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# Utilization of riverine organic matter by macrobenthic communities in a temperate prodelta

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Macrobenthos is an important component of organic carbon storage and energy flow in marine systems, including these impacted by riverine discharge and high share of allochthonous organic matter (OM). Changing environmental conditions, such as lower precipitation and snow cover duration, may affect patterns of riverine input, therefore it is crucial to know how benthic communities utilize different OM sources in areas affected by rivers. Using Bayesian stable isotope mixing models, we assessed the diet composition of common macroinvertebrates forming benthic communities in the transition zone of one of the largest river outlets in the Baltic Sea region, the Vistula River prodelta. Furthermore, we analyzed the spatial and temporal variability in the biomass-weighted resource utilization by those communities. Contribution of riverine OM to the particulate OM in Vistula prodelta decreased with increasing depth. Despite similar distances to the river mouth, the relative contribution of riverine OM to the diet of all studied taxa also decreased with increasing depth, which corresponded to organic matter composition in prodelta waters. Nevertheless, due to synchronous structural changes in benthic communities, and changes in the feeding modes of dominant species, particularly *Macoma balthica* and *Hediste diversicolor*, the riverine organic carbon share in the biomass of benthic communities often remained the highest in the deepest prodelta parts. Our study corroborates that benthic primary consumers act as a gateway for riverine organic matter into the marine food web and illustrates that sediment properties and resource partitioning affects spatial structure of benthic communities and their abilities to utilize allochthonous OM.

## KEYWORDS

food webs,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , primary consumers, stable isotope mixing models, biomass-weighted resource utilization, Baltic Sea, Vistula River

# 1 Introduction

Organic matter (OM) transported to the sea by rivers constitutes a sizable energy source for coastal and estuarine food webs (Hoffman et al., 2008; Dunton et al., 2012). Together with nutrients, it promotes high primary and secondary production in river-ocean transition zones (Valiela and Bartholomew, 2015), making them one of the most productive areas of the world (Polis et al., 1997).

Benthic primary consumers are responsible for a large part of OM utilization, sustaining the carbon cycle and energy flow through the ecosystem (Middelburg, 2018; Snelgrove et al., 2018). Macro-benthic organisms not only sequester carbon in their tissues but also become prey for higher trophic levels, such as benthivorous fish (Darnaude et al., 2004; Nurkse et al., 2016; Silberberger et al., 2018). By transporting and irrigating sediments, benthic fauna takes part in nutrient retention and turnover (Snelgrove et al., 2018), and acts as a coastal filter for excessive loadings transported from land (Thoms et al., 2018). Therefore, vital and productive benthic communities are essential not only for effective carbon pathways but also for maintaining ecosystem health and function. This is especially important in river-impacted areas that are characterized by high sedimentation rates and hence intensive OM burial (Dunne et al., 2007; Damrat et al., 2013).

Riverine discharge may affect benthic communities and their food-web structure through many different factors, e.g., by the amount of OM load and its nutritive quality (Deegan and Garritt, 1997; Antonio et al., 2010). Earlier studies on estuarine food webs suggested that low-quality terrestrial OM (like leaves, wood and soil) is usually not a preferred food source for benthic consumers which rely mostly on autochthonous primary production (Deegan and Garritt, 1997; Peterson, 1999). However, some recent investigations revealed that terrestrial OM may state a substantial part of the benthos diet, especially in food-limited areas (Dunton et al., 2012; Kędra et al., 2012). Moreover, consumption of allochthonous OM by benthos may exceed its consumption by pelagic organisms like zooplankton and planktivorous fish (Hoffman et al., 2008; Bartels et al., 2018) and therefore reinforce the bottom-up transport of riverine OM through the marine food webs (Dias et al., 2016; Peller et al., 2020).

The incorporation of allochthonous riverine OM to benthic food webs depends also on the distance from the freshwater resource (Careddu et al., 2015), as well as pathways of sedimentation, which may vary with depth depending on local currents (Darnaude et al., 2004; Antonio et al., 2010; Bartels et al., 2018). Consequently, allochthonous OM consumption may be greatest close to river mouths in case of shallow estuaries overwhelmed by fluvial sedimentation (Chanton and Lewis, 2002; Vinagre et al., 2019). It can also increase with depth when allochthonous OM is transported to deeper, depositional

zones (Bartels et al., 2018) which is characteristic of deltaic areas (Darnaude et al., 2004).

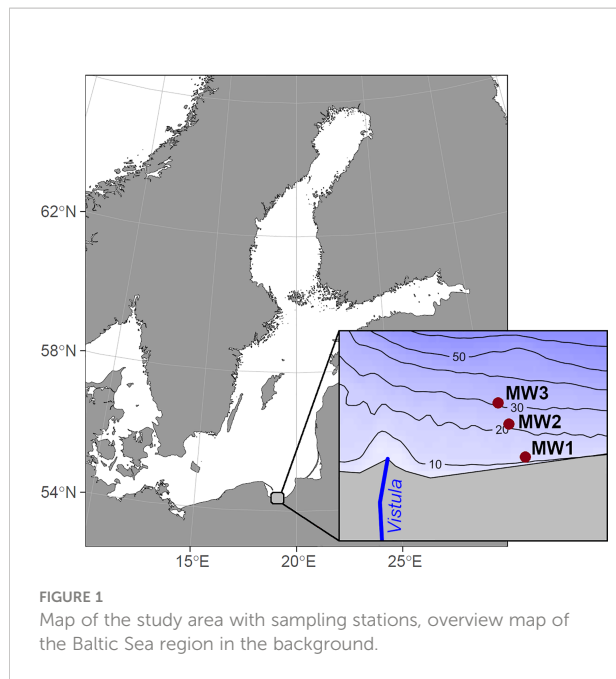
Studies on benthic food webs mostly concentrate on the proportions of different food sources to benthic consumers, putting aside the influence of different food quantities and compositions on the community structure (Arbi et al., 2018). Little is known about the influence of riverine OM supply on standing stocks and feeding habits of different benthic fauna species, which significantly reduces the possibility to predict the influence of hydrological changes (including riverine discharge) on the functioning of benthic faunal communities. In many areas of the world, climate change is predicted to influence freshwater runoff from land (Christensen and Christensen, 2007). These predictions raise concerns about potential effects on coastal food webs (Bartels et al., 2018; Vinagre et al., 2019). The Baltic Sea, a semi-enclosed sea with a large catchment area, is especially susceptible to warming and riverine regime shifts related to increasing precipitation in summer and decreasing snow cover in winter (Christensen et al., 2022). However, the potential impact of altered riverine discharge on benthic communities has not been recognized as a consequence of the ongoing climate change (Viitasalo and Bonsdorff, 2022).

The aim of the present work was to assess the spatio-temporal variability in marine and riverine OM utilization by benthic primary consumers inhabiting a temperate riverine-impacted coast (Vistula River prodelta, southern Baltic Sea). Specifically, we asked: [1] what is the seasonal variation of the quantity, quality, and composition of OM mixtures in the Vistula prodelta, [2] what is the relative contribution of riverine and marine OM to the diet of the nine most common benthic taxa, and [3] what is the contribution of riverine and marine organic carbon ( $C_{org}$ ) to the total  $C_{org}$  comprised in benthic communities. The answers to these questions will provide new insight into allochthonous OM importance for the functioning of the dynamic, coastal ecosystem prone to environmental change and anthropogenic influence.

