group with the most considerable share were Chironomidae (15−76%) larvae with dominant *Glyptotendipes* sp. (Figure 4, Table 1). The proportions of percent shares between the most abundant taxa varied in particular seasons with no discernible patterns.

Next to Chironomidae and Tubificinae (2−51% and 10−73%, respectively), the biomass contained a high share of Chrysomelidae (*Donacia* sp.) (up to 60%) and Amphipoda (1−42%) (Figure 4). Their contribution varied depending on the study term: in April, the majority of sites were dominated by larvae of *Donacia* sp. (up to 60%) and Chironomidae (22−51%), in August Tubificinae (48−73%) and *Donacia* sp. (23−30%), and in October Amphipoda (up to 42%) and Tubificinae (37−56%).

A large majority of the recorded taxa belonged to detritivores, constituting more than 58% of the fauna abundance (Table 1, Figure 5). The second major trophic group were omnivores constituting up to 34% of the fauna abundance. The percent share of particular trophic groups varied depending on the season and zone. A considerable share of herbivores was observed in spring in the middle zone, and a clear increase in omnivores in summer and autumn in the middle and outer zones.

For the purpose of verification of the stability of benthic communities in the reed belt, their abundances were compared in zone M in 2011 and 2013 (Figure 6). In the second year of the study, the density of zoobenthos was more than

Table 1 Density [ind. m^{-2}] of zoobenthos in the inner (I), middle (M), and outer (O) zones of the reed stand in the Vistula Lagoon in 2011. DETR — detritivores, CARN — carnivores, HERB — herbivores, OMNI — omnivores, n. d. — not determined. Mean values ± SE (Standard Error).

	Taxa	Trophic group	I	M	O
NAIDIDAE					
TUBIFICINAE					
	n. det. without hair chaetae (juvenile or damaged), probably *Limnodrilus* sp.	DETR	3 416 ± 591	5 974 ± 1 463	1 206 ± 346
	n. det. with hair chaetae (juvenile or damaged), probably: *Tubifex* sp., *Potamothrix* sp., *Psammoryctides* sp.	DETR	786 ± 397	877 ± 124	55 ± 39
	Tubifex tubifex (Müller)	DETR	219 ± 127	110 ± 63	0 ± 0
	Limnodrilus hoffmeisteri Clapar.	DETR	1 151 ± 443	347 ± 103	420 ± 116
	Limnodrilus claparedeianus Ratz.	DETR	365 ± 199	512 ± 228	18 ± 18
	Limnodrilus profundicola (Verill)	DETR	110 ± 50	128 ± 63	55 ± 39
	Limnodrilus udekemianus Claparède	DETR	37 ± 25	91 ± 74	0 ± 0
	Potamothrix hammoniensis (Mich.)	DETR	0 ± 0	37 ± 37	0 ± 0
	Potamothrix moldaviensis Vejd.	DETR	0 ± 0	55 ± 55	18 ± 18
	Potamothrix heuscheri (Bretscher)	DETR	18 ± 18	146 ± 87	0 ± 0
	Enchytraeidae n. det.	DETR	0 ± 0	37 ± 37	0 ± 0
NAIDINAE					
	Naidinae n. det.	HERB	0 ± 0	18 ± 18	0 ± 0
TOTAL Naididae			**6 102 ± 1 369**	**8 330 ± 1 652**	**1 772 ± 467**
CHIRONOMIDAE					
	Chironomus sp.	DETR	475 ± 117	183 ± 59	18 ± 18
	Glyptotendipes sp.	DETR	694 ± 134	2 503 ± 454	475 ± 299
	Dicrotendipes sp.	DETR	110 ± 43	91 ± 50	274 ± 90
	Polypedilum scalaneum (Schr.)	DETR	37 ± 25	37 ± 25	0 ± 0
	Cladotanytarsus mancus (Walker)	DETR	18 ± 18	347 ± 128	457 ± 305
	Microchironomus tener (Kieff.)	DETR	0 ± 0	0 ± 0	37 ± 25
	Endochironomus albipennis (Mg.)	DETR	0 ± 0	18 ± 18	0 ± 0
	Parachironomus varus (Goetgh.)	CARN	0 ± 0	0 ± 0	37 ± 37
	Cryptochironomus sp.	CARN	55 ± 29	292 ± 102	201 ± 69
	Procladius sp.	CARN	37 ± 25	73 ± 31	18 ± 18
	Orthocladiinae n. det.	HERB	0 ± 0	0 ± 0	18 ± 18

