Functioning of coastal benthic biotopes in the Puck Lagoon

Funkcjonowanie przybrzeżnych biotopów bentosowych w Zalewie Puckim

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Abstract

Coastal areas provide a high variety of benthic habitats that influence the structure and functioning of macrofaunal communities even on small geographical scales. Closely located benthic habitats often vary in geochemical variables such as sediment structure, water dynamics, chemical parameters and benthic vegetation which all can induce patchy distribution of the macrobenthic fauna. Understanding the functioning of benthic communities in different habitats is of great interest in food web ecology since different composition and availability of carbon sources in the system directly affect trophic structure and energy pathways in the resident assemblages.

In this thesis, taxonomic and trophic structure of macrobenthic communities were investigated across closely located benthic habitats in a low diversity system of the semi-enclosed Puck Lagoon (Gulf of Gdańsk, southern Baltic Sea) over four seasons. Traditional community indices (species richness, abundance, biomass and diversity) and food web attributes (estimated based on stable isotope ratios of carbon and nitrogen, $\delta^{13}C$ and $\delta^{15}N$) were integrated to assess spatial and temporal variation of taxonomic and functional diversity. Combining environmental characteristics with species diversity, feeding interactions and food web indicators provided thus an opportunity to bridge the gap between community ecology and ecosystem ecology to highlight small-scale variations related to benthic habitats.

In the first part of the thesis habitat related abiotic and biological variables were shown to exert a clear effect on macrofaunal benthic communities allowing identification of two discrete regions: a region of large biomass of macrophytes and a region of little macrophytes. The quality of the surface sediment organic matter (measured as C/N_{sed} ratio), water depth and composition of benthic macrophytes accounted primarily for within-region variation leading to the identification of four habitats (1) sand with little mixed vegetation (habitat A), (2) *Stuckenia*-dominated sediment (habitat B), (3) *Chara*/*Cladophora* sediment (habitat C) and (4) sand with little *Pylaiella* (habitat D). The next part of the thesis examined which basal resources fueled the food webs of four different macrobenthic communities and how different food sources affect the food web structure and trophic pathways within each community. It was demonstrated that benthic consumers had species-specific carbon and nitrogen isotope composition indicating that they feed mostly on food sources available in their habitats. The third part of thesis addressed trophic niche indices and trophic diversity as well as redundancy of the studied communities as a proxy for assessing the amount of energy and elemental space occupied by species in a given food web. The macrofaunal communities from sandy bottom

with low biomass vegetation showed lower trophic diversity and more compact food webs. Reliance on one dominant resource (suspended particular organic matter and phytoplankton) resulted here in simplification of food web structure with a large proportion of species with one feeding mode. In habitats with dense vegetation, benthic plants appeared to facilitate directly and indirectly development of different trophic niches for consumers by diversification of basic carbon resources. The increased availability and diversification of basal food resources support higher trophic diversity and resilience to disturbance such as species loss or episodic environmental event.

Streszczenie

Przybrzeżne wody morskie charakteryzują się dużą różnorodność siedlisk bentosowych, co powoduje przestrzenne zróżnicowanie struktury i funkcjonowania zbiorowisk makrozoobentosu nawet w niewielkiej skali geograficznej. Siedliska bentosowe położone w niewielkiej odległości od siebie często różnią się pod względem parametrów geochemicznych oraz cech biocenotycznych (obecność roślinności naczyniowej oraz makroglonów), które wpływają na nierównomierne rozmieszczenie zespołów makrofauny. Poznanie mechanizmów funkcjonowania zbiorowisk bentosowych zajmujących siedliska zróżnicowane pod kątem rodzaju i dostępności materii organicznej stanowi interesujące zagadnienie badawcze w ekologii, ponieważ dostarcza informacji o strukturze troficznej zbiorowisk i szlakach przepływu energii w danym ekosystemie.

W niniejszej pracy badania doświadczalne były prowadzone sezonowo na wybranych stanowiskach w Zalewie Puckim i obejmowały pomiary szeregu parametrów geochemicznych i cech biocenotycznych zespołów makrozoobentosu oraz wyznaczenie miar sieci troficznej na podstawie wyników analizy ilościowej stosunku izotopów trwałych węgla i azotu. Zastosowanie tradycyjnych wskaźników biocenotycznych w powiązaniu z wynikami modeli statystycznych opartych na pomiarach $\delta^{13}C$ i $\delta^{15}N$ pozwoliło na określenie zmienności czasowej i przestrzennej różnorodności taksonomicznej i funkcjonalnej. Połączenie różnych metod badawczych dostarczyło nowej wiedzy empirycznej o różnicach w funkcjonowaniu zespołów bentosowych zasiedlających różne siedliska w niewielkiej skali geograficznej Zalewu Puckiego.

W pierwszej części rozprawy przeprowadzone badania wykazały, że czynniki abiotyczne i biologiczne występujące na danym siedlisku kształtują bezpośrednio zbiorowiska makrozoobentosu. Zastosowane metody statystyczne umożliwiły wyodrębnienie dwóch rejonów w Zalewie Puckim: rejonu o dużej biomasie makrofitów i rejonu o niewielkiej biomasie roślin makrobentosowych. Spośród analizowanych czynników abiotycznych i biotycznych, za zróżnicowanie siedliskowe zalewu odpowiadają: jakość materii organicznej osadów powierzchniowych (mierzona jako stosunek ilościowy C/N), głębokość wody oraz skład i biomasa makrofitów bentosowych. Na podstawie powyższych czynników zidentyfikowano cztery siedliska bentosowe: (1) osady piaszczyste z niewielką ilością roślinności bentosowej o różnym składzie gatunkowym (siedlisko A), (2) osady porośnięte przez roślinę naczyniową z rodzaju *Stuckenia* (siedlisko B), (3) osady porośniętego roślinami

Chara/Cladophora (siedlisko C) i (4) osady piaszczyste z niewielką ilością makroglonu z rodzaju *Pylaiella* (siedlisko D). W kolejnej części pracy zidentyfikowano podstawowe źródła materii organicznej, określono jej wpływ na strukturę sieci troficznej oraz główne szlaki przepływu strumieni energii w sieci troficznej w obrębie każdego zespołu makrozoobentosu. Wykazano, że konsumenci charakteryzują się określonym składem izotopowym węgla i azotu, który odpowiada źródłom materii organicznej dostępnym na danym siedlisku. Przedmiotem trzeciej część rozprawy były zagadnienia dotyczące różnorodności oraz redundancji troficznej zbiorowisk na różnych siedliskach. Porównanie zastosowanych wskaźników troficznych pozwoliło na określenie różnorodności troficznej w strukturze zespołów makrozoobentosu oraz zmian czasowych w sieci troficznej. Zbiorowiska makrozoobentosu z piaszczystego dna o niskiej biomasie roślin charakteryzowały się niewielką różnorodnością troficzną sieci pokarmowej, która posiadała bardziej zwartą strukturę. Uproszczenie struktury troficznej było spowodowane wykorzystaniem jednego, dominującego zasobu materii organicznej (zawieszona materia organiczna i fitoplankton) przez organizmy filtrujące, które asymilowały materię z toni wodnej. W siedliskach o dużej biomasie roślin, występujące tam rośliny wpływały pośrednio i bezpośrednio na zwiększenie różnorodności troficznej zespołów makrozoobentosu poprzez dywersyfikację podstawowych zasobów węgla, które były dostępne dla konsumentów. Zwiększona dostępność zasobów pokarmowych w siedliskach o dużej biomasie roślin zwiększała również stabilność sieci troficznej, która cechuje się mniejszą podatnością na potencjalne zakłócenia w ekosystemie takie jak utrata gatunków lub epizodyczne zdarzenia środowiskowe.

Chapter 1. Introduction

A biotope is defined as «the habitat together with its recurring associated community of species, operating together at a particular scale» (Connor et al., 1997). Biotope is therefore considered a unit of the area (topographic unit) characterized by similar environmental (physical) conditions and a specific assemblage of plant and animal species i.e., a set of adjacent places in a given geographic region having more or less similar biotic and abiotic features (Dimitrakopoulos and Troumbis, 2019). The term biotope is used interchangeably with habitat which is generally considered to represent the physical conditions that surround a species, a species population and an assemblage of species or community (Dimitrakopoulos and Troumbis, 2019). The definition adopted in 1997 by the European Union in the EUNIS habitat classification system (EUNIS Habitat Type Code Value; Davies et al., 2004) describes habitat as "a place where plants or animals normally live, characterized primarily by its physical features (topography, plant or animal physiognomy, soil characteristics, climate, water quality, etc.) and secondarily by the species of plants and animals that live there". In this approach, the definition combines both the abiotic characteristics of the environment and its biotic elements.

Coastal zone forms the interface between land and sea which induces high habitat heterogeneity and support diverse communities of vegetation and fauna. In the coastal environments benthic habitat can be defined as an area of the seabed that is distinct from its surrounding in terms of physical, biological and chemical variables which change in space and over time. Habitat is also considered physical space characterized by a combination of variables of different types in which species can survive (Whittaker et al., 1973). Many environmental factors including grain size of sediment, organic matter content in sediments and particulate suspended matter, taxonomic structure and biomass of benthic vegetation and water dynamics shape macrobenthic faunal communities even on small geographical scale. This set of various environmental variables affect also distribution, abundance and functioning of benthic animals (Kostylev et al., 2001; Cogan and Noji, 2007; Brown et al., 2011).

The coastal benthic habitats support species of diverse ecological traits and environmental requirements which maintain local biodiversity and offer essential goods and services for human wellbeing. In the coastal areas, benthic animals play an important role in organic matter transformation and transport, oxygen transport, nutrient cycling, secondary production, physical structuring and benthic pelagic coupling (Graf, 1992; Snelgrove, 1999; Mermillod-Blondin, 2011). Specifically, benthic invertebrates are primary consumers (herbivores and detritivores) that serve as food sources for higher trophic levels (e.g., predatory invertebrates, fish, birds, mammals) and are exploited commercially as harvested species (Vieira and Castello, 1997; Wilson and Fleeger, 2013). For primary consumers, shallow areas provide many food sources such as terrestrial-derived organic matter (Dias et. al., 2014), autochthonic phytoplankton (Yokoyama et. al, 2005) and benthic microalgae (Kang et al., 2003), and coastal macroalgae (Currin et al., 1995). The quality and quantity of basal organic matter sources have a major impact on secondary production, food web complexity and energy pathways (Rooney and McCann, 2011). Due to high variability of organic matter in coastal areas different trophic pathways may arise in benthic food webs (Hoffman et al., 2015). Pelagic pathways, which involve the consumption of phytoplankton and suspended particulate matter, are more efficient than benthic pathways which are based on the use of detritus representing a less labile source of organic matter (Rooney and McCann, 2011). Benthic productivity of an area is partially dependent on the amount of organic matter transferred from the pelagic to the benthic habitats via sedimentation (Hughes et al., 2000; Bergamino and Richoux, 2015). In consequence, it can lead to an increase in estuarine secondary production and food web stability (Huxel and McCann, 1998). Due to the fact that benthic primary consumers can utilize a variety of food sources (Keats et al., 2004) and their diet is directly linked to feeding habits, identifying their respective contributions to trophic links in a given system or habitat remains difficult. This is because some carbon forms can be transported over long distances and because the diets of consumers can vary with endogenic development and nutritional conditions even on small spatial scales (Guest et al., 2004). Previous studies showed that the diet of benthic consumers in coastal ecosystems can be affected by spatial differences in the primary organic matter sources of phytoplankton and detritus (Keats et al., 2004), the relative abundance of seagrass or macroalgae (Olsen et al., 2011) and the quality and availability of animal prey (Fox et al., 2009). Moreover, terrestrial organic matter, phytoplankton and submerged aquatic vegetation all can support benthic faunal communities by providing various food resources which nourish primary consumers in benthic food webs (Bergamino and Richoux, 2014). In addition, benthic vegetation can serve as an indirect food source for benthic fauna in the form of decaying organic matter that enters the sediment detritus pool and changes it composition (Dubois et al., 2012). Due to low palatability and nutritional quality (high C/N ratio) (Michel et al., 20214) vascular plants are considered to be of little trophic importance in the food web but they can exert indirect effect by creating complex substrate for epiphytic algae or enhancing carbon storage in sediment (Jankowska, 2017).

Analyses of stable isotope ratios (SIA) proved useful in ecological studies on the origin of organic matter and reconstructing trophic linkages and energy flows in marine systems.

Stable isotope analysis (mainly $\delta^{13}C$ and $\delta^{15}N$) is a common tool in trophic ecology as it provides a time-integrated measure of the material assimilated by organisms and reflects the proportional use of different carbon sources. The distribution of the isotopes in animal's body is closely related to the isotopic composition of its diet. Incorporation of ingested food into the consumer tissues induces transformation of isotopic ratios (so called trophic fractionation) with enrichment in heavier isotopic forms (e.g., ^{13}C and ^{15}N). ^{13}C varies strongly across primary resources and is therefore useful for differentiating among various organic matter sources, thus enabling tracking of a consumer's diet (DeNiro and Epstein, 1978). $\delta^{15}N$ is employed to define trophic position of an animal in the food web given stepwise enrichment factor when moving up trophic levels (Minagawa and Wada, 1984). The general enrichment factor is estimated to be 0-1‰ per trophic level for carbon and 3-4‰ for nitrogen (Fry, 1988). The use of stable isotope approach to define trophic groups and their trophic links contributes also to delineating ecological functioning of communities (Gray and Elliot, 2009). In this thesis, combining community indices (species richness, abundance, biomass, diversity) with characteristics of trophic groups (such as feeding mode determined by measurements of ratio of carbon and nitrogen stable isotopes) proved a comprehensive method of description of community functioning and was used to define functional (trophic) relationship among species. Moreover, food web approaches provide an opportunity to bridge the gap between community ecology and ecosystem ecology to highlight small-scale variations related to habitats (Thompson et al., 2012; Gravel et al., 2019). Furthermore, the community-level metrics and the calculation of the standard ellipse area under the Bayesian framework allowed comparative studies on community trophic structure across different temporal and spatial scales (Jackson et al., 2011).

Because of strong natural geological, physical and chemical factors harsh ecological conditions are created in some marine water-basins resulting in clear environmental gradients and naturally low diversity, for example in the Baltic Sea. (Gray and Elliot, 2009). The Baltic is the second largest brackish area and a semi-enclosed sea with limited water exchange with the North Sea. The Baltic is often regarded as the most studied area in the world (Chen, 2010). This is also a result of the well-known history of human exploration of the sea and in modern times, well-coordinated collaborative monitoring and legislative effort (HELCOM, 2010). Species diversity is low relative to fully marine areas and ecological characteristics and status of the Baltic species are generally well recognized (Ojaaver et. al., 2010). Due to the higher environmental heterogeneity, the coastal areas of the Baltic host taxonomically and functionally richer plant and faunal assemblages than the open sea areas (Bonsdorff and Pearson, 1999). For example, in the coastal zone of the southern Baltic Sea several types of habitats can be found i.e., species-rich seagrass meadows and macroalgae, deeper muddy anoxic sediments and shallow well-sorted sandy sediments. In a small shallow basin like the Puck Lagoon, geographical variations of environmental variables (e.g., salinity, nutrients, temperature, granulometry, sediment organic matter content) create patches of habitats which are not static in time and can vary on seasonal and spatial scale. Variety of habitats in the lagoon results also from postglacial history of this area and the seabed of shallow parts reflects the lacustrine and reparian accumulation relicts (Sokołowski et al., 2021). The patchy geomorphological structure and benthic vegetation mosaics in this low diversity system form an important reservoirs for local biodiversity. The Puck Lagoon in one of the most valuable part of the Polish Marine Areas (Węsławski et al., 2009) and belong to Special Protection Area (PHL 220032) in Nature 2000 programme. Only one study addressed so far the link between community indices and benthic food web structure in the lagoon but was limited to seasonal changes in the density of the seagrass meadows (Jankowska et. al., 2019). Relations of the structure and functioning of macrofaunal assemblages to environmental conditions (e.g., basic geological variables of surface sediments, hydrological parameters, and the structure of benthic vegetation) across benthic habitats have not been studied yet.The main aim of this thesis was to determine spatial and temporal variation of macrobenthic community in relation to habitat type in a brackish, low-diversity system of the Puck Lagoon. More specifically, taxonomic composition and abundance, biomass and trophic structure of macrobenthic communities were determined along with their variability across different benthic habitat types and over seasons. By combining community analysis and stable isotope measurements it was possible to define spatio-temporal links between biocentoic and functional (trophic) indices. The first part of the study investigated which environmental abiotic and biotic attributes shape faunal community patterns. The second aim of the thesis was to reconstruct trophic links in the benthic communities in different habitats and examine how basal carbon resources vary spatially and over time. The third part of this thesis aimed at describing spatio-temporal changes of trophic diversity and trophic redundancy of the macrofaunal communities and their relationship with taxonomic diversity and habitat characteristics. The results obtained might be of importance for better understanding mechanisms that drive spatial and seasonal variations of macrobenthic faunal communities and can contribute to development of conservation programmers of coastal biodiversity and restoration of degraded ecosystems.

Chapter 2. Research objectives of the thesis

The research hypotheses postulated in this thesis were:

1. Community structure of macrobenthic fauna in the coastal areas is shaped by habitat-related abiotic and biological factors **(Paper 1)**
   a) Species richness and biomass of macrophyte are an essential biotic factor for habitat classification at local scale.
2. Macrobenthic communities occupying different habitats are based on distinct basal resources **(Paper 2)**
   a) The $\delta^{13}C$ and $\delta^{15}N$ of basal resources differ among closely-located benthic habitats
   b) Consumer $\delta^{13}C$ and $\delta^{15}N$ vary among different habitat types
   c) The structure of benthic communities, specifically the relative biomass of dominant consumers, affects carbon flows through benthic food webs
3. Food web attributes of macrobenthic communities differ in relation to habitat type **(Paper 3)**
   a) Trophic diversity and redundancy vary among macrofaunal communities which are fueled by different organic matter sources
   b) Benthic communities vary in niche space of trophic groups in space and over time
   c) Community-wide metrics of the faunal communities are related to their taxonomic diversity.

Chapter 3. List of papers comprising the thesis

Paper 1.

Sokołowski A., Ziółkowska M., Zgrundo A., 2015. Habitat related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea). Journal of Sea Research, 103, 93–102.
https://doi. org/10.1016/j.seares.2015.06.017.
Own contribution - 45%
IF: 2.287, 5-years IF: 2.033, Polish Ministry of Education and Science points: 70

Paper 2.

Ziółkowska M., Sokołowski A., Richard P., 2018. Spatial and temporal variability of organic matter sources and food web structure across benthic habitats in a low diversity system (southern Baltic Sea). Journal of Sea Research 141, 47–60.
https://doi.org/10.1016/j.seares.2018.05.007.
Own contribution - 80 %
IF: 2.287, 5-years IF: 2.033, Polish Ministry of Education and Science points: 70

Paper 3.