## 2 Materials and methods

### 2.1 Study area

The study area is located in the Gulf of Gdańsk, within the vicinity of the Vistula River mouth, in the eastern part of the prodelta (Figure 1). The Vistula River is the second biggest river entering the Baltic Sea (HELCOM, 2018), with a water discharge seasonally ranging from 250 to 8000 m<sup>3</sup> s<sup>-1</sup> [with the maximum outflow during spring and minimum in autumn (Cyberski et al., 2006; Kubiak-Wójcicka, 2020)]. The outflow contributes to 7% of the total annual freshwater discharge into the Baltic Sea (Majewski, 2013). The Vistula River is a very important source of suspended material to the Gulf of Gdańsk. The annual



sediment transport into the Gulf ranges from 0.7 to 2.2 million tons of suspension (Emelyanov and Stryuk, 2002), which causes sedimentation rates of around  $6600 \text{ g m}^{-2} \text{ y}^{-1}$  in the outer Vistula prodelta [the largest sediment load is deposited between February and May, and lowest during summer and autumn; (Damrat et al., 2013)]. The Vistula River is also one of the largest suppliers of OM and nutrients to the Baltic Sea. Kuliński and Pempkowiak (2012) estimated loads of total organic carbon to be  $1.76 \times 10^5 \text{ t y}^{-1}$  and total inorganic carbon of  $1.7 \times 10^6 \text{ t y}^{-1}$ , which accounts for 5.3% and 21.3%, respectively, of the total amount delivered with rivers to the Baltic Sea. The average loads of nutrients to the Baltic Sea between 1995 and 2014 were  $1.0 \times 10^5 \text{ t y}^{-1}$  for total nitrogen and  $6.5 \times 10^3 \text{ t y}^{-1}$  for total phosphorus (HELCOM, 2018). The environmental variability generated by the Vistula River discharges (i.e., physical disturbance, quality and quantity of OM) has a huge impact in shaping benthic communities attributes [i.e., density, diversity and taxonomic composition (Włodarska-Kowalczyk et al., 2016)].

## 2.2 Field Sampling

Samples for the study were collected in the Vistula River prodelta, Gulf of Gdansk (Figure 1) from r/v Oceania, during 5

research cruises (October 2018, January 2019, March-April 2019, October 2019 and January 2020), covering two early autumns, one spring and two winters. Samples were collected at 3 stations – MW1, MW2 and MW3, located at similar distances to the river mouth but representing different depths (Table 1). At each station temperature and salinity profiles were measured with Sea-Bird SBE 19 plus CTD probe.

Samples of water for prodelta particulate OM (pPOM) were collected by a Niskin bottle (bottom water). The water was filtered through pre-weighed and pre-combusted Whatman GF/F filters ( $\phi$  47 mm; pore size:  $0.7 \mu\text{m}$ ) and frozen at  $-20^\circ\text{C}$  until analysis. Additional water samples were filtered for phytopigments analysis [i.e., chlorophyll *a* (chl *a*) and phaeophytin (phaeo)] through Whatman GF/F filters ( $\phi$  25 mm; pore size:  $0.7 \mu\text{m}$ ) and frozen at  $-80^\circ\text{C}$ .

At each sampling station surface sediments for grain size analysis, prodelta sedimentary OM (pSOM; upper 5 cm layer) and phytopigments (upper 1 cm layer) were collected from box corer and frozen at  $-20^\circ\text{C}$  and  $-80^\circ\text{C}$ , respectively.

Sediment samples for macrofauna were collected with a van Veen grab ( $0.1 \text{ m}^2$ ) in four replicates at each station. Sediments were washed over a sieve with a mesh size of 0.5 mm. Three replicates were preserved in a 4% formaldehyde solution buffered with borax for later taxonomic analysis. One replicate sample was used to collect macrofauna for stable isotope analysis. This sample was kept in a fridge for 24h (allowing gut clearance) and then sorted under a stereomicroscope onboard. All taxa present in a sufficient amount for isotopic analysis ( $>2 \text{ mg}$  dry weight) were collected and frozen at  $-80^\circ\text{C}$  until further analysis. For bivalve species (size  $>1 \text{ cm}$ ) only muscle tissues were collected.

Additionally, samples for marine POM (mPOM) and riverine POM (rPOM) for stable isotope analysis were collected at the open coast of the southern Baltic (mPOM), and  $\sim 12 \text{ km}$  upstream in the Vistula River (rPOM) respectively. Marine POM from the open coast was sampled at three stations (ML1:  $54.78^\circ\text{N}$ ,  $17.43^\circ\text{E}$ ; ML2:  $54.84^\circ\text{N}$ ,  $17.42^\circ\text{E}$ ; ML3:  $54.97^\circ\text{N}$ ,  $17.43^\circ\text{E}$ ) during the same research cruises and with the same methodology as in case of samples from prodelta. Samples of rPOM were collected in May 2019 (Silberberger et al., 2021) and November 2020, representing spring and autumn respectively, with water canisters directly from the river shore ( $54.25^\circ\text{N}$ ,  $18.95^\circ\text{E}$ ).

TABLE 1 Geographic coordinates and environmental conditions for each sampling station in the Vistula prodelta.

Station	Latitude	Longitude	Depth	Temperature [ $^\circ\text{C}$ ]	Salinity	Mean grain size [ $\mu\text{m}$ ]
MW1	$54.36^\circ\text{N}$	$19.11^\circ\text{E}$	13 m	2.2 – 14.1	6.2 – 7.5	148.8 – 149.3
MW2	$54.38^\circ\text{N}$	$19.09^\circ\text{E}$	23 m	3.5 – 14.3	6.8 – 7.8	92.17 – 176.4
MW3	$54.40^\circ\text{N}$	$19.08^\circ\text{E}$	32 m	4.4 – 14.4	7.3 – 7.7	191.3 – 245.3

Temperature, salinity and mean grain size are shown as the total range from all sampling events.

## 2.3 Laboratory analysis

The analyses of  $C_{org}$ , as well as total nitrogen ( $N_{tot}$ ) concentrations, and their stable isotopes ( $\delta^{13}C$  and  $\delta^{15}N$ ) were performed in an Elemental Analyzer Flash EA 1112 Series combined with the Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). Samples of benthic animals, sediments and filters with POM were freeze-dried, homogenized and weighed into silver capsules (about 1 mg, 75–80 mg and 35–45 mg, respectively). Afterward, samples were soaked with 2 M HCl to remove carbonates and dried at 60°C for 24 h [the procedure was repeated until a constant weight was obtained (Kuliński et al., 2014)].  $C_{org}$  and  $N_{tot}$  measurements were calibrated against certified reference materials (marine sediments) provided by HEKAtech GmbH (Germany).  $\delta^{13}C$  results were calibrated against IAEA standards: CO-8 and USGS40, and  $\delta^{15}N$  results against N-1 and USGS40. Stable isotope ratios are given in the conventional delta notation, i.e., versus Vienna Pee Dee Belemnite for  $^{13}C$  and versus air for  $^{15}N$  as parts per thousand (‰).

The concentrations of chl *a* and phaeo in bottom water (filters) and surface sediments were analyzed following the EPA 445.0 method (Arar and Collins, 1997) with the use of a Fluorimeter Trilogy<sup>®</sup> (Turner Designs Inc.). Defrosted filters and freeze-dried and homogenized sediments were extracted in 10 ml of 90% acetone for approximately 24 h at 4°C. The centrifuged (3000 rpm for 2 min) supernatant was then analyzed before and after acidification with 100 µl of 0.1 M HCl (Arar and Collins, 1997).

Sediment samples for granulometric analysis were dried (48 h, 60°C) and sieved with a shaker through a set of standard test sieves with mesh diameters of 2, 1, 0.5, 0.25, 0.125 and 0.063 mm (Folk and Ward, 1957). Sediment parameters were calculated using the method of Folk and Ward (1957) in the program GRADISTAT 9.0 (Blott and Pye, 2001).

Benthic community samples were sorted under a stereomicroscope to the lowest possible taxonomic level, counted and weighed (blotted wet weight of formalin preserved samples). Additionally, the biomass/abundance (B/A) ratio for each taxon was calculated, which gives information about an average individual's body size.