Table 1 (*continued*)

|	Taxa	Trophic group	I	M	O
TOTAL Chironomidae			**1 425 ± 234**	**3 544 ± 536**	**1 535 ± 567**
CRUSTACEA, MALACOSTRACA					
	Gammaridae n. det. (probably: *G. tigrinus* and *G. duebeni*)	OMNI	201 ± 87	1 754 ± 370	1 005 ± 341
	Asellus sp.	DETR	0 ± 0	37 ± 25	0 ± 0
INSECTA, CHRYSOMELIDAE					
	Donacia sp.	HERB	183 ± 53	457 ± 227	37 ± 25
HIRUDINEA					
	Hirudinea n. det.	CARN	37 ± 37	0 ± 0	0 ± 0
BIVALVIA					
	Dreissena polymorpha (Pallas)	DETR	18 ± 18	37 ± 37	55 ± 39
OTHERS					
	Diptera larvae n. det.	n. d.	91 ± 57	55 ± 39	0 ± 0
	Nematoda n. det.	DETR	18 ± 18	37 ± 25	0 ± 0
TOTAL DENSITY			**8 075 ± 1 449**	**14 249 ± 1 449**	**4 403 ± 811**
NUMBER OF TAXA			**19**	**24**	**16**
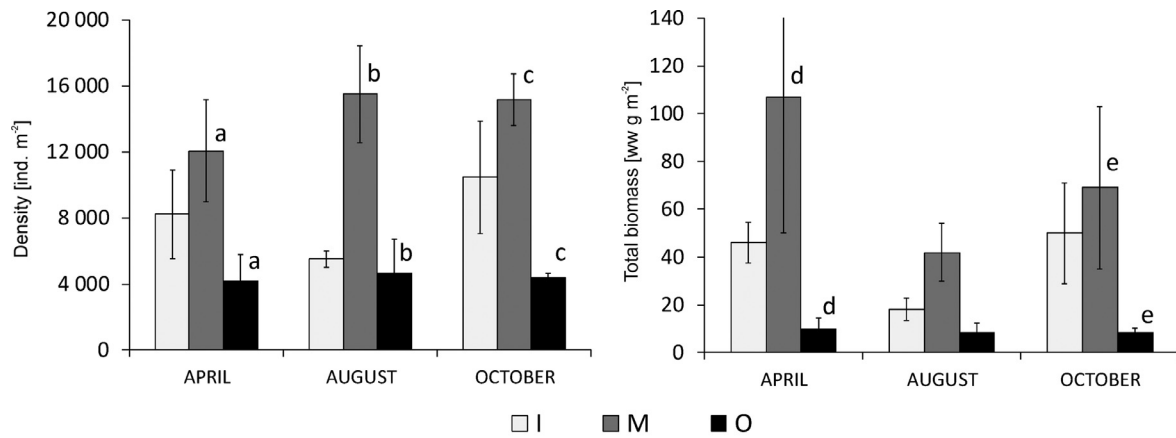
Figure 3 Density [ind. m^{-2}] and total biomass [ww g m^{-2}] of zoobenthos in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon. Small letters denote significant difference (Post-hoc Kruskal-Wallis test, p < 0.05) between areas marked with the same letter. No letter aside bar means no significant difference in density or biomass. Whiskers denote Standard Error.
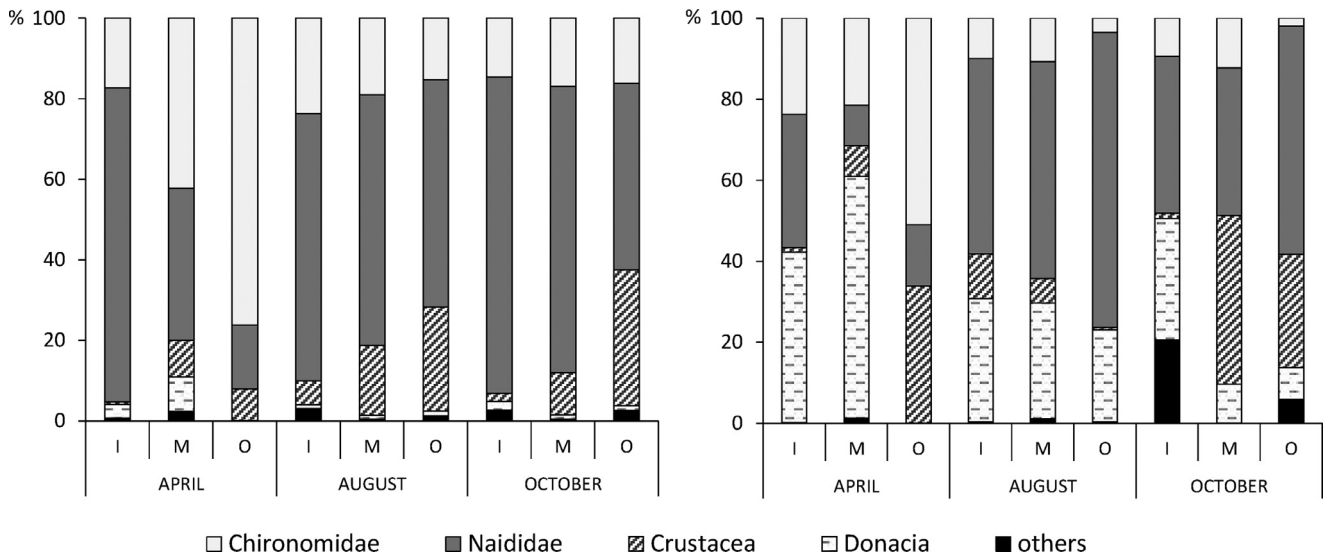