Ziółkowska M., Sokołowski A., 2022. Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics. Estuarine Coastal and Shelf Science 274, 1–14.
https://doi.org/10.1016/j.ecss.2022.107931.
Own contribution - 85%
IF: 3.229, 5-years IF: 2.93, Polish Ministry of Education and Science points: 100

Summary indices of all papers: IF: 7,803; 5-years IF:6,996; Polish Ministry of Education and Science points: 240

Chapter 4. Materials and methods

4.1 Study sites

This study was conducted in the Puck Lagoon, a semi-enclosed water body in the eastern part of the Gulf of Gdańsk, southern Baltic Sea, Poland. It has an area of 104.8 km^2 and a mean depth of 3.2 m. This low salinity lagoon is a productive ecosystem with local vertical water mixing and nutrients loading from the Płutnica and Reda rivers (Gic-Grusza et al., 2009). It is a hydrogeologically and ecologically diverse environment, featuring various benthic habitats, such as bare sands, macroalgae-dominated sediments, and *Zostera* and *Chara* meadows (Gic-Grusza et al., 2009). The lagoon offers thus a good environment in which to study small-scale system response to changing environmental conditions and to make predictions on potential effects of natural and human-induced impacts.

Samples were collected seasonally over 10 months from October 2010 to July 2011 from four sites (A, B, C and D) that were selected based on sediment properties, the presence of benthic vegetation and potential organic matter sources. The sites were chosen in areas where habitat attributes were well defined, distinct and represented typical benthic habitat types in the lagoon (Gic-Grusza et al., 2009). Site A was sand adjacent to the Rybitwia Mielizna sand bank in the outer part of the lagoon; site B had sandy sediments with extensive peat outcrops near the Płutnica River; site C was a very shallow vegetated sand and site D was located in the Reda River plume in the outer part of the lagoon (Fig.1).

4.2. Habitat classification and description

To identify habitat-related abiotic and biological factors, the following attributes were measured to classify environmental conditions at the selected sites: water depth, parameters in the overlying bottom water: concentration of chlorophyll a (chla a), total suspended particular matter (TPM), temperature, salinity and dissolved oxygen concentration, parameters of surface sediments: grain size, organic carbon content (SOC; %), nitrogen organic content (SON; %), C/N_{sed} ratio, taxonomic structure and biomass of macrophytes **(Paper 1)**. Macrobenthic plants and fauna (>1.0 mm) were collected in triplicate with a Van Veen grab (catch area 0.1 m^2) following the HELCOM recommendation (HELCOM, 2003). After sampling, plants and fauna were kept alive in oxygenated sea water taken *in situ* and were not preserved as they were further analyzed for carbon and nitrogen stable isotope analysis.

In laboratory, the sediments were gently sieved through a 1 mm mesh size net to remove organic and inorganic debris, and to sort out the macrobenthic organisms (HELCOM, 2003).

The benthic animals were identified to the species level within two days of collection, except for gammarids, the isopod *Jaera*, and the spionid *Streblospio*, which were identified to the genus. In addition, insects were classified as either the *Chaoboridae* or *Chironomidae* family (larvae), while turbellarians and oligochaetes were classified to the class. The nomenclature followed AlgaeBase (www.algaebase.org) and the World Register of Marine Species (WoRMS, www.marinespecies.org). The abundance of each taxonomic group was determined by counting the individuals. Colonies of colonial species, such as bryozoans, were counted as a single individual. Exoskeleton-bearing animals, such as bivalves and gastropods, were dissected and their individual soft tissues (bivalves, gastropods) were freeze-dried to determine their individual soft tissue dry weight (DW). The species richness (S, total number of species per sample), abundance, and biomass of each faunal taxon were calculated to provide a descriptive overview of the benthic communities.

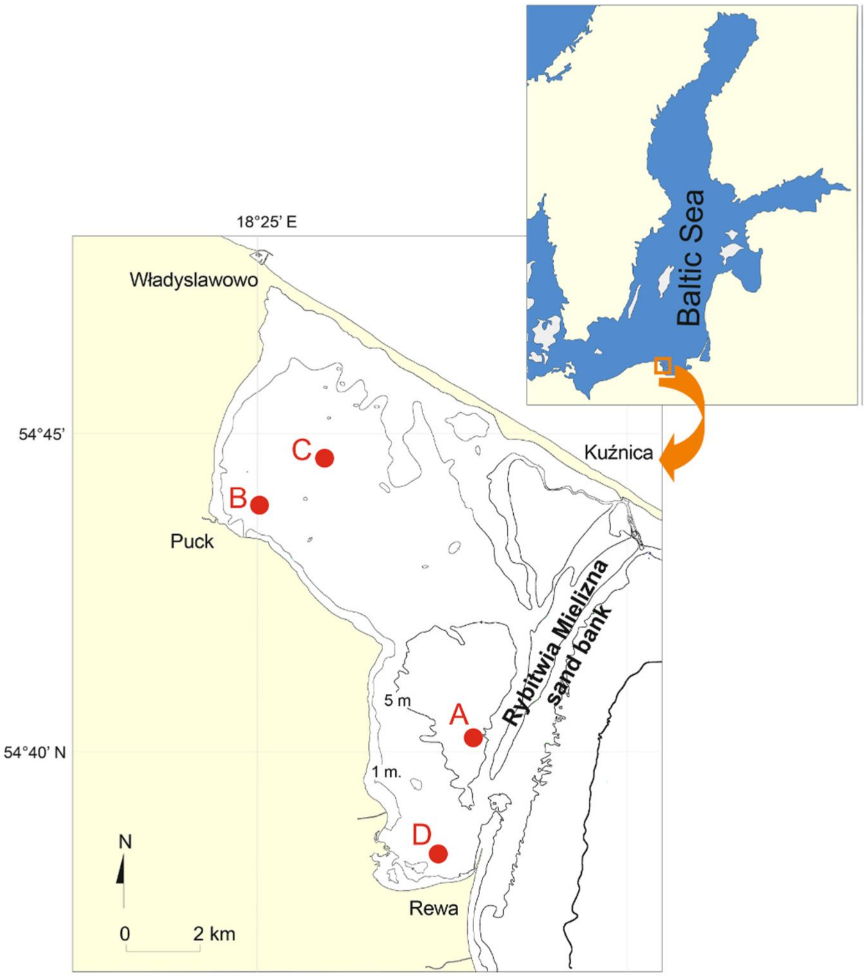

Fig. 1. Location of sampling sites in the Puck Lagoon (southern Baltic Sea) (after Sokołowski et al., 2015).

4.3. Sampling procedure and isotope analyses

The following living and non-living ecosystem components were collected to delineate the trophic organization of benthic communities at the sampling sites using stable isotope approach: suspended particular organic matter (SPOM), sediment organic matter (SOM), phytoplankton, macroflora, macrobenthic and meiobenthic organisms, epiphytes and fishes **(Paper 2 - 3).** Seawater was sampled using a 5 dm^3 GoFlo water sampler and SPOM was collected by filtering water through precombusted (450 °C, 8 h) and preweighed Whatman GF/F filters (glass microfibre filters; 0.7 µm) under a moderate vacuum on a standard filtration system. Surface sediments (0–10 cm) were sampled in triplicate with a Van Veen grab and stored in high-density polyethylene bags at −20°C until analysis. Phytoplankton 25–100 µm in size was collected vertically from above the bottom to the water surface with a WP2 net with 25 µm mesh (diameter 57 cm). The material collected was then sieved gently through 1 mm and 125 µm mesh nets to remove larger free-floating items such as macroalgal thalli, leaves and debris. Subsequently, the material was filtered through Whatman GF/F, stored in polyethylene vial and frozen at−20 °C. Macrofauna (> 1 mm size) and macrobenthic vegetation were collected in triplicate with a Van Veen grab and by dredging with a rectangular bottom dredge (30 × 50 cm with a 1 mm internal mesh net). In addition, benthic fishes were caught with a hoop net that was deployed in site A and B in the summer of 2011.

Five replicates of sediment samples were collected using a Van Veen grab to obtain meiofauna. The top 2 cm of sediment and a 2 cm layer of the overlying bottom water were sieved through a 125 µm mesh net and the aliquot was placed in a collective container. A modified extraction method based on the active downward migration of the meiofauna through sediments (Rzeznik-Orignac et al., 2004) was used. The pooled samples were then centrifuged and stored frozen (−20 °C) until further processing.

For each habitat and sampling event, epiphytes were collected from the vascular plants and macroalgae. To separate them from the host plants, they were put in an ultrasonic bath. The water with the detached organisms was filtered with Whatman GF/F filters on a filtration system, and the filters were kept frozen at −20 °C.

The samples for isotopic analysis were freeze-dried and acidified when necessary. Filters with suspended particulate matter and epiphytes were acidified overnight with 0.1 N HCl while sediment and fauna containing encrusted components such as crustaceans, fishes, gastropods and bivalves were acidified overnight with 1.0 N HCl. After acidification, all samples were frozen (−20 °C) and freeze-dried again. The top-most surface of the filters was gently scrubbed off and special care was taken to avoid collecting glass material that is known to affect the conversion of organic carbon to CO_2 during combustion (Boutton, 1991). The sediment samples were homogenized in a standard mortar, dry sieved through a polypropylene 63 µm mesh net and the aliquot was collected for stable isotope analysis. Benthic plants and animals were ground to a fine powder in a Retsch mixer mill MM 200. The stable isotope ratios of C and N were measured using an Isoprime Micromass IRMS-EA (a Micromass CHN analyzer coupled with a Micromass mass spectrometer) that provides simultaneous data on carbon and nitrogen content. Isotope composition was expressed in standard δ units (‰). Replicate analyses of standards permitted calculation of precision (analytical error; SD) for the overall procedure (i.e., sample preparation and analysis) of ± 0.1‰ for carbon and ± 0.2‰ for nitrogen.

4.4. Data analysis

Different statistical methods were used to analyze benthic communities. They were based on various types of data: environmental data, number of taxa and biomass of macrobenthic vegetation, number of taxa, abundance and biomass of macrofauna as well as carbon and nitrogen contents and stable isotope ratios of C and N of potential food sources and their consumers. A short description of statistical analysis employed is given below.

In Paper 1 the analyses of normality (the Kolmogorov–Smirnov test for goodness of fit) and homogeneity of variances (the Levene's test) were performed as prerequisites to the parametric approach. Abundance (macrofauna) and biomass (macroplants and macrofauna) were converted to units per m^2 (individuals m^{-2} and g m^{-2}, respectively) based on the surface area of the grab. The significance of individual differences between data groups was checked with ANOVA followed by the Bonferroni post-hoc test (α/n) when F was significant. The functional relation between pairs of variables was described with Pearson correlation analysis. Multivariate and univariate analyses were conducted on square-root-transformed grab data (abundance - macrofauna) and biomass (macrofauna and macrophytes)) in order to reduce the dominance of major taxa, and the Bray–Curtis similarity matrix was used throughout with procedures in PRIMER 6.0 (Clarke and Gorley, 2006) and its add-on package PERMANOVA+ (Anderson et al., 2008). Patterns in species structure of plant and animal macrobenthos were presented with ordination non-parametric multidimensional scaling (nmMDS). Distance-based linear modeling (DistLM) with Adjusted R^2 selection criterion was performed to estimate the explained variation in macrophytal and macrofaunal assemblage structures accounted for by each environmental factor. The DistLM model for macrofauna included two additional factors related to plant communities: the number of taxa and biomass. Temporal variability of the relationship between vegetation and the abundance of associated fauna was examined using the two-way PERMANOVA+ model with fixed factors: season (5 levels; Season) and benthic macrophytes of high and low biomass (2 levels: sites B and C were assigned to habitats of massive vegetation while deeper sites A and D were assigned to habitats of poor vegetation; Plants)

In **Paper 2**, the statistical significance of differences in stable isotope ratios among potential food sources and consumers was assessed using the three-way PERMANOVA+ model based on a similarity matrix created from Euclidian distances among samples (Anderson et al., 2008). In order to estimate the proportion of sources that contributed to consumer diets, a Bayesian mixing model approach was applied using the Stable Isotope Analysis in R (SIAR) software package. In order to estimate source-specific invertebrate trophic enrichment factor (TEF) which is based on the isotopic ratio of the food sources: $\Delta\delta^{13}C=-0.113 \times \delta^{13}C_{sources}-1.916$ and $\Delta\delta^{15}N=-0.311 \times\delta^{15}N_{sources}+4.065$, the linear model for invertebrates from Caut et al. (2009) was used. To examine the trophic structure of benthic communities in different habitats, the $\delta^{15}N$ values of the consumers were converted to the relative trophic level (RTL) using the following question:

$$\mathrm{RLT} = \lambda + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{base}}{\Delta n}$$

where λ is the RTL of taxon used to estimate $\delta^{15}N_{base}$, Δ_n is the enrichment in ^{15}N per trophic level, and $\delta^{15}N_{consumer}$ is the direct measurement of $\delta^{15}N$ for the target taxon (Post, 2002). $\delta^{15}N_{base}$ was determined for taxa that met the following criteria: they shared the same habitat as the target species and they integrated the isotopic ratio of the food web on a scale large enough to minimize the effects of short-term variations (Post, 2002). Food chain length (FCL) was defined as the trophic position of the top predator, i.e., the taxon with the highest $\delta^{15}N$ value (Vander Zanden and Rasmussen, 2001).

The normality of the data was verified with the Shapiro-Wilk test and homogeneity of variance with the Levene's test. The functional relation between species richness and FCL (food chain length) was described with parametric Pearson correlation analysis.

In **Paper 3**, community-wide metrics were employed to assess isotopic niche of benthic communities based on the Layman concept (Layman et al., 2007) using package SIBER in R (Stable Isotope Bayesian Ellipses in R) by Jackson et al. (2011). Moreover isotopic indices which were proposed by Layman et al. (2007) were calculated to compere food web structure associated with different benthic habitats: $\delta^{15}N$ range (NR) provides information on the trophic length of the community; ^{13}C range (CR) gives an estimate of the diversity of basal resources;

mean distance to centroid (CD) provides additional information on niche width but also species spacing; mean nearest neighbor distance (MNND) is a measure of density and clustering of species within the community; standard deviation of the nearest neighbor distance (SDNND) forms a measure of evenness of spatial density and packing. In order to calculate niche space, the standard ellipse area SEAc was used which is less sensitive than total area (TA) proposed by Layman et al. (2007). Additionally, overlap in SEAc among benthic communities was calculated for each habitat and season (Jackson et al., 2011).

Chapter 5. Results and discussion

5. 1. Benthic habitat classification in relations to habitat attributes and macrofaunal community structure

In the nmMDS grouping pattern data on macrophytal biomass showed clear separation between the shallower part of the lagoon (sites C and B) and the deeper outer part (sites A and D). The sites C and B in the shallower inner part of lagoon are characterized by high macrophyte biomass of vascular plants (on average 23.2 ± 18.2 g m^{-2}, n = 5 with the dominance of the seagrass *Zostera marina* and the pondweed *Stuckenia pectinate* at site C and 21.2 ± 21.9 g m^{-2}, n = 5 with the dominance of *S. pectinate* at site B). The deeper outer part (sites A and D) showed low macrophyte biomass with the dominance of *Pylaiella littoralis* (on average 1.6 ± 2.9 g m^{-2}, n = 5) at site D and mixed composition of various plant taxa at site A (*Ectocarpus siliculosus, Pylaiella littoralis, Polisiphonia fucoides*). Additionally, distance-based linear modeling (DistLM) demonstrated that two abiotic factors i.e., water depth and C/N_{sed} ratio were most responsible for the spatial differences in the macrophytal assemblage pattern. Allowing for geographical variation of macrophyte biomass and the environmental factors (depth and C/N_{sed} ratio) diagnostic taxa of macrophytes (*Stuckenia* spp., *Chara* spp., *Cladophora* sp. and *Pylailella littoralis*.) have been specified for each sampling site. Taking all above factors into account, the modified EUNIS habitat classification system (Davies et al., 2004) was applied which is based on the following attributes: 1) major granulometric structure of the sediment; 2) local environmental conditions and 3) species composition and biomass of benthic macrophytes. The habitats described in the Puck Lagoon had similar environmental variables but differed substantially in water depth, macrophyte biomass and composition, and sediment quality which led to identification of four benthic habitats with the following characteristic species: 1) sand with little mixed vegetation (habitat A), (2) *Stuckenia*-dominated sediment (habitat B), (3) *Chara*/*Cladophora* sediment (habitat C), and (4) sand with little *Pylaiella* (habitat D) (Fig. 1) **(Paper 1)**. In 2019 the EUNIS system was revised with recoding and renaming the habitat units at levels 1 to 3 (https://www.eea.europa.eu). This revision removed overlaps in definitions of types and extended the typology to all European seas (Chytrý et al., 2019; Sokołowski et al., 2021). The EUNIS 2019 system is based on a criteria that are similar to those in the EUNIS 2004 system (e.g., information on environmental conditions in the area such as water depth, granulometry of surface sediments, hydrological parameters, and macrophyte species composition and biomass; Chytrý et al. (2019) and does not induce large modifications in habit definitions.

Macrobenthic faunal communities in the Puck Lagoon differed significantly in species richness (ANOVA, $F_{3,20}$=15.61, p=0.001), abundance (ANOVA, $F_{3,60}$=8.69, p=0.001) and biomass (ANOVA, $F_{3,60}$=9.86, p=0.001) **(Paper 1)**. Sand with little mixed vegetation (habitat A) and sand with little *Pylaiella* (habitat D) demonstrated relatively high abundance (mostly of gastropods *Peringia ulvae*) and biomass of macrofauna (mainly the infaunal Baltic clam, *Macoma balthica*, the soft shell clam *Mya arenaria* and the cockle *Cerastoderma glaucum*). *Chara*/*Cladophora* sediment (habitat C) did not differ in terms of macrofaunal abundance but had much lower biomass that those at sites A and D. The community occupying this habitat were composed of crustaceans (*Gammarus* spp., *Idotea chelipes*, *Palaemon adspersus*, *Rhithropanopeus harrisii*). The second habitat with high biomass vegetation but higher C/N_{sed} (site B) supported less taxonomically diverse community that was dominated numerically by insect larvae. In addition, distance-based linear modeling (DistLM) demonstrated that habitat related specific abiotic and biotic factors such TPM, depth and biomass of macrophytes have significant impact on the macrofaunal community structure **(Paper 1)**. Interestingly, the effect of macrophytes on the abundance of macrobenthic faunal communities persisted throughout the year with the strongest influence in summer which corresponds to the previous studies by Włodarska-Kowalczuk et al. (2014). It can be therefore concluded that macrobenthic vegetation has a positive effect on macrofaunal taxonomic structure by creating complex spatial structure that promoted diverse fauna, particularly in summer.