## 2.4 Data analysis

### 2.4.1 Organic matter properties

To visualize OM patterns among sampling stations and seasons, a Principal Component Analysis (PCA) was conducted in PRIMER v7 statistical software (Clarke and Gorley, 2015). In total, sixteen variables characterizing OM properties were used i.e.,  $C_{org}$ ,  $N_{tot}$ ,  $\delta^{13}C$ ,  $\delta^{15}N$ ,  $C_{org}/N_{tot}$ , chl *a*, phaeo, and chl *a*/phaeo for both pPOM and pSOM. All data

were scaled to 0 mean and unit variance (i.e., normalize option in PRIMER) prior to the analysis.

### 2.4.2 Mixing models

To quantify the contribution of mPOM and rPOM to the pPOM mixtures, a Bayesian mixing model approach was used (Parnell et al., 2013), which is a statistical framework for quantifying proportional contributions of various sources to a mixture, allowing for application of different extensions, such as trophic discrimination factors (TDFs), concentration dependence and various error structures (Stock et al., 2018). Our approach assumes that the pPOM collected at stations MW1-3 are mixtures of marine and river POM and that the local marine production in the Vistula prodelta is isotopically the same as in the open coast area. However, we are aware that some part of marine primary production may be supplied by riverine dissolved carbon and nitrogen, and if so, our model will take it as riverine source.

The modeling was conducted with the use of MixSIAR package (Stock and Semmens, 2016; Stock et al., 2018) in R version 4.1.2 (R Core Team, 2021). Due to relatively high seasonality of pPOM isotopic values in the study area (Szczepanek et al., 2021), four separate models were run, one for the pPOM data collected during the whole study period (5 sampling campaigns), and three separate models for autumn (2 sampling campaigns), winter (2 sampling campaigns), and spring (1 sampling campaign). The parameters of the model run were set to “extreme” (chain length = 3,000,000; burn = 1,500,000; thin = 500; chains = 3), meaning that 3 Markov chains were each sampled 3000000 times. The first half of the samples were discarded (burn-in) to ensure that the chains converged. This was followed by subsampling (thinning) of the retained second half of each Markov chain, meaning that only every 500th sample was kept, resulting in a total of 3000 samples per chain (i.e., 3 x 3000 = 9000 samples). The thinning is applied, since samples of a Markov chain are correlated, and thinning helps to reduce this correlation. Since the composition of pPOM is exclusively a mixing problem and does not involve a trophic transfer, TDFs for both isotopes were set to 0.

In order to select a group of reliable benthic taxa for the assessment of dietary contributions, the SIMPER analysis was conducted on the square-rooted biomass data that returned the percentage similarity of taxonomic composition within stations (Bray-Curtis similarity) (Table 2). The SIMPER analysis allowed to distinguish 11 common taxa, from which 9 were selected for further analyses, namely: *Cerastoderma glaucum*, *Mya arenaria*, *Macoma balthica*, *Peringia ulvae*, *Corophium* spp., *Oligochaeta*, *Pygospio elegans*, *Marenzelleria* spp., and *Hediste diversicolor*. The two remaining species, i.e. *Diastylis rathkei* and *Streblospio shrubsoli* were rejected due to an insufficient number of isotopic samples. SIMPER was conducted in PRIMER v7 statistical software (Clarke and Gorley, 2015).

For each of the 9 taxa, a separate mixing model was conducted with a fixed effect: station ID in order to estimate the relative contribution of food sources (mPOM, rPOM and pSOM) to their diet at each sampling station (MW1, MW2, MW3). The parameters of the model runs were also set to “extreme”. Since differences between pSOM and mPOM values were not significant (Kruskal-Wallis test,  $p = 0.531$  for  $\delta^{13}\text{C}$  and  $p = 0.474$  for  $\delta^{15}\text{N}$ ), resulting in high uncertainty of modeled probability distributions, those two sources were combined *a posteriori* (Phillips et al., 2005) into a “marine” source, whereas the rPOM represented the “riverine” source. The *a posteriori* summing of particular source proportions is recommended, when some sources are poorly differentiated, since it enables to include all potential sources without losing covariation structure among source proportions (Phillips et al., 2005; Phillips et al., 2014).

For mixing models of macroinvertebrates, we adapted TDFs that have been previously used for one of our sampling station (Silberberger et al., 2021). Accordingly,  $\text{TDF}_{\Delta}^{13}\text{C} = 4 \pm 1.3$  and  $\text{TDF}_{\Delta}^{15}\text{N} = 3.4 \pm 1.0$  were used for the first trophic transfer (i.e., from OM to primary consumers). Since  $\delta^{15}\text{N}$  indicated two species (*H. diversicolor* and *Marenzelleria* spp.) to be secondary consumers,  $\text{TDF}_{\delta}^{13}\text{C} = 4.8 \pm 1.8$  and  $\text{TDF}_{\delta}^{15}\text{N} = 6.8 \pm 2.0$  were used in mixing models for these species.

In our mixing models, we used the residual error structure that is appropriate in applications with an integrated sampling approach [i.e., when consumer sample is pooled from more than one individual (Stock et al., 2018)]. This error accounts for variation in consumer data originating from differences in biochemical reactions of individual consumers, assuming that all consumers equally feed on the source means (Stock and Semmens, 2016).

### 2.4.3 Relative Contribution Index

The measured wet weight (WW [ $\text{g m}^{-2}$ ]) of the 9 common taxa was converted into dry weight (DW) or shell-free DW

(SFDW) in the case of mollusks, according to literature based conversion factors (Rumohr et al., 1987; Gogina et al., 2022). Next, the mean organic carbon content ( $C_{\text{org}}$ ) for those taxa was quantified, based on the mean relative  $C_{\text{org}}$  measured for each species and station. Finally, to quantify the percentage contribution of marine and riverine food sources to the total organic carbon of benthic communities (represented by the common taxa), the relative contribution index ( $\text{RC}_j$ ) (Arbi et al., 2018) was calculated following equations (1) and (2):

$$B_{ji} = C_{\text{org}} \times P_j \tag{1}$$

where  $C_{\text{org}}$  is the organic carbon of the  $i$ th taxon per  $\text{m}^2$  and  $P_j$  is the percentage contribution of the  $j$ th source to the diet of  $i$ th taxon;

$$\text{RC}_j = \sum_{i=1}^n B_{ji} \div B_T \tag{2}$$

where  $B_T$  is the total  $C_{\text{org}}$  [ $\text{g m}^{-2}$ ] in all 9 taxa. In other words,  $\text{RC}_j$  is a percentage sum of organic carbon originating from  $j$  source, accumulated by all species in the community. The  $\text{RC}$  [%] for both food sources was calculated for each grab sample from the probability distribution of these food sources in the diet of each taxon (sum from all analyzed taxa). Additionally, the  $\text{RC}_j$  index (median) was used to estimate the total content of marine and riverine  $C_{\text{org}}$  in benthic communities among seasons and sampling locations.

## 3 Results

### 3.1 Environmental conditions

A clear seasonal variation of OM quantity and quality was observed (Figure 2), both in the bottom water and in surface

TABLE 2 The cumulative percentage similarity (Bray-Curtis) of taxonomic composition and biomass ( $\sqrt{\text{transformed}}$ ) at three sampling stations.