Figure 4 Percent share of the main groups of taxa in total density (left) and total biomass (right) of zoobenthos in the inner (I), middle (M), and outer zone (O) of the reed stand in the Vistula Lagoon.

twice higher (test t = −3.12; p = 0.004). The quantitative proportions between groups did not change, with evident dominance of Tubificinae and Chironomidae in both years.

3.2. Sediments

Reed grew on sandy-muddy sediments (textural group: slightly gravelly muddy sand) (Table 2). In the inner zone, fine muddy fractions were considerably more abundant (17.4%) than in the middle and outer zones located further from the shore (11.3% and 11.7%, respectively). A similar pattern was recorded in reference to the content of organic matter in the sediment (Table 2).

4. Discussion

The diversity of macroinvertebrates found in the lagoon's reed stand was much higher (31 taxa) than that in the

Table 2 Characteristics of sediments in the inner (I), middle (M), and outer (O) zones of the reed stand in the Vistula Lagoon. LOI — organic matter determined as loss on ignition.

	I	M	O
gravel	0.1%	0.3%	0.5%
sand	82.5%	88.4%	87.7%
mud	17.4%	11.3%	11.7%
LOI	3.1%	1.3%	1.1%

open water central part of the lagoon, where only 6 taxa were reported (Kornijów et al., 2021b). It was, however, still much lower than in the littoral of freshwater ecosystems, where many other groups not found in the Vistula Lagoon inhabit the sediments, e.g. Odonata, Ephemeroptera, Trichoptera, Ceratopogonidae, and Gastropoda (Arnold and
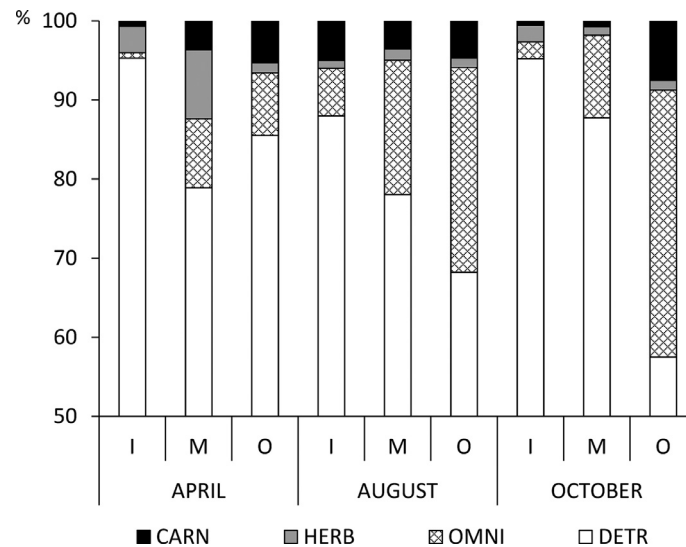
Figure 5 Percent share of particular trophic groups in the total abundance of zoobenthos in the inner (I), middle (M), and outer zone (O). DETR — detritivores, CARN — carnivores, HERB — herbivores, OMNI — omnivores. Note: Y-axis truncated to 50—100% range for clarity.
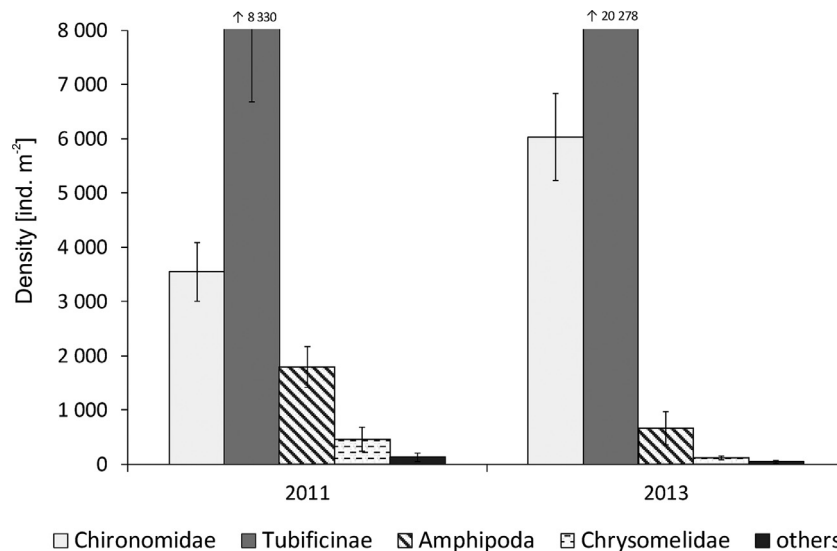

Figure 6 Density [ind. m^{-2}] of the most abundant groups of zoobenthos in the middle zone in 2011 and 2013. The values are means for three sampling occasions. Whiskers denote Standard Error.

Ormerod, 1997; Cardinale et al., 1998; James et al., 1998; Kornijów et al., 2010; Kornijów and Gulati, 1992; Sychra et al., 2010; Yozzo and Osgood, 2013). The reason for this might be elevated salinity which adversely affects some freshwater invertebrates (Arnold and Ormerod, 1997; Brucet et al., 2012; Kornijów et al., 2021a).