5.2. Macrobenthic community trophic structure and trophic pathways in different habitats

In order to achieve the second research goal, it was necessary to answer the question how basal resources vary among habitats. The isotopic analysis of potential food sources showed that individual organic matter sources varied spatially and over time with similar seasonal patterns in all habitats in most cases. Despite of the close geographical proximity of the habitats studied (from 2 to 12 km), habitat-related differences in stable carbon and nitrogen isotope ratios of potential food sources were apparent. Generally, the carbon isotope ratio of SPOM in four benthic habitats were lower than those observed in other regions of the Baltic Sea (e.g. Rolff, 2000; Nordstrom et al., 2009) because $\delta^{13}C$ of SPOM of the Puck Lagoon reflected a large input of allochthonous organic matter from local rivers and anthropogenic sources (Sokołowski, 2009). Interestingly, in all habitats SPOM was more depleted in spring likely due to the increased freshwater discharge of organic matter (from −27.2‰ to −27.9‰) from the local rivers and surface runoff which corresponds to more terrestrial origin of SPOM. Because of hydrodynamics (waves and currents) are not intense here and vertical mixing in the water column is limited, the SPOM deposition rate is high (Uścinowicz, 2011) which strongly affects sediment isotopic ratios. The SOM $\delta^{13}C$ was much lower than typical values for estuarine sediments (Thornton and McManus, 1994; Cifuentes et al., 1996). Similar values of SOM $\delta^{13}C$ in the lagoon was also reported by Szczepanek et al. (2021). Generally, SOM $\delta^{13}C$ in the Puck Lagoon is driven by depleted, terrestrially derived organic matter that is transported by local rivers and strongly enriched submerged vegetation (Pempkowiak, 2020; Sokołowski, 2009). Both carbon and nitrogen stable isotope ratios in the sediments (SOM) varied spatially among the habitats and over time. SOM in the lagoon was composed of a mixture of SPOM and phytoplankton in different proportions (contribution of both >50%) with substantial local input of benthic macroalgae and vascular plants. A dominating contribution of SPOM and phytoplankton to sediment organic matter pool showed strong benthic-pelagic coupling. This pattern was constant during all seasons so, SPOM and phytoplankton provide the most important food sources for benthic species over a year. Due to the fact that in temperate areas the coupling between phytoplankton blooms and zooplankton blooms is delayed (Gray and Elliot, 2009) and nutrient concentration in the Puck Lagoon is relatively high (Dybowski and Dzierzbicka – Głowacka, 2023) much of plant material sinks to the seabed. In areas with high biomass of macrophytes, ^{13}C-enriched SOM was found in the *Chara*/*Cladophora* dominated sediment (habitat C) suggesting that plant tissues were an important component of the sediment detrital pool (up to 20%). A large percentage contribution of benthic plants to SOM (max. 19%) was also noted in *Stuckenia*-dominated sediment (habitat B) but SOM $\delta^{13}C$ was much depleted there than it could be expected. Depleted $\delta^{13}C$ and the poor SOM quality in this area likely result from terrestrial organic matter input from the Płutnica River which tent to support benthic communities of low taxonomic diversity and biomass (**Paper 1-2**). The quality of terrestrial particular organic carbon (TPOC) has been reported by Brett et al. (2009) who indicated that TPOC was a very poor quality carbon resource compared to allochthonous organic matter such as cryptophytes, diatoms, and chlorophytes. The SOM of sandy bottoms with little vegetation (habitats A and D) had intermediate $\delta^{13}C$ values but $\delta^{15}N$ was clearly higher than in other habitats which was probably caused by higher SPOM $\delta^{15}N$ and by decomposing floating macroalgae that entered the sediment pool (Dubois et al., 2012).

Benthic vegetation, water depth and TPM were important factors affecting community structure **(Paper 1)** and utilization of different food sources by macrofauna in the Puck Lagoon **(Paper 2)**. In this study, consumer isotopic ratios varied among taxa and habitats suggesting that different carbon sources supported local food webs in different areas. Benthic invertebrates in the lagoon assimilated carbon mainly from the pool available in their habitats as evidenced by the similar $\delta^{13}C$ values of consumers and the available food sources in in the occupied habitat. Additionally, comparisons of the $\delta^{13}C$ and $\delta^{15}N$ of consumers from different habitats revealed species-specific stable isotope ratios. For example, in habitat C the typical grazing gastropod *P. ulvae* had very high $\delta^{13}C$ values and low $\delta^{15}N$ values which mirrored the increased SOM $\delta^{13}C$ and decreased $\delta^{15}N$ in this habitat. In contrast, the low *P. ulvae* $\delta^{13}C$ values in habitats A and D were consistent with those of the benthic macroalgae and epiphytes in the vegetative season i.e., spring-summer **(Paper 2)**.

One of the concerns in the present ecological studies is understanding the link between diversity, structure and function of communities and in particular how important are the species for the functioning of the benthic systems. Delineating the role each species plays in the ecosystem can be achieved by defining trophic groups which is a set of species having the same function in the food web. Based on energy flow models it is reasonable to presume that the importance of given trophic groups are related to the dominant component species in terms of biomass and/or abundance. Combining biomass of dominant macrofaunal taxa with their carbon and nitrogen isotopic ratios revealed thus the most important trophic groups in the Puck Lagoon, that are represented by set of species, and the main trophic pathways within benthic communities in each habitat **(Paper 2)**. On sandy bottoms with little vegetation (habitats A and D) a large part of biomass was accumulated in suspension feeders (*M. trossulus, C. glaucum* and *M. arenaria*), which were the main primary consumers in the first trophic pathway, and suspension/deposit feeders (*M. balthica*) which together with the omnivorous *H. diversicolor* and the herbivorous *P. ulvae* formed the second pathway of energy transfer. It cab be concluded that the suspension feeders play a major role in pelagic-benthic coupling and in the carbon flow shallow sandy ecosystems, modulating the cycling of nutrients and moving carbon from the pelagic to the benthic realm and *vice versa* (Gili and Coma, 1998). In the Puck Lagoon a significant share of the phytoplankton stock is consumed by benthic suspension feeders, the phenomenon being also observed in Gulf of Riga, the eastern Baltic Sea (Orav-Kotta, 2004) and other estuaries (Dias et al., 2023). In sandy bottom habitats SPOM and phytoplankton were the dominant basal organic carbon resources and three species of suspension feeders (*M. trossulus, C. glaucum* and *M. arenaria*) appeared to control the phytoplankton biomass. The second trophic pathway was based on SOM which provided the main organic matter source for suspension-deposit feeders (*M. balthica*) and omnivores (*H. diversicolor*). During the vegetative season macroalgae with epiphytes also supported consumers and were mostly assimilated by *P. ulvae*. Due to the fact that *P. ulvae* formed assemblages of relatively high biomass in the both habitats **(Paper 1)** and the gastropod shows high trophic plasticity (Riera, 2009), the role of the gastropods in transferring organic matter to higher trophic levels might be substantial. The effect of this small herbivorous hydrobiid, that feed on periphyton associated with macrophytes (Haubois et al. 2005; Papas, 2007), on coastal benthic system is well recognized as an important link in the estuarine food webs (Fenchel, 1975; Dolbeth et al., 2007). In general, benthic macroalgae were of minor importance although their overall percentage contribution to the benthic fauna diet increased in summer up to 27% and 17% in habitats A and D, respectively.

On sediments with a large benthic vegetation biomass (habitats B and C), basal resources were utilized by consumers in a different way. Although *Stuckenia*-dominated sediment (habitat B) was characterized by high biomass of *S. pectinata* and the resident benthic fauna was composed mainly of omnivores (Chironomidae larvae) and herbivores (*T. fluviatilis*, *L. peregra*), the main food sources were SOM and macroalgae throughout the year. The gastropods *T. fluviatilis* and *L. peregra* utilized mainly vascular plants in autumn and summer (19% and 20% of their diet, respectively) and epiphyte consumption was highest in spring (12%) and summer (10%) when *L. hookeri* and *T. fluviatilis* occurred abundantly.

In *Chara*/*Cladophora* sediment (habitat C) different basal resources were utilized more evenly. Benthic primary production was transferred to the first trophic level mainly by small grazers (*P. ulvae, T. fluviatilis, I. chelipes, Gammarus* spp.) that consumed SOM (except *I.*

chelipes), macroalgae, epiphytes and to a limited extent also vascular plants. This food chain created the first trophic pathway in the community. Vascular plants did not appear to be a dominant carbon source for the primary consumers but their tissues provide suitable substrata for numerous epiphytes and macroalgae (e.g., *C. glomerata* which developed on its blades and roots). SPOM and phytoplankton supported suspension/deposit feeders (*C. glaucum, M. balthica, M. arenaria*) that formed the second trophic pathway. The biomass of small grazers (*P. ulvae, T. fluviatilis*, *Gammarus* spp., *I. chelipes*) was similar to that of suspension and suspension/deposit feeders (*C. glaucum, M. balthica, M. arenaria*) indicating that the contribution of plant material and SPOM/SOM to the first trophic level was similar (**Paper 2**).

Estimates of trophic position based on stable isotope ratios of nitrogen provide a measure of a consumer trophic level. In the Puck Lagoon, three trophic levels were identified in macrobenthic communities across all habitats. The longest food chain (FCL, maximum RTL) was detected in habitat C and the shortest in habitat A while intermediate RTLs were noted in the faunal communities in habitats B and C. On sandy bottoms with little vegetation (habitats A and D) the highest trophic position was occupied by gobies, *N. melanostomus* and *G. niger*, the brown shrimp *Crangon crangon* and *P. fluviatilis* (habitat A in summer) or *P. flesus* (habitat D in winter) **(Paper 2)**. Although macrobenthic communities from different habitats had different species richness and taxonomic composition **(Paper 1)**, no significant correlation was observed between the number of species and FCL (correlation analysis).

5.3. Trophic niche, diversity and redundancy of benthic communities in different habitats

It is widely known that both natural and human-induced disturbances affect species distribution and the quantity and quality of available food resources in the coastal areas which consequently leads to potential changes in the trophic structure of community (Gray and Elliot, 2009). In this study, the presence of high biomass of benthic macrophytes was proved to support directly and indirectly development of different trophic niches for consumers by diversifying basal carbon resources (**Paper 2-3**) and providing habitat structure **(Paper 1-3)**. In the Puck Lagoon high SEAc in habitats with massive vegetation (B and C) indicated food resources of different $\delta^{13}C$ and high trophic diversity of macrofaunal communities. An animal community with large isotope space (SEAc) might be composed of diverse trophic specialists (Bearhop et al., 2004) or might consists of trophic generalists that are able to shift among alternative food sources (Layman et al., 2007). Although communities in habitats with high plant biomass had lower species richness (**Paper 1**) the whole community utilized more diverse food resources and had relatively higher trophic diversity. Higher trophic diversity was also observed for some grazers which fed on distinct food items available on the bottom covered with dense vegetation (Jankowska et al., 2019) suggesting that this group was represented by trophic specialist. On the other hand, generalists such as omnivorous *R. harrisii*, which are able to shift among alternative food sources and thus increase CR range of the whole community, were also present e.g., in habitat C. The community at site C, which developed in habitat with dense macrophytal biomass and good quality of sediment organic matter, had the highest CR and NR indicating the widest diversification of basal resources and the longest trophic chain than other communities in the lagoon (CR = 4.3, n = 4; NR = 4.3, n = 4). Higher CR of particular feeding types was also observed by Szczepanek et. al. (2021) confirming that a larger variety of basal resources of varying $\delta^{13}C$ is used by consumers. Diversified organic matter sources resulted in higher variation of primary (small mobile invertebrates, particularly crustaceans and gastropods) and secondary consumers (larger crustaceans and benthic fishes) in this community (**Paper 2**). While grazers utilize preferentially microphytobenthos and epiphytes (**Paper 2**; Voigt and Hovel, 2019), omnivorous animals are able to consume many types of carbon resources and change diet depending on food availability and quality. Increased SEAc of omnivores suggests that they can exert a stabilizing effect on the food webs (Lawler and Morin, 1993; Fagan, 1997; Holyoak and Sachdev, 1998; Lalonde et al., 1999) as together with grazers form one energy pathways which fuel secondary consumers **(Paper 2**).

Communities from sandy bottom with low biomass of macrophytes showed smaller niche width (SEAc = 6,82‰^{2} n = 4 for habitat A and SEAc = 7,84 ‰^{2} n = 4 for habitat D) and CD suggesting more compact food webs of lower trophic diversity **(Paper 3).** This is likely due to less diversified organic matter sources and the limited availability of vegetation that develops only in the vegetative season (**Paper 1-2**). The trophic groups dominating in terms of biomass included suspension and suspension-deposit feeders (**Paper 2**) of small trophic niches. Suspension feeders relied on one dominant resource (SPOM and phytoplankton**)** which resulted here in simplification of food web structure with a large proportion of species with one feeding mode (**Paper 2-3)**. Moreover, high species richness of macrofaunal communities in sandy habitats with little vegetation **(Paper 1)** did not induce higher FCL because these communities were dominated by suspension feeders **(Paper 2)** which do not increase trophic diversity **(Paper 3)**. As a result, trophic niche space of the whole communities was more compressed with a concomitant increase in trophic redundancy. According to Sanders et. al. (2018) great trophic redundancy protects communities from the effects of biodiversity loss in response to habitat modifications or environmental disturbances because loss of one species can be compensated by other species. The communities showed also apparent variation in SEAc over time, individual values ranged from 4.37‰^{2} in sand with little *Pylaiella* in summer to 21.14‰^{2} in *Stuckenia*-dominated sediment in winter. Except habitat B, all communities showed reduced SEAc in a vegetative season (spring-summer) and a substantial increase of SEAc in a cold period (autumn-winter). This observation was not confirmed by Jankowska et. al. (2019) who showed that standard ellipses (SEAc) of communities between vegetated and unvegetated habitats were greater in winter than in summer. On the other hand, Jankowska et al. (2019) reported the same variation pattern of niche position of vegetated and unvegetated communities between summer and winter, and the greater relative overlap between the two standard ellipses for the two habitats in summer than in winter. This can support the hypothesis that in summer the macrobenthic faunal communities relied on the same food sources such as SPOM and phytoplankton as indicated by high trophic niche overlapped among the comunnities. For habitat *Chara*/*Cladophora* sediment (C) and *Stuckenia*-dominated sediment (B) widening of CR and NR in winter was related primarily to the presence of benthic fish that feed on variety of food sources of broad δ^{13}C and δ^{15}N range (**Paper 1-2**). The appearance of these secondary consumers, that show omnivorous and carnivorous feeding modes, increased temporarily local trophic diversity. In contrast, diversity at the base of food web (CR) in habitats B and C, and food chain length in habitat B decreased during a vegetative season and were accompanied by a decrease in trophic diversity. This was due to narrowed isotopic range of primary producers i.e., phytoplankton and macroalgae **(Paper 2**) which incorporated from the water biogenic substances of similar carbon and nitrogen isotopic ratios. The above observation was also noticed during spring for communities from all habitats when the overlap between SEAc's of communities were much lower than in cold period (autumn-winter). Specifically, the highest niche overlap (0.74) was observed between communities in habitats B and C in winter and the lowest (0.23) between communities occupying habitats B and D in summer **(Paper 3)**. The higher SEAc' overlap for all communities in spring results from fact that consumers exploited isotopically similar resources.

In order to link taxonomical diversity with food web structure, relationship between species richness and Bayesian indices was assessed. A positive correlation between the number of species (S) and both CR and NR provided evidence for the hypothesis that species-rich food webs utilize a wide range of organic matter resources and have longer food chains. These communities possess more trophic links and more links per species (linkage density; Yen et al., 2016) making them less susceptible to disturbances (Calizza et al., 2019). Taxonomically diverse assemblages with a variety of feeding strategies and food preferences, display thus higher levels of resilience to disturbance, including species loss, due to their greater redundancy. The presence of a large proportion of species with similar trophic ecologies also boosts the stability of trophic links in these faunal communities.

Chapter 6. Conclusions

The thesis identified dominant patterns of spatio-temporal variations in community composition and food web structure of four benthic macrofaunal communities in a low diversity, brackish system of the Puck Lagoon (the Gulf of Gdańsk, southern Baltic Sea). It was unrevealed strong association of environmental factors with macrobenthic community composition and trophic structure in different habitats. Linking the community indices with food web attributes provided a novel insight into how trophic structure is related to functional traits i.e., feeding interactions.

Based on macrophytal biomass and two environmental parameters i.e., water depth and C/N_{sed} ratio, four distinct benthic habitats were defined with the characteristic species: 1) sand with little mixed vegetation (habitat A), (2) *Stuckenia*-dominated sediment (habitat B), (3) *Chara*/*Cladophora* sediment (habitat C), and (4) sand with little *Pylaiella* (habitat D). The most influential factor was macrophyte biomass which strongly affected composition and structure of faunal communities in space and time. The effect of large biomass of macrophytes on the abundance of communities persisted throughout most of the year with the strongest influence in summer when macrophytes created complex spatial and nutritional structures.

In the Puck Lagoon, macrofaunal communities have access to a range of organic matter sources, including SPOM, phytoplankton (during the vegetative season) and SOM which includes considerable amounts of vascular plants and macroalgae in areas with high biomass vegetation. Benthic invertebrates feed primarily on the carbon sources, that are available in their habitats, and display species-specific stable carbon and nitrogen isotope ratios.

The presence of rich and dense macrophyte vegetation and sediment organic matter of high nutritive value (habitat C) supports a variety of consumers of different feeding modes, thus increasing the trophic niche size of the entire community. The nutritive value of the surface sediment in this habitat results primarily from the presence of deposited vascular plant tissues that form an important component of the sediment detrital pool. Although the plant organic matter is not a direct carbon source for the macrofauna it fuels primary consumers indirectly by providing a substrate for macroalgae and epiphytes which develop on their blades and roots.

In habitat C, SPOM and phytoplankton support suspension feeders while macroalgae and epiphytes promote grazers and omnivores, creating two parallel trophic pathways. Grazers actively consume epiphytes and macroalgae, preventing algal overgrowth. The increased availability and diversification of basal food resources support higher trophic diversity and resilience to disturbance.

Faunal communities inhabiting sandy bottoms with low macrophyte biomass (habitats A and D) have simpler food webs of lower trophic diversity. This is due to the reliance of benthic animals on a single resource, leading to a large proportion of species with the same feeding mode. In the faunal assemblages containing taxa of similar feeding strategies (high trophic redundancy) large proportion of species shares similar trophic ecologies, increasing stability of trophic links.

At a temporal scale, communities in habitats with high vegetation biomass have higher trophic diversity in winter and lower in spring and summer, while those in sandy habitats are more diverse in autumn. This is attributed to a wider range of organic matter sources and the presence of omnivorous and carnivorous fish that migrate to the shoreline in the cold season in habitats with high vegetation biomass

The results obtained can be used to support effective management strategies aimed at conserving the structure and functioning of ecological communities in light of ongoing environmental changes (natural and anthropogenic) and shifts in species distribution.

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Chapter 8. Habitat related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea)

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Habitat-related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea)

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ABSTRACT

Coastal areas provide a high variety of sedimentary habitats that influence the structure of resident fauna even on small geographical scales. Therefore, examinations of spatial variations in benthic assemblages require background knowledge of the environmental and biotic heterogeneity of habitats in order to understand ecological processes in such areas. The effect of habitat-related abiotic and biological variables on macrofaunal benthic assemblages was studied seasonally in 2010 and 2011 in the brackish, semi-enclosed Puck Lagoon (Gulf of Gdańsk, southern Baltic Sea). Based on macrophytal biomass, two discrete benthic regions were identified in the lagoon: a region of large biomass and a region of few macrophytes. The quality of the surface sediment organic matter (measured as C/N_{sed} ratio), depth, and benthic macrophyte composition accounted for within-region variation, which led to the identification of four habitats. Shallow sandy sediments with low C/N_{sed} ratios provide high quality sedimentary food for animals that, together with species-rich, dense macrophyte vegetation, support diverse assemblages. High C/N_{sed} ratios and peat outcrops in shallow sands exert a negative effect on macrofaunal diversity. Two deeper sandy habitats with less massive, species-poor vegetation tend to host distinct faunal assemblages of higher abundance and biomass. The importance of benthic vegetation for macrofaunal assemblages in the southern Baltic Sea is suggested to stem from its complex spatial structure that offers a number of microniches for infaunal and epifaunal species. The effect of macrophytes on benthic faunal assemblages was consistent throughout most of the year with the strongest influence in summer when macrophytes reached the highest biomass.