MW1 (73.85% of similarity)		MW2 (70.24% of similarity)		MW3 (72.41% of similarity)	
Taxon	Cum.%	Taxon	Cum.%	Taxon	Cum.%
<i>Cerastoderma glaucum</i>	21.61	<i>Macoma balthica</i>	27.13	<i>Macoma balthica</i>	62.04
<i>Peringia ulvae</i>	42.63	<i>Peringia ulvae</i>	50.36	<i>Peringia ulvae</i>	71.79
<i>Mya arenaria</i>	61.28	<i>Cerastoderma glaucum</i>	68.42	<i>Hediste diversicolor</i>	79.54
<i>Macoma balthica</i>	79.81	<i>Mya arenaria</i>	79.87	<i>Marenzelleria</i> spp.	87.07
<i>Corophium</i> spp.	85.28	<i>Hediste diversicolor</i>	86.49	<i>Corophium</i> spp.	91.98
<i>Marenzelleria</i> spp.	89.87	<i>Corophium</i> spp.	91.17	Oligochaeta	94.41
<i>Hediste diversicolor</i>	94.06	Oligochaeta	94.56	<i>Mya arenaria</i>	96.82
Oligochaeta	96.36	<i>Marenzelleria</i> spp.	97.94	<i>Pygospio elegans</i>	98.48
<i>Pygospio elegans</i>	98.30	<i>Pygospio elegans</i>	99.49	<i>Diastylis rathkei</i>	99.93
<i>Streblospio shrubsoli</i>	99.11				



sediments of the Vistula prodelta (Supplementary Table 1). In winter, the water column at all stations was characterized by low values of chl *a* (0.2 – 1.2  $\mu\text{g L}^{-1}$ ) and chl *a*/phaeo (0.12 – 0.32) and depleted  $\delta^{13}\text{C}$  (-29.7 – -26.4 ‰). In spring, the water at all stations was characterized by high concentrations of chl *a* (3.8 – 5.1  $\mu\text{g L}^{-1}$ ), chl *a*/phaeo (2.01-2.49) and  $C_{\text{org}}$  (0.36 – 0.48  $\text{mg L}^{-1}$ ). In contrast, during both autumns OM parameters were more variable among sampling stations, and chl *a*, chl *a*/phaeo and  $C_{\text{org}}$  in sediments were increasing with depth. Additionally, in autumn,  $\delta^{15}\text{N}$  values in the water column were depleted in comparison to other seasons (0.97 – 1.81 ‰, excluding MW1 in 2019 – 4.8 ‰).

### 3.2 Organic matter composition

The isotopic composition of rPOM did not differ among sampling campaigns ( $-31.94 \pm 0.45$  ‰ for  $\delta^{13}\text{C}$  and  $9.96 \pm 0.31$  ‰ for  $\delta^{15}\text{N}$ ). Marine POM was more variable among seasons, especially in case of  $\delta^{15}\text{N}$  values ( $-26.56 \pm 0.89$  ‰ for  $\delta^{13}\text{C}$  and  $3.32 \pm 1.61$  ‰ for  $\delta^{15}\text{N}$ ). In general, the contribution of rPOM to the mixtures of pPOM in the study area decreased from MW1 towards MW2 (from 27.1% to 4.3%), and only slightly further to MW3 (1.7%) (Figure 3). The relative contribution of rPOM at all stations was higher during winter in comparison to other seasons.

### 3.3 Benthic community structure

The highest abundance was observed at station MW1 (up to 70,640 ind.  $\text{m}^{-2}$ ) and was associated with high numbers of *M.*

*arenaria*, *P. ulvae*, *C. glaucum* and *M. balthica* (Table 3). Those four species also evenly dominated benthic biomass and benthic  $C_{\text{org}}$  at MW1. At stations MW2 and MW3 the abundance of macrofauna was lower (3387 – 10,683 ind.  $\text{m}^{-2}$  and 3617 – 10,840 ind.  $\text{m}^{-2}$ , respectively) and the number of species that dominated the biomass decreased with depth – *C. glaucum* and *M. balthica* at MW2 and only *M. balthica* at MW3. The average individual body size (B/A ratio) was rather stable across depths for small-bodied taxa, whereas it varied for bivalve species and particularly for polychaete *H. diversicolor* with the highest values at MW3 (Table 3).

### 3.4 Benthic food-web structure

The isotopic composition of the benthic fauna ranged from -24.64 to -22.21 ‰ and from 4.46 to 12.56 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Figure 4). The lowest  $\delta^{15}\text{N}$  values were characteristic for *C. glaucum* and *M. arenaria* whereas the highest for *H. diversicolor* and *Marenzelleria* spp.

The dietary contribution of rPOM for all taxa in this study was the highest at station MW1, with the highest values for *M. balthica* (47.7%) and *Marenzelleria* spp. (42.3%) (Figure 5). The contribution of rPOM decreased from MW1 toward MW2, and further toward MW3 for most species. *C. glaucum*, *M. arenaria* and *P. ulvae* had the lowest overall contribution of rPOM (2-12%).

### 3.5 Relative Contribution index

The average RC for rPOM decreased with depth and was 26.05% (10.97 – 42.35 [95% credible interval – CI<sub>95</sub>]) for MW1, 19.52% (6.98 – 35.50 [CI<sub>95</sub>]) for MW2 and 14.80% (3.55 – 31.49 [CI<sub>95</sub>]) for MW3. The total  $C_{\text{org}}$  content in benthic communities decreased after autumn 2018 at all stations (Table 4) and then increased next autumn at MW1 and MW3. In general, the total  $C_{\text{org}}$  content was the highest at MW3. Thus, although the RC for rPOM at this station was lower in comparison the station MW1, the riverine  $C_{\text{org}}$  at MW3 was the highest during three out of five campaigns.

## 4 Discussion

Our study shows that utilization of riverine OM differed among feeding groups of benthic primary consumers in the Vistula River prodelta. Common species of obligatory and facultative deposit feeders i.e., Oligochaeta (Atrill et al., 2009), *P. elegans* (Brey, 1991), *Marenzelleria* spp. (Dauer, 1997) and *H. diversicolor* (Fauchald and Jumars, 1979) showed a higher contribution of rPOM in their diet in comparison to obligatory suspension feeders (*C. glaucum*, *M. arenaria*).

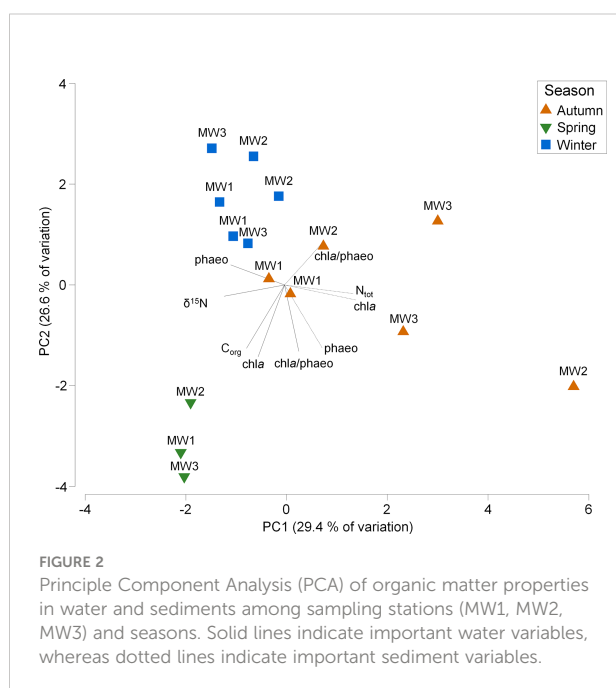


FIGURE 2  
Principle Component Analysis (PCA) of organic matter properties in water and sediments among sampling stations (MW1, MW2, MW3) and seasons. Solid lines indicate important water variables, whereas dotted lines indicate important sediment variables.