In both habitats of the lagoon, namely the littoral and open waters, Tubificinae and chironomid larvae showed the highest abundance. In the reed stand, Tubificinae were dominated by *L. hoffmeisteri*, like in the central part of the lagoon. *Potamothrix hammoniensis*, very abundant in the central part, barely marked its presence in the littoral. Among Chironomidae, the larvae of *Glyptotendipes* sp. were the most abundant in the littoral. As typical dwellers of sediments overgrown with vegetation (Kornijów and Gu-

lati, 1992; Pinder, 1995), they were not present in the central lagoon, where chironomid larvae were instead dominated by *Chironomus balatonicus* Devai, Wuelker & Scholl (Kornijów et al., 2021b). Mean total density was comparable (2 806—16 269 ind. m^{-2} in the central part vs. 4 165—15 510 ind. m^{-2} in the reed stand). Functional feeding groups were dominated by detritus eaters in both habitats.

In the inner littoral zone, the highest densities were reached by a tubificid *L. hoffmeisteri* and *Chironomus* sp. larvae, known for tolerating oxygen deficits and coexisting under such conditions (Kornijów et al., 2021b). A significant percentage of omnivores (mainly *Gammarus* sp.) and herbivores also occurred. The latter were represented almost exclusively by larvae of the root-piercing beetle *Donacia* sp.

The mean density of reed stems in the analysed stand (132—158 stems m^{-2}) was within the mean range of values (60—250 stems m^{-2}) reported from different wetland European habitats (Haslam, 1973), and corresponded with the top determined values, e.g. in freshwater and brackish ecosystems of the North America (Meyerson et al., 2000). Although the reed zones designated in the Vistula Lagoon were separated by a short distance of approx. 10 m, they differed remarkably in terms of habitat conditions. It particularly concerned afternoon water oxygenation the values of which were proportional to the distance from the shoreline and ranged from 59% (5.4 mg dm^{-3}) to 109% (9.5 mg dm^{-3}) (Pawlikowski and Kornijów, 2019).