1. Introduction

Patchy geomorphological structure, variable water dynamics, and benthic vegetation mosaics all combine to ensure that sedimentary areas in shallow coastal water-basins encompass an array of benthic habitats that impact resident macrofaunal communities (Zajac et al., 2003). The patchy distribution of infauna and epifauna on the soft bottom is influenced by many environmental factors including grain size and organic carbon content in sediments and food quality and availability (Ramey and Bodnar, 2008). Geographical variability in the structure of benthic fauna is also related to biological properties such as habitat selection and food preferences (Snelgrove and Butman, 1994). This constraint imposed by natural geographical variation applies not only to large scale patterns (e.g., the UK coast; Bremner et al., 2006 and the deep Baltic Sea; Laine, 2003), but also to smaller scales within estuaries and semi-enclosed bays that often display high within-system variability of benthic properties (Boström and Bonsdorff, 1997; Zettler and Bick, 1996). On small scales, the presence and composition of macrophytes, particularly rooted vascular plants that are important habitat forming species, also influence zoobenthos (Connell and Gillanders, 2007). Moreover, seagrass beds have been shown to host taxonomically more diverse, abundant communities than adjacent bare sands (Battley et al., 2011; Włodarska-Kowalczuk et al., 2014), and they serve as vital reproduction and nursery systems for many invertebrates and fish species as well as feeding grounds for migratory birds. Thus, examinations of spatial variation in faunal assemblages require background data on the environmental and ecological heterogeneity of benthic habitats. Quantification of such assemblages with respect to habitat diversity provides clues about habitat-specific community structure (Fraschetti et al., 2005). Thus, detailed studies are necessary to describe local habitat variation. Further, they can be used to generate large-scale patterns (Irving et al., 2004; Wootton, 2001), and to detect the first alterations in faunal communities caused by environmental disturbances (Terlizzi et al., 2005).

In the Baltic Sea, areas with a variety of habitat types and the associated fauna include primarily sheltered bays, lagoons, and inlets in both the northern Baltic, e.g., the Gulf of Bothnia (Bergström et al., 2002) and the Åland archipelago (Boström and Bonsdorff, 1997), and in the southern Baltic, e.g., Puck Bay (Graca et al., 2004) and the Curonian Lagoon (Bubinas and Vaitonis, 2005). The Puck Lagoon (the inner part of Puck Bay) with a total area of 104.8 km^2 and a mean depth of

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3.2 m, is located in the western part of the Gulf of Gdańsk (southern Baltic Sea) and provides an exceptionally diverse environment covering a range of benthic habitats, i.e., bare sands, macroalgae dominated sands, *Zostera* beds, and *Chara* meadows (Gic-Grusza et al., 2009). The lagoon is also subject to varying degrees to nutrient loading from rivers and streams and to anthropogenic pressures (tourism, fishery, municipal effluents) that exert additional stress on benthic assemblages. Consequently, the lagoon is a good area in which to study fine-scale macrofaunal variations in relation to habitat conditions. A previous quantitative macrofaunal study in the Puck Lagoon showed high spatial variation in taxonomic diversity and abundance (Gic-Grusza et al., 2009). Specifically, polychaete-dominated communities were observed in the northwestern (inner) shallow (<3 m) zone, while bivalves and gastropods prevailed on unvegetated sands in the eastern (outer) part (e.g., Haque et al., 1997). The patchiness of sedimentary food resources and the presence of benthic vegetation coupled with nutrient loading are likely to influence the structure of the resident benthic communities. Patterns in macrofaunal assemblages related to habitat type remain, however, largely unexplored.

This study aimed to determine the geographical and temporal variability of macrofaunal assemblages in relation to benthic conditions (habitat type) in a brackish, low-diversity system in the southern Baltic Sea. By simultaneously quantifying basic geological variables of surface sediments, hydrological parameters, and the structure of benthic vegetation over a full seasonal cycle, the principal factors that are responsible for faunal assemblage patterns were identified. The consistency of the influence of benthic vegetation on macrofauna over time was also investigated. This paper focuses on the structure of macrobenthic communities as the first part of a larger study on the Puck Lagoon ecosystem, while trophic relations and other functional aspects will be addressed in other publications.

2. Material and methods

2.1. Field sampling

Sampling sites were selected based on the spatial distribution of sediment properties and benthic vegetation as well as potential organic matter sources to the lagoon. The sites were chosen in areas where habitat attributes were well-defined, distinct, and represented typical benthic habitat types in the lagoon (Gic-Grusza et al., 2009). Special care was taken to locate the sites in areas where environmental and ecological conditions were homogenous on a scale sufficient to avoid the influence on benthic macrofauna of small habitat mosaics within larger habitat types. Site A is sand adjacent to the Rybitwia Mielizna sand bank in the outer part of the lagoon; site B represents sandy sediments with extensive peat outcrops in the vicinity of the Płutnica River; site C is very shallow vegetated sand, while site D is located in the Reda River plume in the outer part of the lagoon (Table 1; Fig. 1). Samples of overlying bottom water, surface sediments, and macrobenthic organisms were collected at seasonal intervals (July 2010, October 2010, February/March 2011, May 2011, July 2011) over 13 months. Overlying bottom water was sampled in triplicate using a 5 dm^3 GoFlo water sampler at a constant height of 20 cm above the sea bottom to avoid sediment resuspension from sampler action. Water was filtered within 1 h after collection through Whatman GF/F filters (glass microfiber filters; 0.7 μm) on a standard filtration system for determinations of chlorophyll *a* concentrations (chl *a*) and total suspended particulate matter contents (TPM). Temperature (T), salinity (S), and dissolved oxygen concentrations (O_2) in the water were measured immediately after sampling with a WTW Universal Pocket Meter MultiLine P4 equipped with TetraCon 325 (accuracy 1.5%) and CellOx 325 (accuracy 1–5%) sensors. Surface sediments (0–10 cm) were sampled in triplicate with a Van Veen grab (0.1 m^2 catch surface area). The top 10 cm section is the fraction of sediment that most benthic invertebrates can penetrate, and is the biologically relevant portion of the sediment. On each sampling occasion, the vessel was anchored and the exact geographical position of the on-board working platform was monitored with a DGPS device during the grab operation so the horizontal distance among grab replicates at a given sampling site was <5 m. Macrobenthic plants and fauna (>1.0 mm) were collected in triplicate with a Van Veen grab. Using the grab ensured areal random sampling of floating and rooted macrophytes as well as epifaunal and infaunal species from exactly the same set of area of the bottom allowing quantitative analyses of both benthic vegetation and animals (Martin et al., 2013). The sediments were gently sieved through a 1 mm mesh size net to reduce the amount of sediment and inorganic debris, and to sort out the macrobenthic organisms (HELCOM, 2003). Plants and fauna (carnivores separately from other animals) were then kept alive in oxygenated Whatman GF/F filtered sea water taken in situ in a cool place. The

Table 1
Environmental and biological characteristics of the selected habitat types in the Puck Lagoon.

Site	A	B	C	D
Location in the lagoon	Adjacent to the Rybitwia Mielizna sand bank	Inner part; the vicinity of the Płutnica river	Inner part	The Reda river plume in the outer part
Depth (m)	5.2	3.6	2.6	4.2
Surface sediments				
Grain-size class	Fine-grained sand	Fine-grained sand	Fine-grained sand	Fine-grained sand
C_{org} content (SOC; %)[a]	1.8 ± 0.5	1.5 ± 0.5	3.2 ± 1.2	1.5 ± 0.3
N_{org} content (SON; %)[a]	0.24 ± 0.04	0.19 ± 0.10	0.45 ± 0.22	0.18 ± 0.07
C/N_{sed} ratio[a]	7.4 ± 2.0	9.0 ± 2.4	7.5 ± 1.2	8.6 ± 1.8
Overlying-bottom water				
T (°C)[a]	13.9 ± 7.4	14.0 ± 9.9	13.9 ± 10.2	15.2 ± 8.4
S[a]	6.5 ± 0.2	6.4 ± 0.2	6.5 ± 0.3	6.0 ± 0.1
TPM (mg dm^{-3})[a]	2.85 ± 1.99	6.12 ± 6.10	4.72 ± 3.45	3.70 ± 0.44
O_2 concentration (mg dm^{-3})[a]	8.1 ± 4.1	8.1 ± 3.9	8.3 ± 4.9	8.7 ± 2.8
Macrophytes				
Community structure	Mixed composition	*Stuckenia* dominance	*Zostera*/*Stuckenia* dominance	*Pylaiella* dominance
Biomass (g m^{-2})[a]	3.80 ± 5.71	21.18 ± 21.93	23.24 ± 18.17	1.62 ± 2.89
EUNIS classification (code)	Baltic level sandy bottoms of the infralittoral zone with little or no macrophyte vegetation (A5.211)	Sublittoral macrophyte-dominated sediment (A5.2)	Sublittoral macrophyte-dominated sediment (A5.2)	Baltic level sandy bottoms of the infralittoral zone with little or no macrophyte vegetation (A5.211)
Habitat type defined	Sandy bottom with little macroalgae of mixed species composition	Sublittoral *Stuckenia*-dominated sediment	Sublittoral *Chara*/*Cladophora*-dominated sediment	Sandy bottom with little *Pylaiella* vegetation

[a] Mean annual value and standard deviation based on seasonal measurements (n = 5).

Fig. 1. Location of sampling sites in the Puck Lagoon (southern Baltic Sea).

organisms were not preserved as they were further analyzed for carbon and nitrogen stable isotope composition. An extra Van Veen grab was taken on two occasions, i.e., in summer and fall 2010, for granulometric analyses.

2.2. Hydrological and geological variables

Chlorophyll *a* concentrations and TPM were analyzed according to standard methods recommended for marine waters. Granulometric analyses of surface sediments were performed using Gradistat 5.11 PL BETA software. The mud fraction (<63 μm) was further analyzed for the contents of sediment organic carbon (SOC), sediment organic nitrogen (SON), and the weight C/N_{sed} ratio (C/N_{sed} ratio) with a EUROVECTOR CHN analyzer.

2.3. Macrobenthic community structure of plants and fauna

Macrobenthic algae and vascular plants were identified to the lowest possible taxonomic level within two days of collection using the taxonomic key by Braune and Guiry (2011). The nomenclature followed AlgaeBase (www.algaebase.org) and the World Register of Marine Species (WoRMS, www.marinespecies.org). All representatives of identified taxa were freeze-dried to determine their biomass ($g\ m^{-2}$).

Benthic animals were identified alive within two days of collection to the species, except gammarids, the isopod *Jaera* and the spionid *Streblospio*, which were identified to the genus. In addition, insects were classified either as the family Chaoboridae or Chironomidae (larvae), while turbellarians and oligochaetes were classified to the class. Individuals from each taxonomic group were then counted to assess abundance. Each colony of colonial species such as bryozoans was counted as a single individual. Animals with exoskeletons, such as bivalves and gastropods, were dissected and whole individuals or individual soft tissues (bivalves, gastropods) were freeze-dried to determine individual soft tissue dry weight (DW). The species richness (*S*, total number of species per sample), abundance, and biomass of each faunal taxon were calculated to provide descriptive statistics of benthic communities.

2.4. Statistical analysis and habitat classification

Analyses of normality (the Kolmogorov–Smirnov test for goodness of fit) and homogeneity of variances (the Levene's test) were performed as prerequisites to the parametric approach. The significance of individual differences between data groups was checked with ANOVA followed by the Bonferroni post-hoc test (α/n) when F was significant. The functional relation between pairs of variables was described with Pearson correlation analysis.

Abundance (macrofauna) and biomass (macrofauna and macroplants) were converted to units per m^2 (individuals m^{-2} and g m^{-2}, respectively) based on the surface area of the grab. Multivariate and univariate analyses were conducted on square-root-transformed grab data (abundance and biomass) in order to reduce the dominance of major taxa, and the Bray–Curtis similarity matrix was used throughout with procedures in PRIMER 6.0 (Clarke and Gorley, 2006) and its add-on package PERMANOVA+ (Anderson et al., 2008). The exceptions were correlation analyses that were performed on square-root-transformed averaged data. Because of the different scales of the environmental data, they were normalized prior to analyses. Macroplant and macrofauna biomasses showed good relative discriminatory power and were used in further analyses to discriminate between benthic habitats. Patterns in plants and faunal macrobenthic species structure were presented with ordination non-parametric multidimensional scaling (nmMDS). Distance-based linear modeling (DistLM) with Adjusted R^2 selection criterion was performed to estimate the explained variation in macrophytal and macrofaunal assemblage structures accounted for by each environmental factor. The DistLM model for macrofauna included two additional factors related to plant communities: the number of taxa (taxveg) and biomass (bioveg). Since regression-based models are sensitive to intercorrelation among factors, environmental factors with a significant correlation of ≥0.9 were recorded (SOC and SON) and one of the correlated pair (SON) was discarded from the analysis. The significance of environmental factors in habitat delineation within the Adjusted R^2 model was then examined using marginal and sequential tests for the distance-based linear modeling procedure (Schulz et al., 2014). The direction and magnitude of the relationship between environmental variables and biological assemblages were presented visually in distance-based redundancy analysis (dbRDA) biplots. Benthic habitats, which were predefined by Gic-Grusza et al. (2009), were then verified based on nmMDS and DistLM, and indicator species analysis with the point biserial correlation coefficient (Pearson's *phi* coefficient of association) (Chytrý et al., 2002) for phytal biomass data corrected for unequal group size was conducted in R to determine the diagnostic species associated with each habitat (De Cáceres and Legendre, 2009). Dissimilarity values in the biomass data of macrobenthic plants among habitats were obtained with SIMPER analysis. Indicator species analysis was also used to determine the ecological preferences of faunal taxa among habitats (De Cáceres and Legendre, 2009). The temporal variability of the relationship between vegetation and the abundance of associated fauna was examined using the two-way PERMANOVA+ model with fixed factors: season (5 levels; Season) and benthic macrophytes of high and low biomass (2 levels: sites B and C were assigned to habitats of massive vegetation while deeper sites A and D were assigned to habitats of poor vegetation; Plants). When the interaction of Season × Plants was significant, pair-wise tests for differences between habitats of massive and poor vegetation within five seasons were performed. The p-level for all tests was set as <0.05.

Benthic habitats were classified using the modified EUNIS habitat classification system (Davies et al., 2004), which is based on the following attributes: (1) major granulometric structure of the sediments; (2) local environmental conditions and (3) species composition and biomass of benthic macrophytes. The nomenclature of the habitats identified was attributed to phytal diagnostic species. Although the HELCOM Underwater Biotope and habitat classification system, HELCOM HUB (HELCOM, 2013) was developed recently for the Baltic Sea and is applied successfully in some regions (e.g. Schiele et al., 2014), its classification criteria for benthic biotopes could not be met because of the lack of data on the coverage percentage of the bottom by macroscopic epibenthic flora and fauna (Level 4 — Functional characteristics) and on the height of the plants (Level 6 — Dominating taxon). Additionally, the HELCOM HUB system does not differentiate between macrophytes and epifauna at the classification mid-level, which was crucial in the present study to assess the effect of habitat-specific environmental variables and benthic vegetation on macrofaunal assemblage patterns.

3. Results

3.1. Hydrological and geological variables

The salinity of the overlying bottom water differed significantly among sites (ANOVA, $F_{3,20} = 5.85$, $p = 0.007$), with significantly lower salinity at site D than at sites A and C (Bonferroni post-hoc test, $p = 0.012$ and $p = 0.017$ for site A and C, respectively). Water temperature and chlorophyll *a* concentrations varied with season (ANOVA, $F_{4,20} = 122.51$, $p < 0.001$ and $F_{4,20} = 4.88$, $p = 0.01$ for T and chl *a*, respectively; Table 1 and Fig. A in Appendix A). Dissolved oxygen concentrations in the overlying bottom water did not vary geographically and ranged between 1.1 mg dm^{-3} and 12.5 mg dm^{-3}, i.e., within hypoxic and normoxic values. In the inner part of the Puck Lagoon, TPM had one major peak in winter (February) when maximums of 16.84 mg dm^{-3} and 10.63 mg dm^{-3} were recorded at sites B and C, respectively. In contrast, the maximum TPM in the outer part of the lagoon was in summer (6.23 mg dm^{-3} and 3.88 mg dm^{-3} at sites A and D, respectively). During intense biological production, the contribution of chl *a* (phytoplankton) to TPM was as high as 97.8% (site D), which suggests that phytoplankton was the principal source of organic matter in the water column. In the cold months, the contribution of phytoplankton diminished to 10.1–37.2%.

Grain-size analysis revealed a similarly high contribution of sand facies at sites A, C, and D (from 94.4% to 99.1%), but it was lower at site B (85.3%) (Table 1). The surface sediments in all parts of the lagoon were classified as moderately sorted fine-grained sand with medians ranging from 142.8 μm at site B to 231.1 μm at site D. The content of carbon and nitrogen in surface sediments varied significantly among sites (ANOVA, $F_{3,20} = 5.81$, $p = 0.008$ for SOC; $F_{3,20} = 4.56$, $p = 0.02$ for SON) with particularly elevated SOC and SON at site C (Bonferroni post-hoc test, $p = 0.018$ and $p = 0.039$ for SOC and SON, respectively). Surface sediments at site B showed an increased C/N_{sed} ratio relative to other sites (ANOVA, $F_{3,20} = 5.81$, $p = 0.008$).

3.2. Benthic macroplants as a habitat-forming factor

Eighteen macrophytal taxa were recorded, including 12 macroalgae from four classes, namely Charophyceae, Ulvophyceae, Phaeophyceae, and Florideophyceae and six angiosperms representing one class of Spermatopsida. Spermatopsida was represented by the highest number of taxa followed by Ulvophyceae (5 taxa), Charophyceae (3 taxa), and red algae Florideophyceae and brown algae Phaeophyceae (2 taxa each). The number of taxa (*ANOVA*, $F_{3,60} = 12.24$, $p < 0.001$) and total macrophyte biomass (ANOVA, $F_{3,60} = 4.88$, $p = 0.004$) varied spatially. Nearly a two-fold higher number of taxa was observed at sites C (9) and A (7) than at sites B and D (both 4 taxa; Table A in Appendix A). The macrophyte community at site C also showed the highest total biomass (on average 23.2 ± 18.2 g m^{-2}, $n = 5$) with the dominance of seagrass, *Zostera marina*, and pondweed, *Stuckenia pectinata*, which together comprised on average 78.2% of the total phytal biomass during the vegetative season (Fig. 2). A dense pondweed community was found at site B (average biomass 21.2 ± 21.9 g m^{-2}, $n = 5$) contributing on average 97.5% to the total biomass in spring-fall. The loose-lying, floating mats of brown algae, *Pylaiella littoralis*, occurred mostly at site D (77.6%), where total macrophyte biomass averaged 1.6 ± 2.9 g m^{-2} ($n = 5$). Low macrophytal biomass was also observed at site A (3.8 ± 5.7 g m^{-2}, $n = 5$) where benthic plants comprised various taxa of seasonally varying dominance, i.e., *Ectocarpus siliculosus* in summer 2010 (84.6%) and *P. littoralis* in spring 2011 (93.5%).