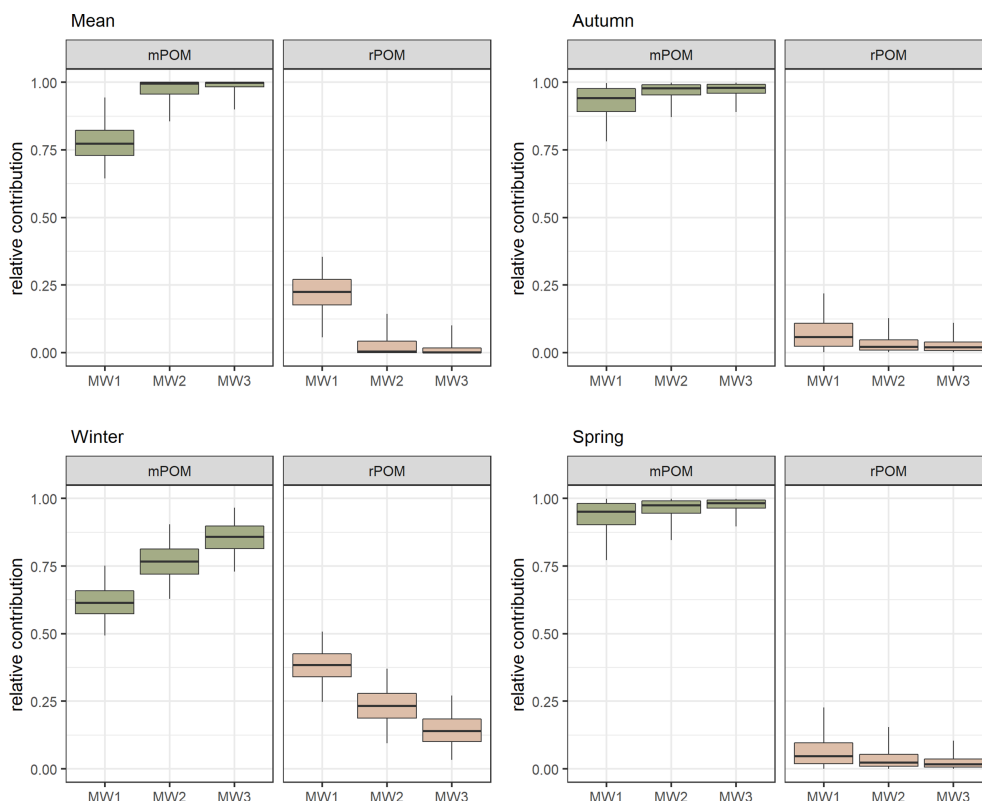
Populations of *M. balthica*, which is known for the ability to switch between suspension- and deposit-feeding mode (Ólafsson, 1986), differed in the biomass and abundance as well as dietary proportions of food sources depending on depth, and the availability of fresh marine OM. Although the consumption of rPOM decreased with increasing depth for all species, changes in the community structure with depth resulted in similar levels of riverine  $C_{org}$  utilization in the shallow and deepest areas of this riverine impacted coast.

### 4.1 Contribution of riverine OM to benthic diet

The relative contribution of rPOM to the pPOM (prodelta POM) mixture decreased with increasing depth. Similarly, a decreasing contribution of riverine OM to the diet of benthic fauna was noted from the shallowest to deepest station. Similar pattern was observed in other riverine impacted areas e.g., in Chesapeake Bay (Hoffman et al., 2008) or Tyrrhenian Sea

(Careddu et al., 2015). However, other studies observed also the opposite trend i.e., increasing contribution of allochthonous OM with increasing depth (Darnaude et al., 2004; Premke et al., 2015; Bartels et al., 2018). These contrary observations were suggested to result from different topology and hydrological conditions of estuaries and river deltas, which lead to higher sedimentation of allochthonous material in deeper deltaic areas. In the Vistula River prodelta, the highest sedimentation is observed close to the river mouth, however, the sedimented material largely becomes resuspended and transported to Gdańsk Deep, a depositional area outside the Gulf of Gdańsk (Damrat et al., 2013). This may explain lower abundance of riverine material at our outermost station.

Nevertheless, the contributions of rPOM to the pPOM at sampling stations were lower than those observed in the benthic fauna diet, especially at the deepest station. It is possible that we did not always detect riverine OM in pPOM, especially at deeper stations, since the vertical extent of Vistula waters was found to reach up to 10 m from the surface (Grelowski and Wojewódzki, 1996). However, in the long term, the suspended material from



**FIGURE 3**  
The probability distribution of relative contribution [%] of mPOM (collected at the open coast of western Poland) and rPOM (collected ~12 km upstream in the Vistula River) to the pPOM (prodelta POM, collected at sampling stations). Boxplots depict median (horizontal line) with 50% (box) and 95% credible intervals (vertical line).

riverine flow can to some extent get to the bottom layer and surface sediments and affect the diet composition of fauna (Darnaude et al., 2004). It is worth mentioning that pycnocline was observed in the study area during both winter samplings, with less saline waters transported along the surface. However, differences in the isotopic values from bottom and surface water layers ( $\delta^{13}\text{C} = -28.39 \pm 1.43$  and  $\delta^{15}\text{N} = 4.70 \pm 1.05$  for bottom and  $\delta^{13}\text{C} = -27.19 \pm 0.39$  and  $\delta^{15}\text{N} = 3.89 \pm 0.81$  for surface waters respectively) indicated more allochthonous OM in the bottom water (Maksymowska et al., 2000), most probably originating from more intensive discharge typical for late autumn. In remaining seasons, water column was usually well-mixed and therefore ordinary sedimentation should be assumed. It is important to recognize that Gulf waters have naturally low salinity of approximately 7 and therefore both water masses usually mix immediately.

## 4.2 Depth-related patterns of rPOM availability

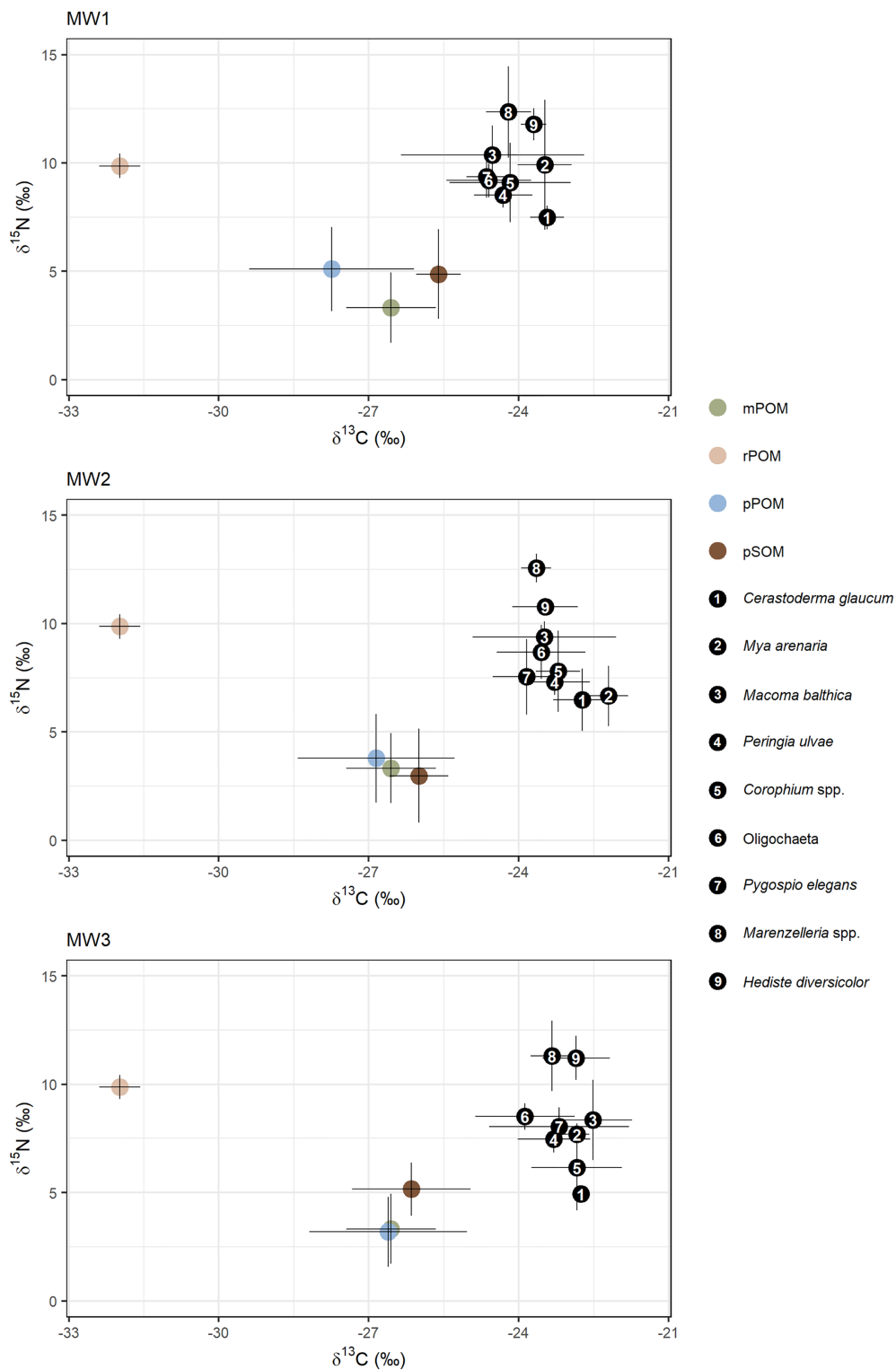
All stations in our study were located at a similar distance from the river mouth in the east of the outflow which is a prevailing direction in which riverine water masses are introduced into the Gulf (Grelowski and Wojewódzki, 1996; Voss et al., 2005). It is because of prevailing westerly winds that push riverine waters eastwards in this area. Thus, the observed decrease of riverine OM contribution with depth to both the pPOM mixture and the diet of macrofauna is most likely caused by an increasing contribution of marine primary production to the vertical OM flux with increasing volume of the water column (Careddu et al., 2015). Indeed, the most effective summer primary production in the study area is observed further in the offshore zone (Ochocki et al., 1995), and chl *a* concentrations in the surface layer were shown to