The relationship between the oxygen conditions and the diversity and density of bottom fauna, regardless of the type of aquatic environment, is a generally known pattern (Berezina and Golubkov, 2008; Jacobsen, 2020; Maasri et al., 2019; Verberk et al., 2011). It was also evident in our research. The highest diversity, density, and biomass were found in the middle zone, where oxygenation was clearly higher than in the inner near-shore zone. The exception was autumn, when the highest diversity was found in the inner zone. It can be assumed that at low water temperature and at plant density too low to impede water circulation, the oxygenation conditions could be aligned across the reed stand, and oxygenation might be no longer the structuring factor for the occurrence of some, at least less oxygen-demanding taxa (Warfe and Barmuta, 2004). A proportion of Amphipoda, known to be sensitive to hypoxia (Meijering, 1991), in the inner zone remained negligible in autumn. The larvae of *Donacia* sp. which rely on the plant for oxygen (Houlihan, 1969) showed the highest biomass in the inner and middle zones, regardless of the season.

Oxygen shortage can be partially compensated by the release of oxygen by macrophyte roots (Reddy et al., 1990; Sand-Jensen et al., 1982) that may support the development of some benthic macroinvertebrates (Sagova-Mareckova and Kvet, 2002). The process, however, was probably insufficient in the stand studied, particularly in summer under the conditions of increased temperature and drying out of the bottom.

A characteristic feature of the littoral of freshwater ecosystems with periodic hypoxia is the occurrence of a high number of invertebrates that respire atmospheric oxygen, such as pulmonate snails or beetles (Dvorak, 1970). They were, however, not present in the brackish waters of the Vistula Lagoon.

Temporary oxygen shortage in shallow coastal Baltic waters seems to be a common phenomenon not only in the reed stand. It can also be the result of the decomposition of drifting algal mats, leading to a strong depletion of benthic macrofauna (Berezina and Golubkov, 2008; Conley et al., 2011).

In the reed stand, a much higher content of organic matter in the sediments of the inner zone was not accompanied by the highest densities of all detritivores, with the exception of *L. hoffmeisteri* and *Chironomus* sp. The probable reason was the astatic nature of this habitat, associated with periodic drying, and the aforementioned strong fluctuations in oxygenation with periodic hypoxia, favoured by the elevated content of sediment organic matter, and limited water exchange with the open water (Cardinale et al., 1997; Dvorak, 1970; Pawlikowski and Kornijów, 2019).

According to Żbikowski et al. (2021), the occurrence and rate of growth of *L. hoffmeisteri* may be determined by the content of the sand fraction with a diameter of 60—160 μm in mud. Swallowed by worms, it may accelerate digestion and nutrient assimilation. Due to the different classification of sand grain size adopted in this paper, however, we could not verify this theory.

The relatively lowest total density and biomass, as well as the diversity of macroinvertebrates in the outer zone adjacent to the well-oxygenated open water, could have resulted from predation pressure by fish migrating here by day from the free water area in search for refugia from predators (Macneil et al., 1999; Okun et al., 2005). An additional factor might be the instability of the habitat conditions due to the strong and frequent wave action that could not damp by the vegetation sufficiently (Kairesalo, 1983). Interestingly, we found no pattern in terms of distribution of invertebrate predators, as previously pointed out by e.g. Dvorak (1970).

In conclusion, with some minor exceptions, the presented data support our hypothesis predicting the existence of a spatial variation pattern in the composition and distribution of macroinvertebrates in response to the changing zonal habitat conditions within the reed stand.

Our main research program lasted for one year. Therefore, in order to verify the long-term stability of the fauna composition, we repeated the research two years later in the middle zone (Pawlikowski and Kornijów, 2022). We recorded a more than double increase in density, but the proportions between the main faunal components did not change much. This suggests that while the density may fluctuate from year to year, the specificity of the assemblage composition remains relatively constant. Our results are generally in agreement with Cardinale et al. (1998), who claimed that distance from open water may be of primary importance for the spatial distributions of macroinvertebrates throughout coastal emergent vegetation.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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