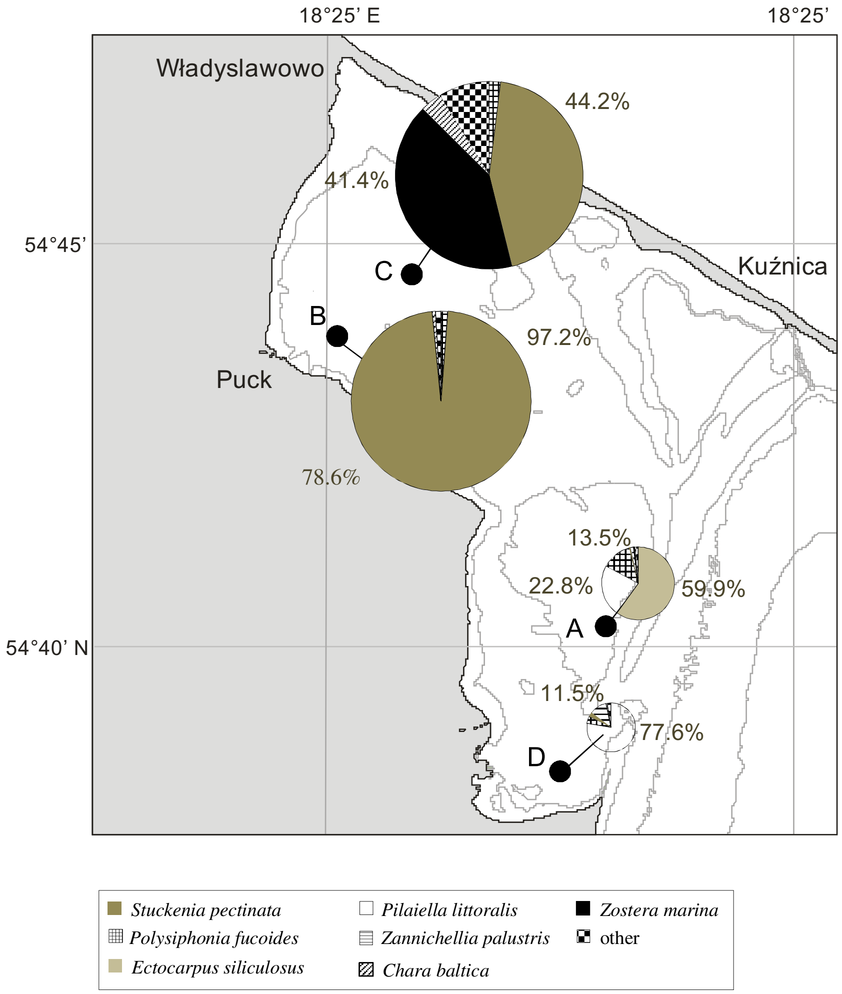

Fig. 2. Percentage contribution of different taxa to the total biomass of macrophytal communities in different habitats in the Puck Lagoon. Data are presented as means of all sampling seasons (n = 5). Diagrams are proportional to the respective total biomass. Numbers show percentage contribution >4.0%.

3.3. Benthic habitat classification

Only the analysis of macrophytal biomass data from all seasons and sites showed an nmMDS grouping pattern with clear separation between the shallower inner part of the lagoon (sites B and C) and the deeper outer part (sites A and D) (Fig. 3). Marginal and sequential tests in distance-based linear modeling (DistLM) demonstrated that two environmental factors, i.e., depth and C/N_{sed} ratio were significant in isolation (Table 2) for the Adjusted R^2 selection criterion. The adjusted R^2 model explained 32.6% of the total variation. The first two dbRDA axes explained 71.0% of the fitted variation (Fig. 4); the first dbRDA axis correlated with depth ($\rho = 0.861$), while the C/N_{sed} ratio correlated closely with the second axis ($\rho = 0.810$). These factors are most responsible for the spatial differences in the macrophytal assemblage patterns. The nmMDS grouping and DistLM model indicated two benthic regions in the Puck Lagoon corresponding to the following sampling sites: (1) shallow sublittoral sediments with large vegetation biomass (sites B and C), and (2) sandy bottom with little vegetation (sites A and D). By examining the point biserial correlation coefficient, however, different diagnostic species were associated with different sites, including *Ulva intestinalis*, *E. siliculosus*, *S. pectinata*, *Chara balthica*, *Cladophora glomerata*, and *P. littoralis* (Table 3a). Allowing for this taxonomic variation and geographical delineation by environmental factors (depth and C/N_{sed} ratio), four habitats were defined based on the modified EUNIS classification system:

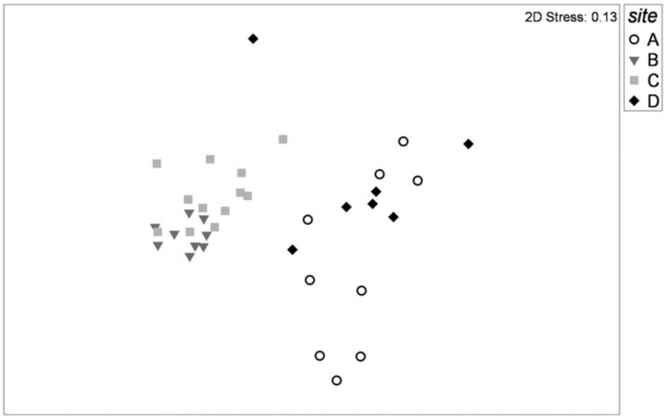

Fig. 3. Non-metric multidimensional scaling ordination (nmMDS plot) of macrophytal biomass (n = 37) in different habitats of the Puck Lagoon. Data were square-root-transformed prior to analysis. Each symbol represents one sample in a given habitat. See Section 3.3 for assignation of sites to different habitat types.

(1) Sandy bottom with few macrophytes of mixed species composition (abbreviation: sand with little mixed vegetation; site A) habitat in a deeper (outer) part of the lagoon with little benthic vegetation;
(2) Sublittoral *Stuckenia*-dominated sediment (*Stuckenia*-dominated sediment; site B) — habitat of species-poor but massive

Table 2
Results of marginal and sequential tests for the distance based linear modeling (DistLM) procedure using step-wise selection and 9999 permutations within the Adjusted R^2 selection criterion, examining the effect of environmental factors on macrophytal biomass. Significant effects are marked in bold.

Variable	Adjusted R^2	SS (trace)	Pseudo-F	p	Prop. (%)	Cumul. (%)
Marginal tests						
Temperature		7948.9	2.765	**0.017**	7.3	
Salinity		3136.3	1.041	0.376	2.9	
O_2		2742.9	0.907	0.472	2.5	
TPM		2643.1	0.873	0.497	2.4	
chl *a*		4061.7	1.360	0.199	3.7	
SOC		7848.9	2.727	**0.022**	7.2	
C/N_{sed}		7197.7	2.485	**0.026**	6.6	
Depth		23,885.0	9.870	**<0.001**	22.0	
Sequential tests						
Depth	0.19769	23,885	9.870	**<0.001**	22.0	22.0
C/N_{sed}	0.23889	6645	2.895	**0.008**	6.1	28.1
Temperature	0.25594	3992	1.779	0.086	3.7	31.8
SOC	0.26719	3330	1.507	0.148	3.1	34.9
TPM	0.30015	5292	2.507	**0.025**	4.9	39.8
chl *a*	0.31669	3607	1.750	0.098	3.3	43.1
O_2	0.32108	2444	1.194	0.275	2.3	45.4
Salinity	0.32612	2473	1.217	0.266	2.3	47.7

Significant values are shown in bold.

benthic vegetation and low-nutritive sediment organic matter (high C/N_{sed} ratio);

(3) Sublittoral *Chara*/*Cladophora* sediment (*Chara*/*Cladophora* sediment; site C) — habitat of rich, high biomass macrophytal communities;

(4) Sandy bottom with little *Pylaiella* vegetation (sand with little *Pylaiella*; site D) — another habitat in a deeper part of the lagoon with a high C/N_{sed} ratio because of riverine input of terrestrial organic matter (Table 1).

SIMPER analysis of macrophytal biomass revealed high dissimilarity by biomass among sites (habitats), with the highest average dissimilarity between sites A and B (91.1%) (Table 3b).

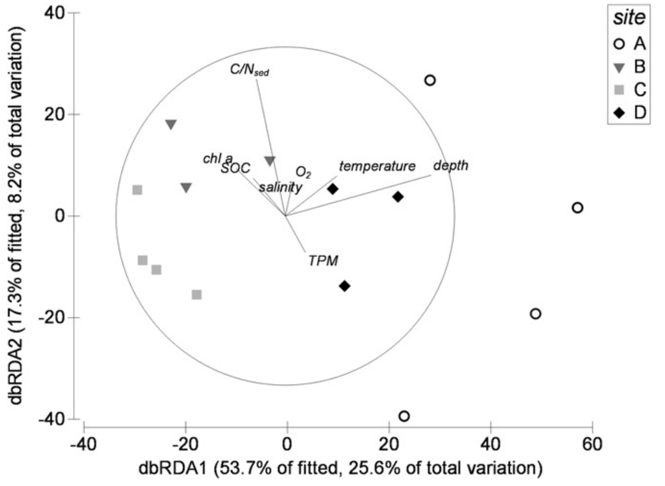

Fig. 4. Distance-based redundancy analysis plot of habitat variables using average macrophytal biomass ($n = 14$). Data were square-root-transformed prior to analysis. Vectors are showed only for the most important environmental variables in the modeling ($\rho > 0.3$). Length and direction of vectors indicate the strength and direction of the relationship.

Table 3
Diagnostic species associated with each site (habitat), point biserial correlation coefficients (φ) and p-values of the analysis of indicator species based on macrophytal biomass data (a) and SIMPER derived average biomass internal pair-wise dissimilarity levels between sites (habitats). Values expressed as percentages (%) (b). Significant effects in Table 3a are marked in bold. See Section 3.3 for assignation of sites to different benthic habitat types.

(a)

Site (habitat)	Species	φ	p
A	*Ulva intestinalis*	0.537	0.010
	Ectocarpus siliculosus	0.492	0.024
B	*Stuckenia pectinata*	0.746	0.001
C	*Chara baltica*	0.427	0.024
	Cladophora glomerata	0.395	0.038
A + D	*Pylaiella littoralis*	0.442	0.030

(b)

Site (habitat)	A	B	C
A			
B	91.1		
C	88.6	53.3	
D	74.8	90.3	86.6

3.4. Variation in macrobenthic faunal communities

Thirty faunal taxa were identified representing nine classes. The most diverse class was Crustacea with ten species or genera, followed by Gastropoda (5 species), Bivalvia, and Polychaeta (4 species each). Species richness (*S*) ranged from four on *Stuckenia*-dominated sediment (summer and fall 2010) to 19 on sandy bottom with little mixed vegetation (fall 2010), and it varied significantly among different habitats (*ANOVA*, $F_{3,20} = 15.61$, $p = 0.001$), but not over time (Table B in Appendix A). The total abundance of macrobenthic fauna ranged from 693 ind. m^{-2} on *Stuckenia*-dominated sediment (spring) to 25,783 ind. m^{-2} on sand with little *Pylaiella* (summer 2011) and varied significantly among habitats (ANOVA, $F_{3,60} = 8.69$, $p = 0.001$). The average total abundance of macrozoobenthos was the highest on sand with little *Pylaiella* (11,539 ± 11,497 ind. m^{-2}, $n = 5$) and lowest on *Stuckenia*-dominated sediment (2617 ± 1864 ind. m^{-2}, $n = 5$) (Fig. B in Appendix A). Gastropods (mostly *Peringia ulvae*) were the most numerous class in three habitats (sand with little mixed vegetation, *Pylaiella*-dominated sediment, and *Chara/Cladophora sediment*) throughout most sampling seasons, while Chironomid larvae were most abundant on *Stuckenia*-dominated sediment. Geographical differences in macrobenthic fauna species composition and abundance are reflected in nmMDS ordination (Fig. 5).

The total biomass of faunal communities also differed among habitats (*ANOVA*, $F_{3,60} = 9.86$, $p = 0.001$), and varied from 0.85 g m^{-2} on *Stuckenia*-dominated sediment (spring) to 48.17 g m^{-2} on sand with little mixed vegetation (fall 2010), which generally reflected the presence of numerically dominant classes (Fig. C in Appendix A). Bivalves (mainly the infaunal Baltic clam, *Macoma balthica*, and the soft-shell clam, *Mya arenaria*) comprised most of the total macrozoobenthic biomass on sand with little mixed vegetation and on sand with little *Pylaiella* in all seasons (on average from 51.2% to 82.4%; Figs. B and C in Appendix A). Macrofaunal biomass on *Chara*/*Cladophora* sediment was dominated by crustaceans (49.9%), particularly the estuarine mud crab, *Rhithropanopeus harrisii*. Insect larvae had the greatest biomass on *Stuckenia*-dominated sediment in most seasons (mean contribution 71.5%).

Seasonal variability was noted only for total macrobenthic biomass (*ANOVA*, $F_{4,60} = 6.40$, $p = 0.001$), but no significant differences were detected over time for species richness or total faunal abundance. On sandy bottom with little mixed vegetation the number of species tended to increase during fall (up to 19 taxa), while in the remaining habitats elevated *S* was observed in summer 2011 (up to 17 species on sandy

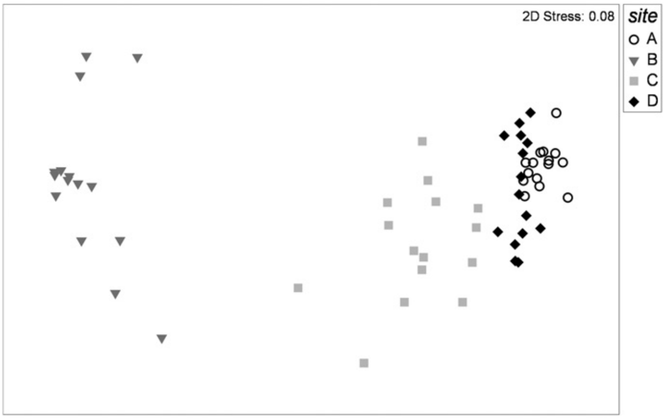

Fig. 5. Non-metric multi-dimensional scaling (nmMDS) ordination showing the relationship among abundance of faunal assemblages from four different benthic habitats in the Puck Lagoon (n = 60). Data were square-root-transformed prior to analysis. See Section 3.3 for assignation of sites to different habitat types.

bottom with little *Pylaiella*). On sandy bottoms with little mixed vegetation and with little *Pylaiella*, high macrofaunal abundance was recorded in spring (maximum 14,457 ind. m^{-2} and 25,783 ind. m^{-2}, respectively), while in the inner part of the lagoon, an increase in abundance occurred in summer 2011 (5540 ind. m^{-2} on *Stuckenia*-dominated sediment) and fall (8900 ind. m^{-2} on *Chara*/*Cladophora* sediment). In three habitats, a substantial increase in biomass occurred in the fall months (up to 48.2 g m^{-2} on sand with little mixed vegetation), which was followed by a decrease during winter (down to 8.83 g m^{-2} on sandy bottom with little *Pylaiella*) and spring (1.65 g m^{-2} on *Chara*/*Cladophora* sediment). The fall increase in biomass was mainly caused by the increased biomass of bivalves (*M. balthica*, *M. arenaria*, *Cerastoderma glaucum*), particularly on sandy bottoms with little mixed vegetation and with little *Pylaiella*, where their contribution to the total biomass was 79.9 and 64.8%, respectively. The ragworm, *Hediste diversicolor*, also added to the elevated biomass in fall with percentage contributions of 11.6 and 33.2%, respectively, while *R. harrisii* was an important component on *Chara*/*Cladophora* sediment (64.5%) in this season. On *Stuckenia*-dominated sediment the maximum total biomass was noted in summer 2011 (8.26 g m^{-2}) and coincided principally with the increased biomass of the common pond snail, *Radix labiata* (50.1% of the total macrofaunal biomass).

3.5. Relations between habitat attributes and macrofaunal community structure

The number of faunal taxa was positively correlated with the number of plant taxa (correlation analysis on averaged data; $S_{\text{macrofauna}} = 0.497\, S_{\text{macrophyte}} + 9.219$, R = 0.451, p = 0.046, n = 20). Total macrophyte biomass did not affect either species richness or the total abundance and biomass of macrobenthic animals. Total macrofaunal biomass was negatively correlated with the C/N_{sed} ratio of surface sediments (correlation analysis on averaged data; biomass = $-3.540 C/N_{sed}$ ratio + 41.547, R = 0.522, p < 0.022, n = 20). Marginal and sequential tests in distance-based linear modeling (DistLM) on environmental variables, biomass (bioveg), and the species richness of benthic macroplants (taxaveg) indicated that TPM, bioveg, and depth were significant (Table 4) for the Adjusted R^2 selection criterion. The Adjusted R^2 model explained 59.9% of total variation. The first two dbRDA axes explained 75.5% of the fitted variation; the first dbRDA axis correlated with TPM (ρ = 0.585), depth (ρ = −0.439), and bioveg (ρ = 0.334). These factors are most responsible for spatial differences in macrofaunal assemblage patterns (Fig. 6). The ecological preferences of faunal species were defined using indicator species analysis in R which showed 18 taxa to be specifically associated with habitats (Table 5). The influence of benthic plants on macrofaunal assemblages was dependent on season (PERMANOVA+) with significant effects of vegetation in all seasons except spring (pair-wise tests; Table 6).

Table 4
Results of marginal and sequential tests for the distance based linear modeling (DistLM) procedure using step-wise selection and 9999 permutations within the Adjusted R^2 selection criterion, examining the effect of environmental factors and biomass and species richness of benthic macroplants on macrofaunal biomass. Significant effects in are marked in bold.

Variable	Adjusted R^2	SS (trace)	Pseudo-F	p	Prop. (%)	Cumul. (%)
Marginal tests						
Temperature		618	0.2667	0.969	4.6	
Salinity		1939	0.8644	0.425	1.5	
O_2		614	0.2650	0.963	16.1	
TPM		6810	3.4526	**0.018**	5.3	
chl *a*		2231	1.0021	0.347	4.2	
SOC		1774	0.7878	0.494	6.9	
C/N_{sed}		2939	1.3437	0.258	4.4	
taxaveg		1870	0.8320	0.435	12.1	
Bioveg		5140	2.4890	**0.047**	16.1	
Depth		6805	3.4498	**0.020**	4.6	
Sequential tests						
Temperature	−0.04015	618	0.2667	0.960	1.5	1.5
Salinity	−0.04577	2104	0.9033	0.394	5.0	6.5
O_2	−0.08563	908	0.3757	0.880	2.1	8.6
TPM	0.02886	6242	2.8862	**0.042**	14.8	23.4
chl *a*	0.03336	2303	1.0698	0.349	5.4	28.8
SOC	0.05280	2716	1.2873	0.240	6.4	35.2
C/N_{sed}	0.00027	706	0.3170	0.830	1.7	36.9
Taxaveg	−0.04884	1023	0.4381	0.717	2.4	39.3
Bioveg	0.20393	7965	4.4928	**0.022**	18.8	58.1
Depth	0.29131	3524	2.2329	0.091	8.3	66.4

Significant values are shown in bold.

4. Discussion

4.1. Benthic habitats in the Puck Lagoon

The European Nature Information System (EUNIS) habitat classification (Davies et al., 2004; Schiele et al., 2014) is based on the univariate assessment of various ecosystem properties (e.g., salinity, depth, substrate type, macrophytes) which are organized in a hierarchical scheme. Although the system is complex, as it applies to both terrestrial and marine environments, it has been used broadly in many European coastal areas. However, the EUNIS system does not classify fine details of the macrophyte community structure within similar biotopes, e.g., vegetated sublittoral sediments (Levels 5 and 6), which can conceal

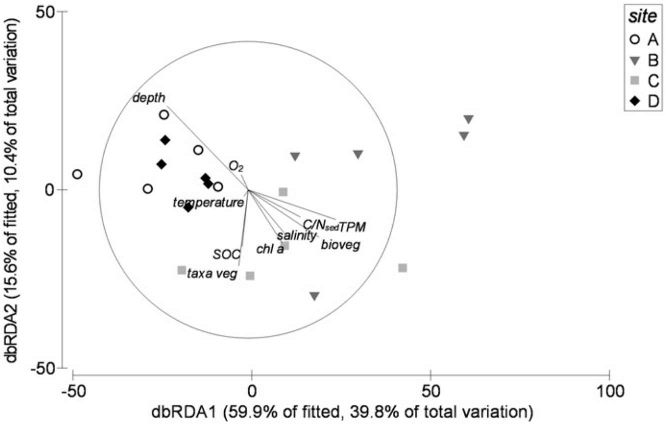

Fig. 6. Distance-based redundancy analysis plot of habitat variables using average biomass of benthic macrofauna (n = 20). Data were square-root-transformed prior to analysis. Vectors are showed for all environmental variables in the modeling (ρ > 0.3). Length and direction of vectors indicate the strength and direction of the relationship.