TABLE 3 The mean abundance [ind. m<sup>-2</sup>], biomass [WW g m<sup>-2</sup>], biomass/abundance ratio (B/A) [mg ind.<sup>-1</sup>], and C<sub>org</sub> [DW g m<sup>-2</sup>; SFDW for mollusks species] of the common benthic taxa at the sampling stations.

Station	Taxon	Abundance	Biomass	B/A	C <sub>org</sub>
MW1	<i>Cerastoderma glaucum</i>	1382 (60 - 6067)	22.32 (5.81 - 43.06)	71.8 (6.1 - 155.4)	0.47 (0.12 - 0.91)
	<i>Mya arenaria</i>	12490 (795 - 45837)	25.09 (13.55 - 33.14)	15.2 (0.7 - 39.7)	0.63 (0.34 - 0.83)
	<i>Macoma balthica</i>	972 (53 - 3570)	25.85 (4.35 - 67.2)	146.4 (1.9 - 364.6)	0.61 (0.1 - 1.58)
	<i>Peringia ulvae</i>	7190 (2300 - 14653)	17.02 (3.29 - 40.08)	2.2 (1.2 - 3.1)	0.15 (0.02 - 0.59)
	<i>Corophium</i> spp.	477 (60 - 960)	0.96 (0.23 - 1.76)	2.5 (1.5 - 3.9)	0.03 (0.01 - 0.06)
	Oligochaeta	497 (133 - 1023)	0.20 (0.04 - 0.44)	0.4 (0.3 - 0.5)	0.01 (0 - 0.01)
	<i>Pygospio elegans</i>	506 (60 - 987)	0.24 (0.03 - 0.41)	0.5 (0.4 - 0.7)	0.01 (0 - 0.03)
	<i>Marenzelleria</i> spp.	402 (90 - 795)	3.44 (0.29 - 13.56)	5.6 (1.9 - 15.2)	0.20 (0.02 - 0.78)
	<i>Hediste diversicolor</i>	257 (190 - 287)	1.03 (0.36 - 2.15)	3.9 (1.6 - 7.7)	0.05 (0.02 - 0.11)
	other	248 (70 - 513)	0.25 (0.08 - 0.58)		
MW2	<i>Cerastoderma glaucum</i>	527 (23 - 2483)	31.25 (6.44 - 90.48)	350.9 (36.4 - 559.8)	0.66 (0.14 - 1.9)
	<i>Mya arenaria</i>	264 (53 - 563)	3.04 (1.67 - 5.53)	17.8 (6.3 - 40.7)	0.08 (0.04 - 0.14)
	<i>Macoma balthica</i>	242 (122 - 353)	23.61 (10.67 - 38.06)	116 (34.8 - 220)	0.56 (0.25 - 0.9)
	<i>Peringia ulvae</i>	3179 (1293 - 5623)	8.95 (4.03 - 15.65)	3.1 (1.9 - 4)	0.08 (0.02 - 0.18)
	<i>Corophium</i> spp.	230 (53 - 410)	0.45 (0.24 - 0.6)	2.5 (1.2 - 4.6)	0.02 (0.01 - 0.02)
	Oligochaeta	689 (135 - 970)	0.24 (0.09 - 0.39)	0.4 (0.2 - 0.7)	0.01 (0 - 0.01)
	<i>Pygospio elegans</i>	417 (50 - 943)	0.15 (0.01 - 0.36)	0.3 (0.2 - 0.4)	0.01 (0 - 0.02)
	<i>Marenzelleria</i> spp.	121 (50 - 197)	0.36 (0.12 - 0.46)	4.3 (1.1 - 8.8)	0.02 (0.01 - 0.03)
	<i>Hediste diversicolor</i>	522 (273 - 793)	1.21 (0.32 - 2.24)	2.2 (1.2 - 3.4)	0.06 (0.02 - 0.11)
	other	203 (20 - 753)	0.87 (0 - 4.01)		
MW3	<i>Cerastoderma glaucum</i>	40 (10 - 70)	0.15 (0.07 - 0.23)	12 (1 - 23)	<0.01 -
	<i>Mya arenaria</i>	73 (30 - 183)	3.21 (0.04 - 7.9)	33.7 (1.2 - 105.4)	0.08 (0 - 0.2)
	<i>Macoma balthica</i>	772 (417 - 1493)	96.13 (50.35 - 170.81)	143.2 (43.9 - 226.4)	2.26 (1.18 - 4.02)
	<i>Peringia ulvae</i>	1637 (433 - 4747)	3.27 (0.88 - 9.81)	2.2 (0.7 - 3.5)	0.03 (0.01 - 0.11)
	<i>Corophium</i> spp.	346 (75 - 827)	0.66 (0.2 - 1.14)	3.4 (1.4 - 8.2)	0.02 (0.01 - 0.04)
	Oligochaeta	593 (195 - 1573)	0.18 (0.08 - 0.35)	0.4 (0.2 - 0.5)	<0.01 (0 - 0.01)
	<i>Pygospio elegans</i>	394 (40 - 837)	0.17 (0.01 - 0.32)	0.4 (0.3 - 0.6)	0.01 (0 - 0.02)
	<i>Marenzelleria</i> spp.	396 (110 - 580)	2.07 (0.55 - 4.87)	5.5 (0.9 - 8.9)	0.12 (0.03 - 0.28)
	<i>Hediste diversicolor</i>	183 (113 - 287)	3.73 (0.52 - 12.23)	17.4 (2.5 - 42.6)	0.19 (0.03 - 0.62)
	other	160 (23 - 340)	0.18 (0.01 - 0.57)		

Values in brackets show the min-max range among sampling campaigns.





**FIGURE 4**

Biplots of carbon and nitrogen isotopic ratios of the common benthic taxa (indicated by numbers 1-9) and their food sources: mPOM – marine POM from the open Polish coast; rPOM – riverine POM from ~12 km upstream in the Vistula River; pPOM – prodelta POM collected at sampling stations; pSOM – prodelta sedimentary OM collected at sampling stations. Points indicate the mean (all sampling campaigns) and whiskers indicate standard deviation. Figure represent raw data before applying trophic enrichment factors.