Table 5
Diagnostic species associated with each habitat, point biserial correlation coefficients (φ) and p-values of the analysis of diagnostic species based on faunal biomass data. See Section 3.3 for assignation of sites to different benthic habitat types.

Site (habitat)	Species	φ	p
A	*Mytilus trossulus*	0.918	0.001
	Cerastoderma glaucum	0.789	0.001
	Macoma balthica	0.738	0.001
	Cyathura carinata	0.732	0.001
	Mya arenaria	0.695	0.021
	Peringia ulvae	0.692	0.001
	Oligochaeta	0.640	0.011
	Amphibalanus improvisus	0.627	0.004
	Pygospio elegans	0.577	0.027
B	*Chironomidae*	0.977	0.001
	Theodoxus fluviatilis	0.624	0.021
	Lekanesphaera hookeri	0.571	0.014
	Radix labiata	0.447	0.050
C	*Rhithropanopeus harrisii*	0.758	0.002
D	*Marenzelleria neglecta*	0.834	0.001
	Corophium multisetosum	0.749	0.001
	Hediste diversicolor	0.700	0.028
	Streblospio spp.	0.531	0.041

ecologically important differences on microgeographical scales of some regional seas in Europe, such as the Baltic Sea (Gic-Grusza et al., 2009; HELCOM, 2013). Specific geological conditions and the ecological variety of the Baltic seafloor were accounted for recently in the HELCOM Underwater Biotope and habitat classification system, HELCOM HUB (HELCOM, 2013), which combines two ecological terms, i.e., habitat and biotope, of which only the former is used in EUNIS. HELCOM HUB was designed to be EUNIS compatible and classifies benthic biotopes to a fine level in a hierarchical system with descriptions of abiotic environments (e.g., light availability, substrate type) and associated biotic community structures. At mid-level 4, the split rule is based on coverage of substrates (%) by macroscopic epibenthic biotic structures, and an additional level 6 is based on the height of visible plants. Proper estimates of these parameters requires high-quality underwater images and/or direct measurements and expert judgment. Because of technical limitations and adverse meteorological conditions, particularly in cold, stormy seasons, underwater imaging/video or SCUBA-diving observations were not done during the sampling campaigns in this study. Thus, macrophytal biomass data were used to characterize benthic vegetation and a modified EUNIS benthic habitat classification system for classifying the benthic habitats in the Puck Lagoon in order to comply with local phytal variety.

Patterns of benthic habitat structure in the Puck Lagoon are clearly influenced by depth and C/N_{sed} ratio in surface sediments (DistLM model; Table 2), all operating over a small spatial scale (i.e., distances among sampling sites). These factors are most responsible for driving the structure of benthic vegetation in discrete habitats. While the growth of vascular plants is dependent on depth-related light conditions, macrophytal production is considered nutrient-limited (Duarte, 1995). In the Puck Lagoon, eutrophication-induced increases of suspended matter in the water column decrease light penetration depth and affect vascular plant biomass.

Table 6
Two-way PERMANOVA+ model and pair-wise tests for differences in macrofaunal abundance among seasons (Season) and habitats of massive and poor benthic vegetation (Plants). *Stuckenia*-dominated sediment and *Chara*/*Cladophora* sediment were assigned to habitat of massive vegetation while sand with little mixed vegetation and sand with little *Pylaiella* were assigned to habitat of poor vegetation. Significant effects in are marked in bold. Pair-wise tests were performed separately for five months and months where difference was significant at $p < 0.05$ are listed.

Factor	df	SS (trace)	Pseudo-F	p
Season	4	10,392	1.4902	0.1085
Plants	1	3082	1.7677	0.1281
Season × Plants	1	46,187	6.6233	<**0.001**
Pair-wise test			July 2010	**0.002**
			October 2010,	**0.043**
			February/March 2011	**0.002**
			May 2011	0.168
			July 2011	**0.002**

Significant values are shown in bold.

Dense macrophyte communities composed almost exclusively of pondweed, *S. pectinata*, (diagnostic species; Table 3a) develop on very shallow sandy sediments with peat outcrops in the vicinity of a small river (site B). Surface sediments in this area had a relatively high C/N_{sed} ratio, which indicated recent nutrient mineralization through organic matter diagenesis, which represents low quality food for fauna (Sokołowski, 2009). In the neighboring area, *C. balthica* and *C. glomerata* (including *Z. marina*) form another macrophyte-rich community (site C) that provides a suitable habitat for phytophilic benthic animals. The sandy sediments underneath the plants receive fresh phytal organic matter with low C/N_{sed} ratios, which can serve as a nutritive sedimentary source of carbon for animals. Not surprisingly, the northwestern part of the lagoon is considered to be the most diverse, richest region of the Gulf of Gdańsk floristically (Kruk-Dowgiałło, 1998). Macrophyte growth in this shallow-water area is favored by limited hydrodynamics (wind waves, sea currents), good light penetration, and advantageous thermal conditions in warm seasons. Enhanced hydrodynamics and lower nutrient availability in sediments support taxonomically less diverse and less massive macrophytes in two other habitats: sand with little mixed vegetation and sand with little *Pylaiella* (sites A and D, respectively). The deeper, less sheltered outer part of the lagoon is subject to intense water movement, which, together with worse light conditions, prevent large benthic plants from developing. In this area, benthic vegetation consisted of various species with a dominance of opportunistic filamentous brown algae, *E. siliculosus* and *P. littoralis*. The variety of habitats in such a small water-basin underscores its unique biological value and esthetic quality, which provides an impetus for protection and management. The lagoon has been designated as a Special Protection Area (*PLB* 220005) and Special Area of Conservation (*PHL* 220032) as described in the EU-wide network of nature protection areas Natura 2000.

4.2. Macrofaunal assemblage patterns across benthic habitats

In the marine environment, benthic faunal communities are strongly influenced by habitat type (Gogina et al., 2010; Zajac et al., 2003), so examining habitat macrofauna preferences is an important prerequisite for developing an understanding of ecosystem functioning. Diverse patterns and rates of ecosystem processes can be expected in systems with a large diversity of habitats. The spatial heterogeneity of benthic habitats and the resultant asynchrony of associated fauna preclude scaling processes that were established in a particular area to the whole ecosystem (Rooney et al., 2006). Regional or even habitat-specific investigations are, therefore, required to unravel patterns of faunal assemblages in the area of interest and to allow for local divergence of environmental and ecological conditions.

Multivariate and univariate analyses highlighted the importance of benthic habitat type for the structure and composition of faunal assemblages. Based on macrophytal biomass and two environmental parameters, i.e., depth and C/N_{sed} ratio, four distinct benthic habitats were identified that affect benthic macrofauna biomass and taxonomic diversity differently. Dense benthic vegetation in the inner part of the lagoon exerts a negative impact on faunal biomass by reducing large, long-lived macroinvertebrates. Macrophytal communities here are dominated by so-called structural engineering taxa such as *S. pectinata*, *Chara baltica*, and *Z. marina*, which restrict infauna living space. In addition, the reduced effect of benthic plants on resident fauna might be associated with harmful exudates and low oxygen concentrations (Pihl et al., 1999), as well as on dissolved NH_4^+, which can be toxic (Hauxwell et al., 1998).

Taxonomically rich, massive vegetation (*Chara*/*Cladophora* sediment) tended, in turn, to host taxonomically diverse macrofaunal assemblages. These bottoms have a complex spatial and nutritional structure offering a number of microniches for infaunal and epifaunal species (Boström and Bonsdorff, 2000). The occurrence of annual filamentous algae and the development of vascular rooted plants (*Z. marina*) are both beneficial for benthic invertebrates, particularly during the vegetative season; this was also observed earlier in the Puck Bay by Włodarska-Kowalczuk et al. (2014) and in the northern Baltic Sea by Boström and Bonsdorff (1997, 2000). Shallow vegetated sandy sediments are recognized as favoring diverse macrofaunal assemblages, particularly in more sheltered areas, as would be expected given the scope of colonization of these sediments by actively moving species (Rees et al., 1999). The estuarine mud crab *R. harrisii* was, indeed, associated specifically with *Chara*/*Cladophora* sediments, which were seasonally inhabited by other motile crustaceans such the Baltic prawn *Palaemon adspersus*, the omnivorous *Gammarus* spp., and the phytophilic isopod *Idotea chelipes*. The input of plant debris and its fast mineralization processes at increased water temperature result in the production of decaying organic matter that is an important food source for detritivorous animals (Sokołowski, 2009). The prevalence of motile epibenthic crustaceans over tube-dwelling sedentary polychaetes suggests, however, that faunal assemblages in this part of the Puck Lagoon are sustained largely by benthic macrophytes. Increased species diversity and abundance of fauna in complex vegetated areas have also been documented in other coastal areas, e.g., the Puck Bay (Włodarska-Kowalczuk et al., 2014), the northern Baltic Sea (Boström and Bonsdorff, 1997), the Wadden Sea (Polte et al., 2005), and the coastal waters of New Zealand (Battley et al., 2011).

The habitat with massive but species-poor vegetation (*Stuckenia*-dominated sediment) adjacent to the Płutnica River supports less diverse macrofaunal assemblages that were dominated numerically by insect larvae. Run-off of allochthonous organic particles along with peat outcroppings and a large load of decaying plants increase sediment organic matter locally. The elevated C/N_{sed} ratio of sediments in this location is consistent with nitrogen-depletion and lower food quality. Such conditions promote organic matter-resistant infauna such as Chironomidae and active herbivores such as *Lekanesphaera hookeri* and *Theodoxus fluviatilis* (diagnostic taxa for this habitat; Table 4). In addition, the high load of plant-derived organic matter and peat outcrops lead to temporary hypoxia/anoxia and even the production of hydrogen sulfide in these organic-rich sediments during summer when the water column stagnates (authors' own observations) exerting a deleterious effect on the resident fauna (Levin et al., 2009).

Two sandy habitats in the outer part of the lagoon (sand with little mixed vegetation and sand with little *Pylaiella*) host faunal assemblages with the highest biomass. The resident fauna in this area responds positively to the presence of opportunistic macroalgae that attract mobile species, and to the supply of suspended, sedimentary food supporting suspension and deposit feeders. Because of the input of terrestrial riverine organic matter, which increases locally suspended particles in the water column and decreases the quality of organic matter, benthic assemblages on sand with little *Pylaiella* (close to the river mouth) comprised mainly sediment-dwelling polychaetes and crustaceans (Table 5). On sand of little mixed vegetation (i.e. away from the river), long-lived, suspension feeding infaunal (*M. balthica* and *M. arenaria*) and epifaunal (*Cerastoderma glaucum*) bivalves dominated the biomass structure, followed by detritivorous gastropods (*P. ulvae*) and polychaetes (*H. diversicolor*).

4.3. Consistency of patterns among habitat types over time

The effect of macrophytes on the abundance of benthic faunal assemblages persisted throughout the year (except in spring) with the strongest influence in summer, which corresponds to other studies in temperate coastal waters, e.g., Puck Bay (Włodarska-Kowalczuk et al., 2014) and the Lagoon of Venice (Pranovi et al., 2000). Although in this study shallow communities of massive vegetation were not dominated by one species and consisted of mixed vascular plants and algae (e.g., *Stuckenia*, *Zostera*, *Chara, Cladophora*), the impact of the macrophytes on zoobenthos was evident; this highlights the important structural and nutritional roles of benthic plants. This finding also suggests that the positive effect of vegetation on macrofaunal diversity can be achieved by multi-taxon engineering plant communities and, thus, providing architectural complexity and food variety to benthic animals (Harley and O'Riley, 2011). The most pronounced effect was observed in summer when macrophytal biomass was the highest, and vascular plants and associated algae created complex spatial structures that promoted diverse fauna. It is also possible that the accumulation of organic matter and its increased nutritive value (low C/N_{sed} ratio) in surface sediments in warm months also attracts benthic detritivorous invertebrates.

5. Conclusions

Despite its small area, relatively homogenous hydrological conditions, and sediment grain-size structure, the Puck Lagoon provides a zonation of benthic habitats on a microscale that affects soft-bottom macrofaunal assemblages. The patterns evident from the study support the relevance of benthic macrophyte biomass and taxonomic structure, and surface sediment organic matter (C/N_{sed} ratio) quality as important structuring factors for fauna. Sandy sediments with little mixed vegetation and relatively low C/N_{sed} ratio provide good nutritional conditions for long-lived deposit and suspension feeders (bivalves), which account primarily for elevated macrozoobenthos biomass in the outer, deeper part of the lagoon. However, the presence of brown algae, *Pylaiella*, and riverine inputs of low-quality terrestrial organic matter promote deposit-feeding polychaetes and crustaceans in the area close to the river mouth. Species-rich, dense macrophyte vegetation and sediment organic matter of high nutritive value host more diverse faunal assemblages of low biomass offering favorable microniches for infaunal and epifaunal species. On the other hand, massive but species-poor *Stuckenia*-dominated macrophyte communities together with the low-quality of organic matter from the river tend to support faunal assemblages of low taxonomic diversity. The effect of large biomass macrophytes on the abundance of benthic faunal assemblages persisted throughout most of the year with the strongest influence in summer when macroplants created complex spatial and nutritional structures. Spatial variation of the structure of zoobenthic assemblages in this brackish lagoon is driven by various habitat-related factors which act on different scales, highlighting the unique biological value of this water body.

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Appendix A. Supplementary data

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8. 1. Supplementary files

Appendix

Table A Species richness (*S*) and taxa which dominated in the biomass of macrophyte communities at different sites in the Puck Lagoon between July 2010 and July 2011. Empty cells - no macrophytes recorded.

	S				Dominating taxon			
season *site**	A	B	C	D	A	B	C	D
2010								
summer	5	0	0	0	*Ectocarpus siliculosus*			
autumn	3	2	7	1	*Polysiphonia fucoides*	*Stuckenia pectinata*	*Zostera marina*	other
winter	9	0	6	0	*Zostera marina*		*Zostera marina*	
2011								
spring	12	9	9	8	*Pilaiella littoralis*	*Stuckenia pectinata*	other	*Pilaiella littoralis*
summer	0	4	9	5		*Stuckenia pectinata*	*Zostera marina*	*Pilaiella littoralis*

* - see section 3.3 for assignation of sites to different benthic habitat types.

Table B Species richness (*S*) of macrobenthic faunal communities at different sites in the Puck Lagoon between July 2010 and July 2011.

		S			
season	*site**	A	B	C	D
2010					
summer		15	4	10	13
autumn		19	4	14	13
winter		15	5	11	14
2011					
spring		16	7	14	14
summer		10	9	15	17

* - see section 3.3 for assignation of sites to different benthic habitat types.

Figure captions in Appendix

Figure A. Seasonal variations in a) temperature, b) salinity, c) concentration of dissolved oxygen, O_2, d) total particulate matter, TPM and e) chlorophyll *a*, chl *a* in the overlying bottom water at different sites (microhabitats) in the Puck Lagoon between July 2000 and July 2011.

Figure B. Abundance (mean contribution > 1.0% of the total abundance) of major macrozoobenthic taxa at different sites (microhabitats) in the Puck Lagoon between July 2000 and July 2011.

Figure C. Biomass (mean contribution > 1.0% of the total biomass) of major macrozoobenthic taxa at different sites (microhabitats) in the Puck Lagoon between July 2000 and July 2011.

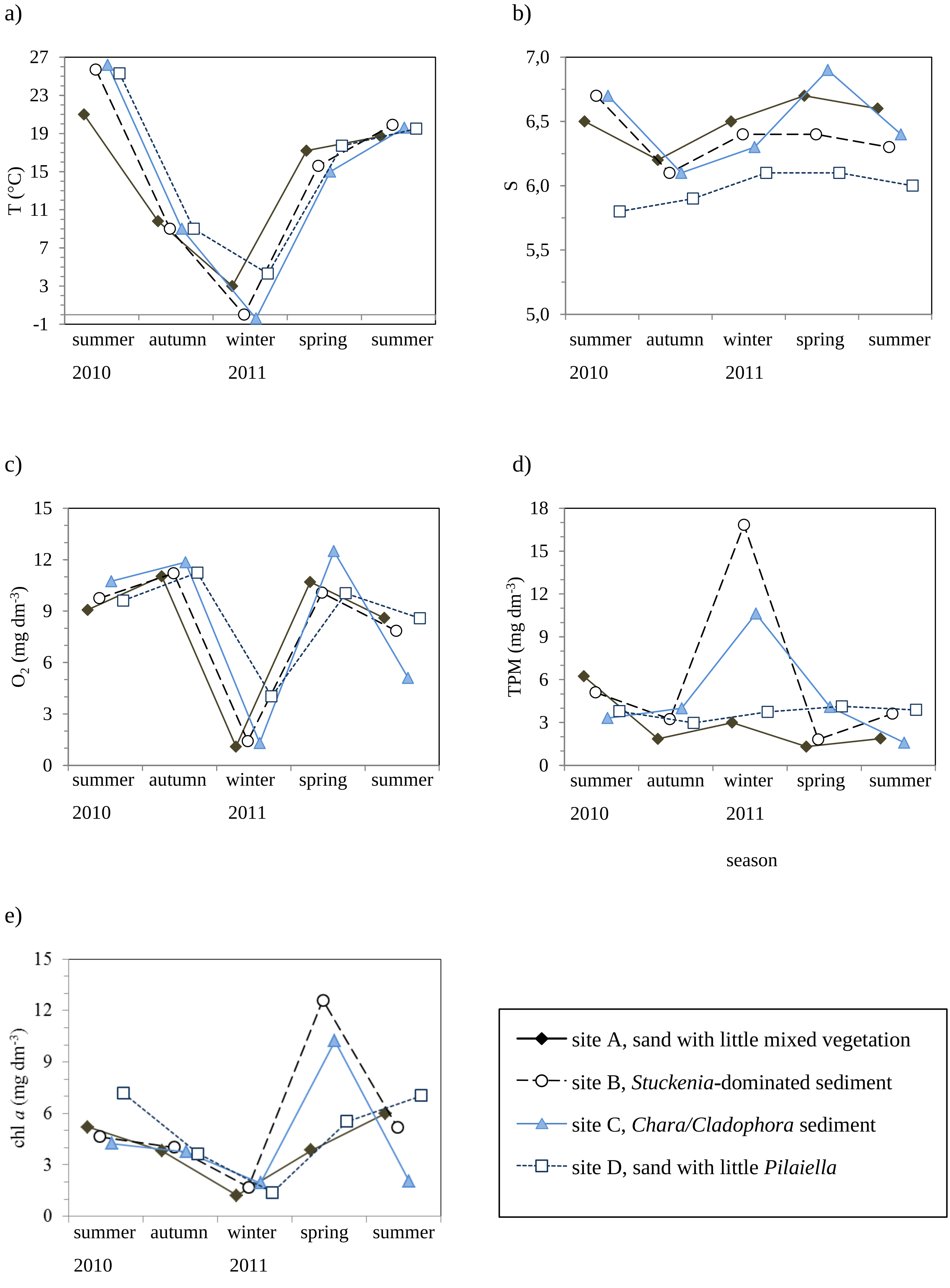

a)
27
23
19
15
11
7
3
-1
T (°C)
summer
autumn
winter
spring
summer
2010
2011
b)
7,0
6,5
6,0
5,5
5,0
S
summer
autumn
winter
spring
summer
2010
2011
c)
15
12
9
6
3
0
O_2 (mg dm^{-3})
summer
autumn
winter
spring
summer
2010
2011
d)
18
15
12
9
6
3
0
TPM (mg dm^{-3})
summer
autumn
winter
spring
summer
2010
2011
season
e)
15
12
9
6
3
0
chl *a* (mg dm^{-3})
summer
autumn
winter
spring
summer
2010
2011
season
site A, sand with little mixed vegetation
site B, *Stuckenia*-dominated sediment
site C, *Chara/Cladophora* sediment
site D, sand with little *Pilaiella*

Fig. A.

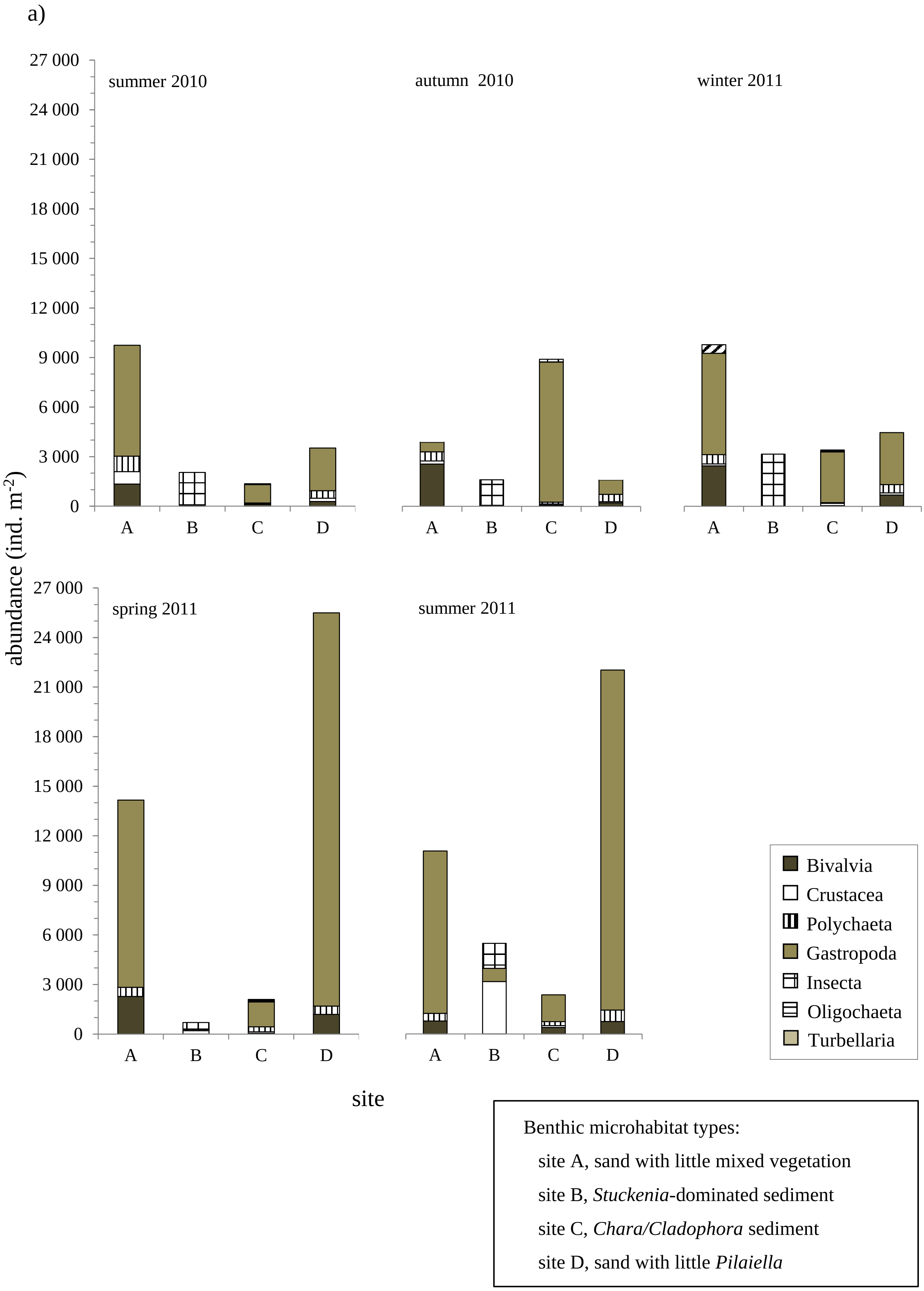
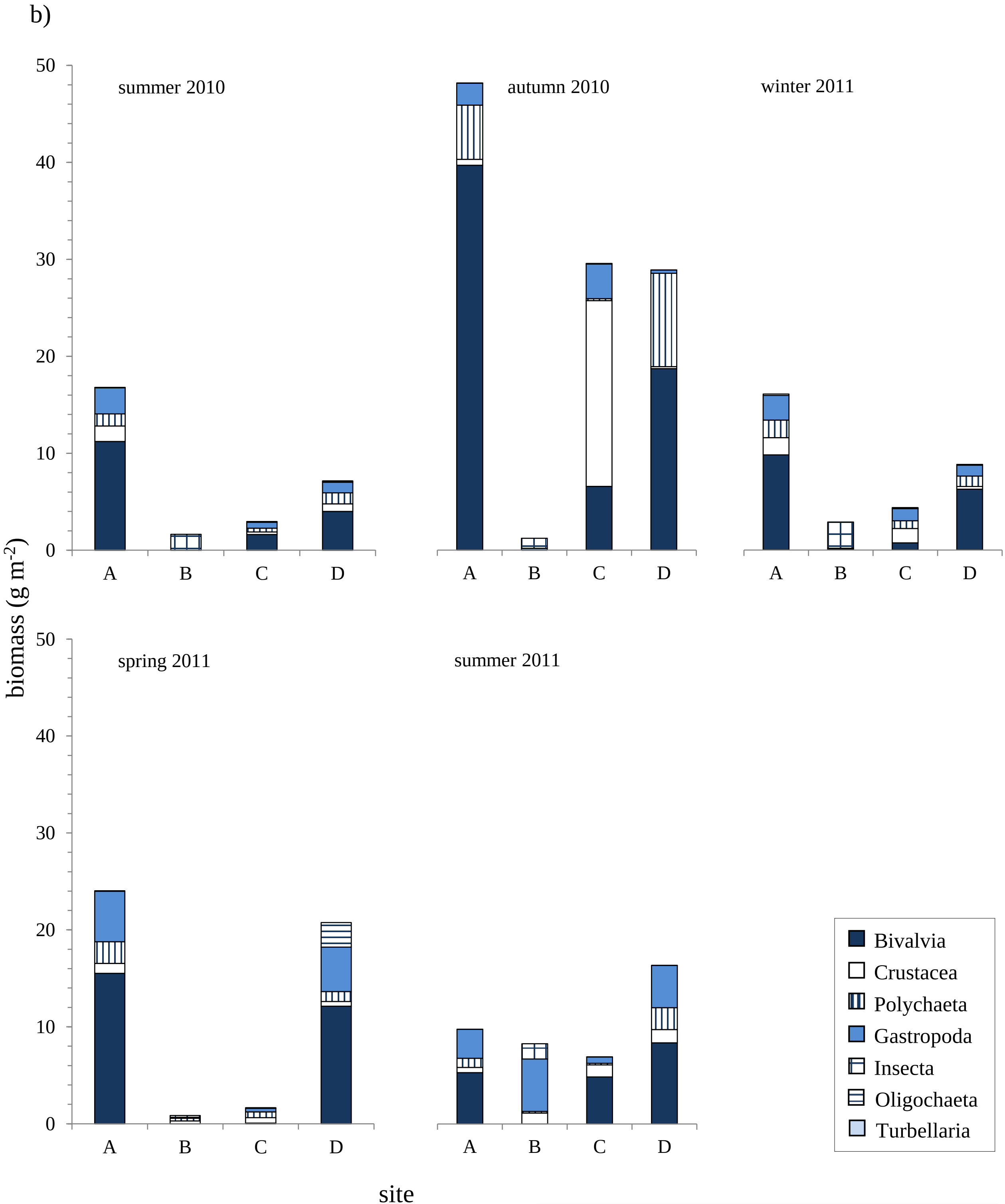

a)
abundance (ind. m-2)
27 000
24 000
21 000
18 000
15 000
12 000
9 000
6 000
3 000
0
summer 2010
autumn 2010
winter 2011
spring 2011
summer 2011
A
B
C
D
site
Bivalvia
Crustacea
Polychaeta
Gastropoda
Insecta
Oligochaeta
Turbellaria
Benthic microhabitat types:
site A, sand with little mixed vegetation
site B, *Stuckenia*-dominated sediment
site C, *Chara/Cladophora* sediment
site D, sand with little *Pilaiella*

Fig. B.



Benthic microhabitat types:

site A, sand with little mixed vegetation

site B, *Stuckenia*-dominated sediment

site C, *Chara/Cladophora* sediment

site D, sand with little *Pilaiella*

Fig. C.

8.2. Author contribution statement

Author contribution statement

We hereby confirm, that the specific contributions to the publication:

Sokołowski, A., Ziółkowska, M., Zgrundo, A., 2015. Habitat related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea). Journal of Sea Research, 103, 93–102. https://doi. org/10.1016/j.seares.2015.06.017.

were as follows:

Marcelina Maria Ziółkowska - 45 %

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conceptualization and design of the study, field sampling, laboratory work, statistical analyses, interpretation of the results preparation of figures and tables, writing the manuscript, revision and editing, contribution of the response to the reviews, correspondence with editor

....

Adam Sokołowski - 48 %

Faculty of Oceanography and Geography, Univeristy of Gdansk

field sampling, conceptualization and design of the study, revision and commenting on the manuscript, funding acquisition

....

Aleksandra Zgrundo - 7%

Faculty of Oceanography and Geography, Univeristy of Gdansk

field sampling, laboratory work, interpretation of the results, revision and commenting on the manuscript

Aleksandra
....

Chapter 9. Spatial and temporal variability of organic matter sources and food web structure across benthic habitats in a low diversity system (southern Baltic Sea)

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Spatial and temporal variability of organic matter sources and food web structure across benthic habitats in a low diversity system (southern Baltic Sea)

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ABSTRACT

Understanding the effects of basal resources on the functioning of coastal ecosystems is of great interest in ecology since the different composition and availability of food sources directly affect trophic pathways and energy flow in systems. In this study, we determined which basal resources fuel the food webs of four benthic communities from different habitats in the shallow, low diversity Puck Lagoon (Gulf of Gdańsk, southern Baltic Sea) over a full seasonal cycle. Using $\delta^{13}C$ and $\delta^{15}N$ values, the relative contribution of various potential carbon sources to the diets of dominant consumers were estimated with a mixing model in R (SIAR). The organic matter pool assimilated by macrofauna included primarily suspended particulate matter (SPOM), phytoplankton, and sediment detritus (SOM) that contained degraded vascular plants and macroalgae in areas with high vegetative biomass. Benthic invertebrates fed mostly on food sources available in their habitats and had species-specific carbon and nitrogen isotope compositions. On sediments with little vegetation, two separate trophic pathways included SPOM, phytoplankton, and suspension feeders, while SOM supported deposit feeders and omnivores in a sheltered environment close to a river mouth. On sediments dominated by *Stuckenia*, SOM and macroalgae supported the benthic food web that was dominated by opportunistic and tolerant omnivores and herbivores. In contrast, the large biomass of benthic vegetation and high SOM quality on *Chara*/*Cladophora* sediment induced high trophic diversity with two main trophic pathways, SPOM and phytoplankton supported suspension feeders, and macroalgae and epiphytes promoted grazers and omnivores. Vascular plants were found not to have been consumed by benthic invertebrates or fishes, but they provided suitable substrata for the macroalgae that developed on their blades and roots.

1. Introduction

Coastal ecosystems are characterized by a combination of benthic habitats of specific physical, chemical, and biological attributes that change in space and over time (Livingston, 2014). Geographical variations of environmental variables (e.g., salinity, nutrients, and primary production) in shallow areas create patches of habitats that can serve as reservoirs for local biodiversity. Long-term (multiannual) and seasonal changes of the gross production of organic matter in a system directly influence species distribution and abundance, and, thus, the structure of food webs (Bergamino and Richoux, 2014). Moreover, terrestrial organic matter, phytoplankton, and submerged aquatic vegetation all support benthic food webs by providing various potential food resources (Livingston, 2014). Benthic consumers can utilize a variety of food sources including phytoplankton, bacteria, benthic micro- and macroalgae, vascular plants, and suspended organic matter (Kang et al., 2003), but identifying their respective contributions to trophic links in a given system or habitat can be difficult. This is because some carbon sources (e.g., suspended material) can be transported over long distances and because the diets of consumers can vary even on small spatial scales (Guest et al., 2004). Previous studies show that the diets of benthic consumers in coastal ecosystems can be affected by spatial differences in the primary organic matter sources of phytoplankton and detritus (Keats et al., 2004), the relative abundance of seagrass or macroalgae (Olsen et al., 2011), and the quality and availability of animal prey (Fox et al., 2009). Moreover, benthic vegetation can serve as an indirect food source for benthic fauna in the form of decaying organic matter that enters the sediment detritus pool and changes its composition (Dubois et al., 2012). Due to the low palatability (hard tissue containing a lot of structural carbohydrates) and nutritional

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quality (high C/N ratios) (Michel et al., 2014), vascular plants (e.g., eelgrass) are considered to be of little trophic importance in the food web, but they can exert an indirect effect by providing complex substrata for epiphytic algae or enhancing carbon storage in sediments (Jankowska, 2017). It is documented that the epiphytic algal assemblages growing on seagrass may be the primary food source of resident animals as opposed to seagrass tissues (van Montfrans et al., 1984; Pollard and Kogure, 1993).

The Puck Lagoon, which is located in the southern Baltic Sea, provides an exceptionally diverse environment with a range of semi-isolated and fragmented benthic habitats, including seagrass meadows, peat outcrops, and bare sediments covered by massive, fast-growing macroalgae (Gic-Grusza et al., 2009; Sokołowski et al., 2015). The patchy spatial distribution of benthic habitats results in small-scale variations in the diversity and abundance of macrobenthic fauna that may have further consequences for trophic interactions and carbon pathways in local food webs (Layman et al., 2007; Nordström et al., 2015; Arroyo and Bonsdorff, 2016). Recent studies in the lagoon reveal that the key structuring factors for benthic communities are taxonomic composition and macrophyte biomass, sediment quality (C/N ratio), and depth (Sokołowski et al., 2015). How benthic food webs respond to the availability of basal resources in this brackish, low diversity system is poorly understood.

The aim of this work was to reconstruct the food webs of benthic communities in different habitats over four seasons and to examine how basal organic carbon resources vary geographically and over time. By assessing the contribution of different resources to the diets of dominant macrofauna species, we tested the hypothesis that benthic communities from different habitats on a small geographical scale (the Puck Lagoon) are based on distinct basal resources. The study combined community structure and trophic ecology over time and space by tracking changes in species biomass and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$). The specific hypotheses tested were: (H_1) the $\delta^{13}C$ and $\delta^{15}N$ of basal resources differ among benthic habitats that are in close proximity to one another, (H_2) consumer $\delta^{13}C$ and $\delta^{15}N$ vary among different habitat types, and (H_3) the structure of benthic communities, specifically the relative biomass of dominant consumers, affects carbon flows through benthic food webs.

Stable isotope analysis (SIA, $\delta^{13}C$ and $\delta^{15}N$) is a common tool in trophic ecology as it provides a time-integrated account of the material assimilated by organisms and reflects the proportional use of different resources. $\delta^{13}C$ is useful for differentiating among different organic matter sources at the food web base, while $\delta^{15}N$ is used to define trophic position in the food web (Wada et al., 1991; Minagawa and Wada, 1984; Michner and Schnell, 1994; Post, 2002).

2. Materials and methods

The study was conducted in the Puck Lagoon (southern Baltic Sea, Poland) which is the inner part of Puck Bay with a total area of 104.8 km^2 and a mean depth of 3.2 m. The lagoon is a productive, low salinity, semi-enclosed water body, with local vertical water mixing and nutrient loading from rivers and streams (e.g., the Płutnica and Reda rivers) (Gic-Grusza et al., 2009). The lagoon is a hydrogeologically and ecologically diverse ecosystem with variety of benthic habitats, i.e., bare sands, macroalgae dominated sediments, and *Zostera* and *Chara* meadows (Gic-Grusza et al., 2009). Sampling sites were located in four different benthic habitats with the following characteristic species: 1) sand with little mixed vegetation (habitat A), (2) *Stuckenia*-dominated sediment (habitat B), (3) *Chara*/*Cladophora* sediment (habitat C), and (4) sand with little *Pylaiella* (habitat D) (Fig. 1). These habitats had similar environmental variables, but they differed substantially in macrophyte biomass and composition, sediment quality, and impact from local rivers (for more details see Sokołowski et al., 2015).

2.1. Sample collection and pre-treatment

The following living and non-living ecosystem components were collected to delineate the trophic organization of the benthic biocenosis in the lagoon: suspended particulate organic matter (SPOM), phytoplankton, mesozooplankton, macrobenthic and meiobenthic organisms, epiphytes, fishes, and sediment organic matter/detritus (SOM). The samples were collected at seasonal intervals over 10 months from October 2010 to July 2011.

Seawater was sampled using a 5 dm^3 GoFlo water sampler and passed through a 1 mm mesh net to remove large particles and debris. SPOM was obtained by filtering water through precombusted (450 °C, 8 h) and preweighed Whatman GF/F filters (glass microfibre filters; 0.7 µm) under a moderate vacuum on a standard filtration system. The filters containing the retained particulate matter were then stored individually in polystyrene Petri dishes at −20 °C.

Phytoplankton 25–100 µm in size was collected vertically from above the bottom to the water surface with a WP2 net with 25 µm mesh (diameter 57 cm). The material collected was then sieved gently through 1 mm and 125 µm mesh nets to remove larger free-floating items such as macroalgal thalli, leaves, and debris. Sampling was repeated several times to acquire sufficient material for SIA. The plankton was placed in a cool container with aerated seawater collected in situ and then transported to the laboratory. Next, the samples were fractionated through two sieves with 25 µm and 100 µm mesh nets (phytoplankton) using a modified method by Rolff and Elmgren (2000). The method is based on a vacuum set of polyethylene bottles with different mesh size sieves, and it permits segregating plankton fractions by size. After fractionation, the phytoplankton was filtered through Whatman GF/F filtered seawater and Milli-Q water and stored in polyethylene vials. The filters and vials were then frozen at −20 °C.