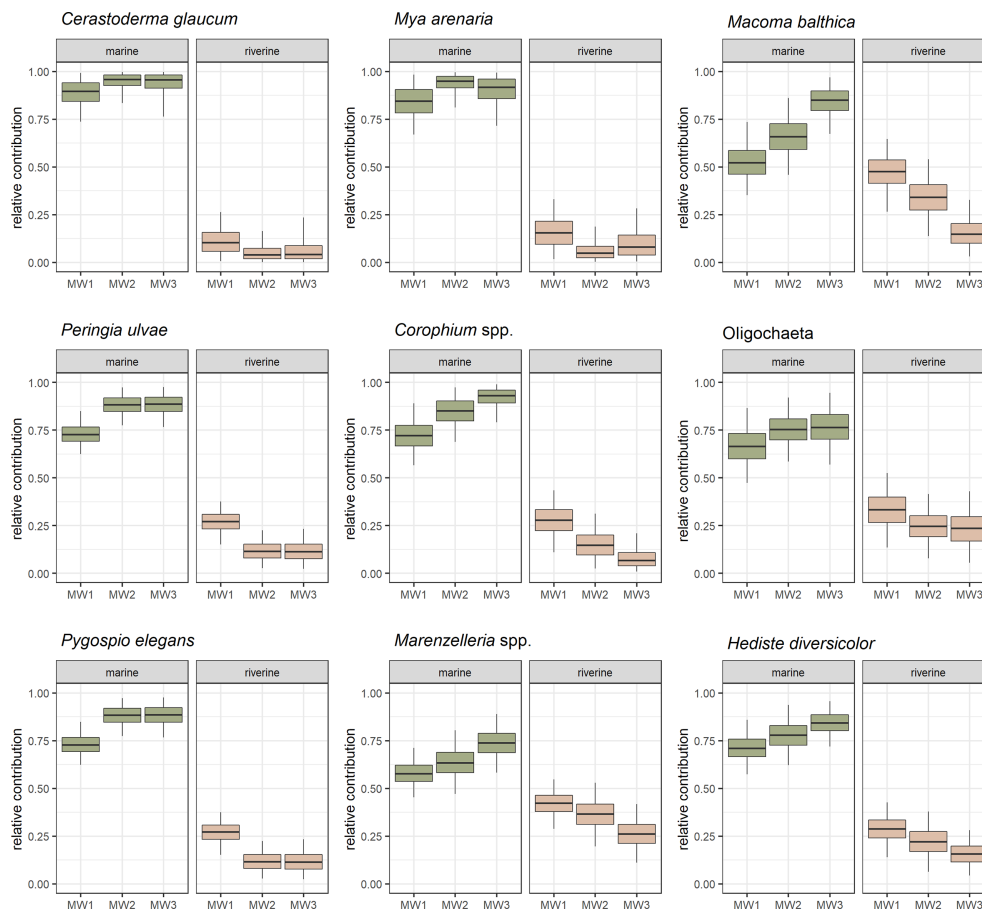


FIGURE 5

The probability distribution of relative contribution [%] of marine and riverine food sources in the diet of the common benthic taxa at sampling stations (MW1, MW2, MW3). Boxplots depict median (horizontal line) with 50% (box) and 95% credible intervals (vertical line).

increase with increasing bottom depth (and distance from the shore) during spring (this study) and autumn (Ochocki et al., 1995). Moreover,  $C_{org}$  concentrations in sediments were usually higher at MW3 in comparison to shallower stations (Supplementary Table 1), which supports this statement.

During calm weather and winds from the north, the outflow of the Vistula can be blocked to some extent close to the river mouth (Matciak and Nowacki, 1995; Grelowski and Wojewódzki, 1996). Under such conditions surface water pockets are formed and transported in both directions along the coast which prevents deeper areas from the river influence. These may additionally explain why the decrease of riverine food in the benthos diet is particularly prominent between MW1 and MW2, whereas it decreases further at MW3 only for particular taxa.

### 4.3 The role of feeding modes in rPOM consumption

In our study, deposit feeders (Oligochaeta and polychaetes, *M. balthica*) showed higher reliance on rPOM in their diet, which

reflected the pPOM composition in winter. In contrast, the diet composition of suspension-feeding taxa (*M. arenaria*, *C. glaucum*) and selective feeding *P. ulvae* and *Corophium* spp. (Fenchel and Kofoed, 1976; Nielsen and Kofoed, 1982) resembled the pPOM composition during the productive period (spring and autumn), confirming their preference for higher-quality, autochthonous food source. Therefore, it is likely that the diet of deposit feeders originated from rPOM carried by riverine flow during periods of higher detrital abundance (winter) or that they were outcompeted by suspension feeders for fresh primary production (spring, autumn). This is further supported when differences in the response time to fresh primary production among different feeding groups are taken into account. Populations of deposit feeders were shown to react to primary production supply later than suspension feeders which was demonstrated by faster population growth of the latter (Lessin et al., 2019). Lessin et al. (2019) explained that it may be a mechanism of suspension-feeding fauna control on the fresh food supply to deposit feeders.

Deposit feeders rely on OM accumulated in or at the surface of the bottom and the quantity and nutritional value of accumulated

TABLE 4 The abundance [ind. m<sup>-2</sup>], biomass [g WW m<sup>-2</sup>] and total, riverine, and marine C<sub>org</sub> contents [g DW m<sup>-2</sup>] in benthic communities among stations and sampling campaigns.

Sampling	Stations	Abundance	Biomass	C <sub>org</sub> total	C <sub>org</sub> riverine	C <sub>org</sub> marine
Autumn 2018	MW1	70,640 ± 27,592	181.10 ± 67.09	3.71 ± 1.20	1.12 ± 0.35	2.59 ± 0.85
	MW2	10,683 ± 1646	152.04 ± 111.12	3.18 ± 2.33	0.43 ± 0.26	2.75 ± 2.07
	MW3	10,840 ± 1157	86.34 ± 23.76	1.95 ± 0.54	0.21 ± 0.11	1.74 ± 0.53
Winter 2019	MW1	18,470 ± 8627	41.86 ± 7.57	0.84 ± 0.21	0.19 ± 0.09	0.65 ± 0.12
	MW2	3970 ± 862	48.59 ± 11.08	1.04 ± 0.19	0.18 ± 0.08	0.85 ± 0.20
	MW3	3727 ± 962	68.38 ± 38.49	1.85 ± 1.00	0.31 ± 0.16	1.54 ± 0.84
Spring 2019	MW1	5617 ± 1347	56.07 ± 7.83	1.31 ± 0.16	0.44 ± 0.07	0.87 ± 0.10
	MW2	3387 ± 280	55.40 ± 9.38	0.98 ± 0.59	0.26 ± 0.17	0.72 ± 0.45
	MW3	1880 ± 833	54.67 ± 40.08	1.37 ± 0.91	0.20 ± 0.13	1.12 ± 0.78
Autumn 2019	MW1	9810 ± 2397	93.77 ± 18.38	2.21 ± 0.64	0.53 ± 0.04	1.69 ± 0.68
	MW2	4540 ± 547	38.37 ± 21.71	0.79 ± 0.48	0.16 ± 0.10	0.63 ± 0.38
	MW3	3617 ± 793	190.03 ± 30.45	4.89 ± 0.92	0.75 ± 0.15	4.14 ± 0.77
Winter 2020	MW1	11,777 ± 6512	105.26 ± 10.05	2.26 ± 0.24	0.41 ± 0.06	1.85 ± 0.19
	MW2	8927 ± 4345	34.83 ± 7.44	0.62 ± 0.26	0.13 ± 0.07	0.49 ± 0.19
	MW3	2857 ± 497	148.59 ± 31.76	3.55 ± 0.77	0.52 ± 0.09	3.03 ± 0.67

Riverine and marine OM contributions to C<sub>org</sub> content [g DW m<sup>-2</sup>] are estimated based on the RC<sub>i</sub> index for particular stations and samplings. Values represent the mean and standard deviation summed from the 9 studied taxa.

OM depends on many environmental factors *e.g.*, rates of sedimentation, amount of refractory compounds, and intensity of microbial remineralization (Levinton, 1989; Thornton and McManus, 1994). Thus, the fresh OM supply to this feeding group is potentially more limited than to suspension feeders (Levinton, 1972) which might cause increased importance of allochthonous riverine subsidy in their diet. This can be supported by rather low C<sub>org</sub> concentrations in sediments throughout the year in contrast to water column, where C<sub>org</sub> is only slightly higher during spring bloom comparing to other seasons (Supplementary Table 1; Szczepanek et al., 2021).

Previous findings also showed that deposit feeders may to some degree rely on terrigenous OM (Darnaude et al., 2004; McGovern et al., 2020) that is one of the main components of OM transported by rivers. Attrill et al. (2009) suggested that higher reliance of Oligochaeta on terrigenous matter is probably the result of their evolutionary association to freshwater ecosystems that to a large extent are subsidized by terrigenous detritus. Since most deposit feeders feed rather non-selectively on sedimentary detritus (Levinton, 1989), it is likely that terrigenous OM contribution in the diet of other deposit-feeding species is higher than for obligatory suspension feeders. This probability may additionally increase with getting closer to freshwater resource and associated increase of terrigenous OM to available sedimentary OM pool.

#### 4.4 Changes in community structure with depth

In connection to changes in the diet composition of benthic fauna, the structural changes in community abundance and

biomass among stations were also noticeable. The most prominent changes with depth were visible for the bivalve species. Suspension-feeding bivalves like *M. arenaria* and *C. glaucum* are found specifically in shallow sandy areas of the southern Baltic Sea (up to 25 m, Gic-Grusza et al., 2009; Gogina and Zettler, 2010). Thus, the limited abundance of *M. arenaria* and *C. glaucum* at station MW3 (32 m) could be related to limited depth range of those species. Kube (1996) also observed the highest abundance and biomass of *M. arenaria* close to the shore in sandy sediments of the Pomeranian Bay (southern Baltic Sea).

The absence of large individuals of suspension feeders at the shallowest station could be also the result of increased turbidity and resuspension by the river current which is unfavorable for their growth and survival (Archambault et al., 2004). However, the sampling stations in the study have been located by design at a greater distance from the river mouth, to not be directly affected by salinity changes or increased water turbidity and sedimentation (Włodarska-Kowalczyk et al., 2016).

Changes in the structure of benthic species populations across depth may be the result of sediment-dependent species distributions, together with their causes and effects (Snelgrove and Butman, 1994). Many previous studies reported that sediment grain size affects the distribution and densities of benthic species, including bivalves (Thrush et al., 2003; Compton et al., 2009; Gerasimova et al., 2019). It was shown that distribution of juvenile and adult populations of different bivalve species can be driven by sediment type selection during post-settlement migrations (Huxham and Richards, 2003; Compton et al., 2009). Compton et al. (2009) reported that while juvenile and adult individuals of deposit-feeding *M.*

*balthica* inhabited separate sedimentary habitats across wide spatial scale, the same pattern was not observed for suspension feeders (*C. edule* and *Scrobicularia plana*). Similar effect on spatial distribution of *M. balthica* could be also induced by sediment-dependent feeding activity (Ólafsson, 1986; Kamermans et al., 1992). Ólafsson (1986) observed that in muddy sediments *M. balthica* preferred to feed on deposited material, whereas, in sediments dominated by sands, individuals actively suspension-fed. In our study, a positive correlation was observed between the biomass of *M. balthica* and mean grain size (Pearson's  $r$ , 0.56), whereas weaker, negative correlations were observed for suspension feeders (-0.19 and -0.31 for *C. glaucum* and *M. arenaria*, respectively). This suggests that sediment grain size plays an important role in shaping populations of these species in the Vistula River prodelta.

Differences in spatial distributions could be also the result of resource partitioning between suspension-feeding and deposit-feeding species (Levinton, 1972; Ólafsson, 1986). It was shown that in areas of high abundance of bivalves, the interspecific competition between suspension feeders occurred, leading to a switch of *M. balthica* to deposit-feeding (Kamermans et al., 1992). This may explain the much higher contribution of riverine OM to the diet of this species at the shallow station. In contrast, at deepest station, the diet of *M. balthica* was dominated by marine OM (this study, Silberberger et al., 2021). This suggests that the resource limitation for this species was no longer the case, and suspension-feeding strategy was predominant (Ólafsson, 1986). At a greater depth, marine food supply is larger and this decreases the level of intraspecific food competition. Interestingly, the biomass and individual body size of deposit-feeding *H. diversicolor* in our study also increased with depth. We suggest that this can be linked to the likely switch in the diet of *M. balthica*. When *M. balthica* feeds on suspended material at MW3 it results in a larger niche size and higher food availability for other deposit feeders (Levinton, 1972). As previously mentioned, at MW3  $C_{org}$  concentrations in the sediment were higher throughout the year in comparison to shallower stations (Supplementary Table 1). Thus, higher biomass of *H. diversicolor* at MW3 could result from both lower competition from *M. balthica* and higher detrital abundance.

#### 4.5 Riverine $C_{org}$ utilization

In our study, the riverine share in the biomass of benthic communities remained similar among the shallow and deepest prodelta parts. This is a result of above-described structural changes in benthic communities, specifically for *M. balthica* and *H. diversicolor* which biomass and feeding habits switch between both areas. These suggests that the riverine supply plays an

important role in the coastal system of the Gulf of Gdańsk. Although the riverine OM sustains around 15% of  $C_{org}$  demand ( $RC_j$ ) to the benthic species at 30 m depth, high biomass of *M. balthica* that effectively utilizes riverine  $C_{org}$  surely supports substantial transport of allochthonous  $C_{org}$  to higher trophic levels e.g., demersal fish (Nurkse et al., 2016). Additionally, due to their typically long life span (Gilbert, 1973; Kube, 1996) and production of calcium carbonate shells, marine bivalves act as an effective carbon sink supporting ecosystem functions and counteracting the negative effects of climate change (Filgueira et al., 2018).

The high content of riverine OM in benthic biomass shown in our study confirms that allochthonous OM is an important food subsidy to benthic secondary production in coastal riverine-impacted systems (Hoffman et al., 2008; Dunton et al., 2012). The observed and predicted climate change, and related decrease in snow cover and riverine discharge in Europe (Christensen and Christensen, 2007; Christensen et al., 2022) may lead to reduced allochthonous OM supply by the river (Vinagre et al., 2019). As shown in our study, changes in community structure and dietary contributions of benthic primary consumers may be directly linked to food composition. Thus, any changes in allochthonous OM supply may substantially affect the functioning and ecosystem services provided by coastal macrobenthic communities.

## 5 Conclusion

Our study shows that riverine OM supports benthic food web in the Vistula River prodelta. The importance of riverine OM decreases with depth affecting the community structure and functional feeding roles of benthic fauna. In the shallowest waters, the diet of benthic species is supported by riverine OM supply the most, and abundant populations of small-sized suspension feeders are favored most likely due to suitable depth range and sediment sorting. With increasing depth, the predominance of dietary-flexible *M. balthica* and *H. diversicolor* increases and we suggest that it is the result of the decrease of both inter- and intraspecific competition and increasing quantity of marine food supply.

Our results indicate that benthic primary consumers act as a gateway for riverine organic matter into the marine food web and that the structure of benthic fauna communities largely affects the ability and patterns of riverine  $C_{org}$  storage by benthos. Although benthic communities inhabiting the southern Baltic Sea show high plasticity of feeding behaviors (Szczepanek et al., 2021), the observed and predicted changes in the amount of riverine discharge (Christensen et al., 2022) and primary production patterns (Tamelander et al., 2017) may have profound consequences on the benthic community and food-

web structure and thus the functioning of coastal riverine impacted ecosystems.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

MSz, MSi and MK conceptualized the design of the study. MSz, MSi and KK-M conducted field and laboratory work. MSz analyzed data with contribution of KK-M. MSz wrote the original draft. All authors contributed substantially to the final version of the manuscript. MK acquired funding for this research. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.974539/full#supplementary-material>



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