Macrofauna (> 1 mm size) and macroflora were collected in triplicate with a Van Veen grab (catch area 0.1 m^2) and by dredging with a rectangular bottom dredge (30 × 50 cm with a 1 mm internal mesh net). Quantitative samples were first used for community analyses, and then they were combined with qualitative samples to obtain sufficient material for SIA. Benthic fishes were caught with a hoop net that was deployed in habitats A and B in the summer of 2011. Sediments from the grab were gently sieved through a 1 mm mesh net to sort out the macrobenthic animals. These were placed in a cool container with aerated seawater collected in situ and then transported to the laboratory. Special care was taken to remove delicate or enmeshed specimens from the sieve mesh. The benthic macrofauna was kept alive overnight to depurate at the ambient temperature and salinity of the environment from which they were collected. The animals were then sorted out, identified to the species level (except for *Streblospio* spp, *Gammarus* spp., *Jaera* spp., Nematoda, Chaoboridae, Chironomidae larvae, and Oligochaeta) under a stereomicroscope, and counted. The soft tissues of gastropods, bivalves, and barnacles (*Amphibalanus improvisus*) were removed from the shells. A section of white muscle from the caudal region or the abdomen was collected from each of the larger fish and crustacean specimens. Individuals and/or soft tissue of the same taxon were grouped into 3 pools containing 7 individuals/samples each to provide sufficient material for SIA. The exceptions were the fish species *Sygnathus typhle, Nerophis ophidion*, *Perca fluviatilis*, *Pomatoschistus minutus*, *Neogobius melanostomus*, *Gobius niger*, *Platichthys flesus*, *Gasterosteus aculeatus*, *Rutilus rutilus* and *Pungitius pungitius*, and larger crustaceans such as *Crangon crangon*, *Palaemon elegans*, *Palaemon adspersus*, and *Rhithropanopeus harrisii*, which occasionally formed pools of 1–3 individuals. Benthic plants (vascular plants and macroalgae) were placed separately in other containers. In the laboratory, the plants were cleaned of any debris and associated fauna, rinsed with Milli-Q water, and identified to the lowest possible taxonomic level (species in most cases). Additionally, epiphytes were collected from the vascular plants and macroalgae sampled in each habitat and during each sampling event. The epiphytes were separated from the host plants in an

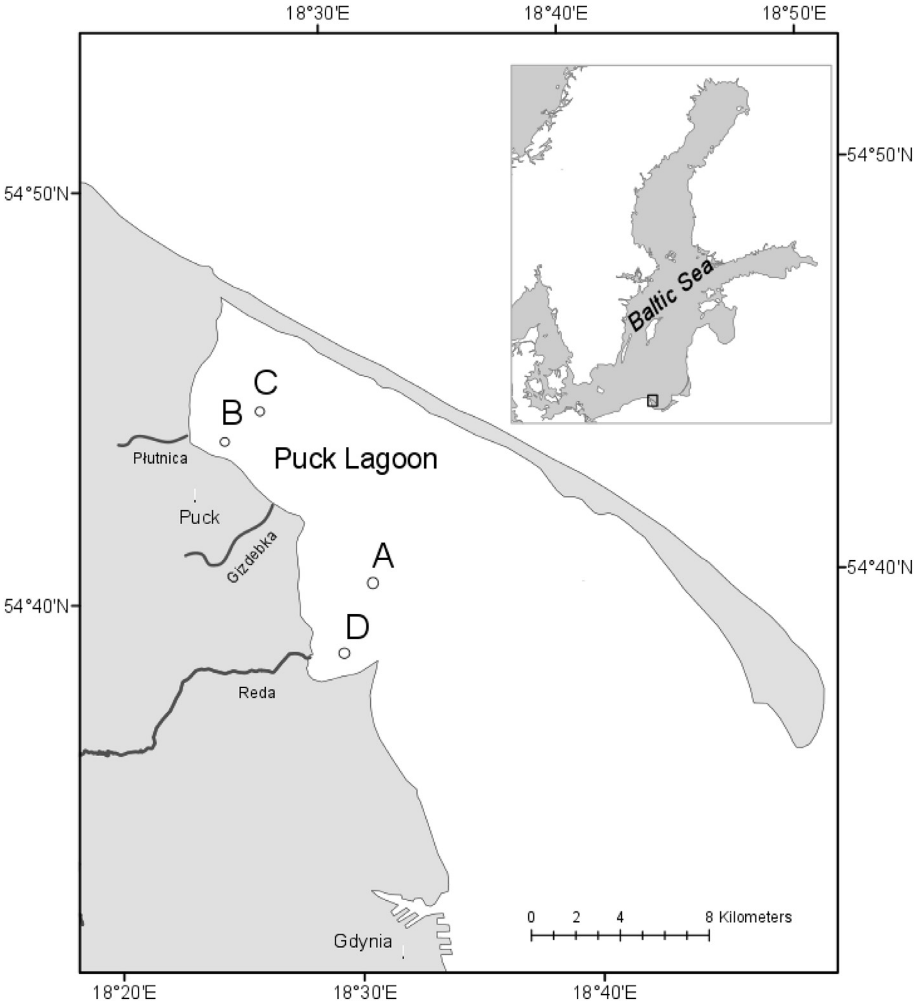

Fig. 1. Location of sampling sites (habitats in the Puck Lagoon) (southern Baltic Sea).

ultrasonic bath. The water with the detached organisms was then filtered through Whatman GF/F filters on a standard filtration system, and the filters containing the epiphytes were stored frozen (−20 °C).

Meiofauna was collected in sediment samples in five replicates with a Van Veen grab. The top 2 cm of sediment and a 2 cm layer of the overlying bottom water were sieved gently through a 125 µm mesh net, and the aliquot was placed in a collective container. A modified method for bulk meiofauna extraction was used that is based on the active downward migration of the meiofauna through sediments (Rzeznik-Orignac et al., 2004). In brief, the sediments were stirred and sieved through a 40 µm mesh net four times to detach the meiofauna from the sediment particles. A mixture of meiofauna and sediment particles was then placed on 1 cm layer of three-time precombusted (450 °C, 8 h) coarse sand, which was covered with a 200 µm net, and irradiated by a light source for 48 h. The net was sprinkled often with seawater to prevent it from drying out. Negative phototaxis led the nematodes to migrate downward, and they were collected in Whatman GF/F filtered seawater in a collector container under the sand. Single individuals were handpicked with a fine needle under a microscope, rinsed twice in seawater to remove adhering particles, and finally pooled in polyethylene vials containing Milli-Q water (at least 80 individuals per pool). The pooled samples were then centrifuged and stored frozen (−20 °C) until further processing.

Surface sediments (0–10 cm) were sampled in triplicate with a Van Veen grab and stored in high-density polyethylene bags at −20 °C until analysis.

2.2. Stable isotope determination

The samples were freeze-dried and acidified when necessary. Filters with suspended particulate matter and epiphytes were acidified overnight with 0.1 N HCl, while sediment and fauna containing encrusted components such as crustaceans, fishes, gastropods, and bivalves were acidified overnight with 1.0 N HCl. After acidification, all samples were frozen (−20 °C) and freeze-dried again. The top-most surface of the filters was gently scrubbed off and special care was taken to avoid collecting glass material that is known to affect the conversion of organic carbon to CO_2 during combustion (Boutton, 1991). The sediment samples were homogenized in a standard mortar, dry sieved through a polypropylene 63 µm mesh net, and the aliquot was collected for stable isotope analysis. Benthic plants and animals were ground to a fine powder in a Retsch mixer mill MM 200. The stable isotope ratios of C and N were measured using an Isoprime Micromass IRMS-EA (a Micromass CHN analyzer coupled with a Micromass mass spectrometer) that provides simultaneous data on carbon and nitrogen content. Isotope composition was expressed in standard δ units (‰). Replicate analyses of standards permitted a calculation precision (analytical error; SD) for the overall procedure (i.e., sample preparation and analysis) of ± 0.1‰ for carbon and ± 0.2‰ for nitrogen.

2.3. Statistical analysis and modeling

The statistical significance of differences in stable isotope ratios among potential food sources and consumers was assessed using the three-way PERMANOVA+ model based on a similarity matrix created from Euclidian distances among samples (Anderson et al., 2008). The statistical model consisted of three factors: habitats (4 levels, fixed); seasons (4 levels, fixed and crossed with habitats); and food type (6 levels, fixed, and crossed with habitats and seasons). PERMANOVA was performed on the Euclidean distance matrices, and a square root transformation was performed on the data. The statistical significance of the PERMANOVA results was assessed using a permutation procedure ($n = 9999$) of the residuals under a reduced model (Anderson et al., 2008). The significance of individual differences between two variables was checked with the pairwise *t*-test. In order to estimate the proportion of sources that contributed to consumer diets, a Bayesian mixing model approach was applied using the Stable Isotope Analysis in R (SIAR) software package. Bayesian statistics combine the isotope ratio variability of consumers and potential food sources with the trophic fractionation factor (Parnell et al., 2010). The trophic enrichment factor (TEF) is no longer considered to be a constant value because many factors can affect the fractionation process in organism tissues (Caut et al., 2009; Martinez del Rio et al., 2009). We used the linear model for invertebrates from Caut et al. (2009) to estimate source-specific invertebrate TEF based on the isotopic ratio of the food sources: $\Delta\delta^{13}C = -0.113 \times \delta^{13}C_{sources} - 1.916$ and $\Delta\delta^{15}N = -0.311 \times \delta^{15}N_{sources} + 4.065$. The results of the source-specific TEF calculation with their standard deviations were included in the Bayesian mixing model to improve the precision of diet analysis. Our results showed that TEF ranged from 0.40 to 0.96‰ for $\Delta\delta^{13}$C and from 1.73 to 3.08‰ for $\Delta\delta^{15}$N (Table 1), i.e., within the ranges of recommended TEFs (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003; Caut et al., 2007).

To examine the trophic structure of benthic communities in different habitats, the δ^{15}N values of the consumers were converted to the relative trophic level (RTL) using the following equation:

$$RTL = \lambda + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{base}}{\Delta_n}$$

where λ is the RTL of taxon used to estimate $\delta^{15}N_{base}$, $\Delta_n$is the enrichment in ^{15}N per trophic level, and $\delta^{15}N_{consumer}$is the direct measurement of $\delta^{15}N$ for the target taxon (Post, 2002). $\delta^{15}N_{base}$ was calculated for taxa that met the following criteria: they shared the same habitat as the target species, and they integrated the isotopic ratio of the food web on a scale large enough to minimize the effects of short-term variations (Post, 2002). Based on the abundance and biomass of macrobenthic fauna in different habitats, a suspension-feeding cockle (*Cerastoderma glaucum*) was used as the $\delta^{15}N_{base}$ in habitats with low biomass vegetation (A, D). The taxa that best reflected the food web base in habitats with massive benthic vegetation were the isopods *Lekanesphaera hookeri* (in habitat B) and *Idotea chelipes* (in habitat C) that feed mostly on plant material in the Baltic Sea (Jankowska, 2017). Food chain length (FCL) was defined as the trophic position of the top predator, i.e., the taxon with the highest δ^{15}N value (Vander Zanden and Rasmussen, 2001).

The normality of the data was verified with the Shapiro-Wilk test, and then the functional relation between species richness and FCL was described with parametric Pearson correlation analysis.

Table 1
Estimates of trophic enrichment factors (TEF) based on the model developed by Caut et al. (2009).

Source	δ^{13}C TEF		δ^{15}N TEF	
	Mean	SD	Mean	SD
SPOM	0.96	0.19	2.25	0.37
phytoplankton	0.81	0.18	2.16	0.40
SOM	0.75	0.11	3.08	0.96
macroalgae	0.40	0.09	1.73	0.32
vascular plants	−0.62	0.16	2.45	0.21
epiphytes	0.48	0.19	2.24	0.32

Table 2
Results of three-way PERMANOVA tests for differences in δ^{13}C and δ^{15}N of organic matter among habitats, seasons, and types of potential food sources (SPOM, phytoplankton, SOM, macroalgae, vascular plants, and epiphytes) for benthic fauna in the Puck Lagoon (statistically significant values are in boldface type).

Factor	*df*	*MS*	*Pseudo-F*	*P*
$\delta^{13}C$				
Habitat	3	20.11	25.24	**0.001**
Season	3	6.01	7.54	**0.001**
Food type	5	345.11	434.22	**0.001**
Habitat × season	9	4.88	6.12	**0.001**
Habitat × food type	14	6.43	8.07	**0.001**
Season × food type	15	7.13	8.95	**0.001**
Habitat × season × food type	34	2.82	3.54	**0.001**
$\delta^{15}N$				
Habitat	3	21.51	65.90	**0.001**
Season	3	18.81	57.64	**0.016**
Food type	5	35.52	108.83	**0.001**
Habitat × season	9	4.30	13.18	**0.001**
Habitat × food type	14	4.69	14.39	**0.001**
Season × food type	15	7.56	23.17	**0.001**
Habitat × season × food type	34	2.07	6.37	**0.001**

3. Results

3.1. Spatial and temporal variations of δ^{13}C and δ^{15}N from organic matter sources

δ^{13}C and δ^{15}N were measured in the following ecosystem components that were potential organic matter sources for benthic consumers: suspended particulate organic matter (SPOM), phytoplankton, sediment organic matter/detritus (SOM), macroalgae, vascular plants, and epiphytes. These organic carbon sources differed statistically in isotope carbon ratios (δ^{13}C spanned a range of −18.9‰ for all habitat and seasons, i.e., from −9.2‰ for *Zostera marina* in habitat C to −28.1‰ for phytoplankton in habitat D) and in stable nitrogen ratios (δ^{15}N spanned a range of 13.3‰, i.e., from −4.2‰ for SOM in habitat A to 9.1‰ for phytoplankton in habitat A). δ^{13}C and δ^{15}N varied significantly among organic matter sources, habitats, and seasons, and the type of organic matter that had the strongest effect on δ^{13}C and δ^{15}N (Table 2). Regardless of habitat and season and in the majority of cases, phytoplankton (from −28.1‰ to −21.3‰) and SPOM (from −27.9‰ to −24.2‰) were the most ^{13}C-depleted. The SOM carbon isotope ratio was within the ranges of SPOM and phytoplankton (from −26.4‰ to −21.6‰), which reflects a combination of pelagic material, and, presumably, the microbial decomposition of SOM. Macroalgae spanned the smallest δ^{13}C range (from −19.2‰ to −22.1‰ for *Cladophora glomerata*), while δ^{13}C ranged from −19.1‰ to −24.7‰ in epiphytes.

Individual organic matter sources varied spatially and over time (Table 3) with similar seasonal patterns in all habitats in most cases. The carbon isotope ratios of SPOM were lower in spring, while ^{13}C-enriched SPOM was noted in the winter and summer seasons (Fig. 2a). In contrast, increased δ^{13}C was observed in phytoplankton in fall, and the lowest carbon isotope ratios occurred in winter. The mean δ^{13}C of SPOM and phytoplankton was lowest in habitat D (−26.5‰ ± 0.4, $n = 12$ and − 25.4‰ ± 1.6, n = 12, respectively) and the highest was in habitat B (−24.7‰ ± 1.8, n = 12 and − 23.5‰ ± 0.9, n = 12, respectively). The pairwise *t*-test indicated significant differences among habitats in phytoplankton δ^{13}C in winter and summer (Table 4) thereby separating habitats into those located in the inner lagoon (habitats B and C) and those in the outer lagoon (habitats A and D). Moreover, SPOM nitrogen isotope ratios were much higher (average for two habitats 6.7‰ ± 0.8, $n = 24$) in the outer lagoon habitats than in those in the inner lagoon (habitats B and C, 5.1‰ ± 0.7, n = 24)

Table 3
Results of two-way PERMANOVA tests for differences in $\delta^{13}C$ and $\delta^{15}N$ of potential organic matter sources among habitats, seasons, taxa (only for macroalgae) and species (only for vascular plants) in the Puck Lagoon (statistically significant values are in boldface type).

Factor	$\delta^{13}C$				$\delta^{15}N$			
	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
SPOM								
Habitat	3	3.13	286.1	**0.001**	3	12.16	489.54	**0.001**
Season	3	14.43	1318.2	**0.001**	3	1.47	59.40	**0.001**
Habitat × season	9	1.24	113.71	**0.001**	9	0.98	39.52	**0.001**
Phytoplankton								
Habitat	3	7.48	20.86	**0.001**	3	11.68	32.53	**0.001**
Season	3	15.62	43.53	**0.001**	3	4.18	11.66	**0.001**
Habitat × season	9	4.71	13.14	**0.001**	9	0.82	2.31	0.051
SOM								
Habitat	3	21.65	2426.8	**0.001**	3	3.51	76.88	**0.001**
Season	3	0.15	17.47	**0.001**	3	39.81	870.72	**0.001**
Habitat × season	9	0.74	83.99	**0.001**	9	8.01	175	**0.001**
Macroalgae								
Taxa	3	1.82	1.1	0.870	3	4.09	7.70	**0.001**
Habitat	3	1.60	1.80	0.149	3	5.90	17.53	**0.001**
Season	3	1.25	1.38	0.270	3	1.39	1.69	0.196
Habitat × season	6	3.28	1.49	0.341	6	1.18	23.22	**0.001**
Vascular plants								
Species	1	3.24	1.71	0.220	1	6.87	17.48	**0.001**
Habitat	2	9.27	83.38	**0.001**	2	4.63	78.13	**0.001**
Season	3	3.83	34.44	**0.001**	3	0.28	4.85	**0.014**
Habitat × season	3	2.04	18.38	**0.001**	3	1.17	19.87	**0.001**
Epiphytes								
Habitat	3	13.14	6.33	**0.002**	3	20.74	29.64	**0.001**
Season	3	5.54	2.62	**0.049**	3	8.70	12.43	**0.001**
Habitat × season	9	8.82	4.22	**0.001**	9	2.75	3.94	**0.004**

Table 4
Pairwise t-test comparison of the $\delta^{13}C$ of phytoplankton and consumers between habitats in winter and summer (9999 permutations in a reduced model). Values in boldface type indicate significant effects. A, B, C, and D – benthic habitats in the Puck Lagoon.

Season	winter		summer	
	t	p	t	p
Phytoplankton				
A vs B	8.08	**0.029**	2.35	0.105
A vs C	5.68	**0.035**	6.78	**0.023**
A vs D	0.44	0.675	5.68	0.108
B vs C	0.26	0.751	1.72	0.165
B vs D	9.69	**0.040**	5.55	**0.030**
C vs D	6.39	**0.029**	12.46	**0.030**
Consumers				
A vs B	3.86	**0.001**	5.08	**0.001**
A vs C	5.03	**0.001**	6.11	**0.001**
A vs D	2.39	**0.011**	1.81	0.053
B vs C	0.54	0.739	1.25	0.231
B vs D	5.03	**0.001**	6.47	**0.001**
C vs D	6.41	**0.001**	7.72	**0.001**

(Fig. 2b). In habitats B and C, SPOM $\delta^{15}N$ temporal variations were similar with lower values in winter and higher values in spring. In habitat D in the vicinity of the Reda River, a notable decrease of SPOM $\delta^{15}N$ was recorded in fall, but this rose gradually through winter and into summer. Spring ^{15}N-enrichment (except in habitat A) was also observed in phytoplankton, which coincided with increased pelagic primary production as was shown by the high concentration of chlorophyll *a* in the water column (Sokołowski et al., 2015). Additionally, the mean $\delta^{15}N$ of SPOM and phytoplankton was the lowest in habitat B (4.8‰ ± 0.5, *n* = 12 and 4.9‰ ± 0.7, n = 12, respectively) and the highest in habitat D (7.1‰ ± 0.6, n = 12 and 7.4‰ ± 0.8, n = 12, respectively).

The highest carbon isotope ratios of SOM were observed in habitat C (mean ± SD for all seasons; −21.9‰ ± 0.2, n = 12) and the lowest were in habitat B (−25.9‰ ± 0.4, n = 12), while the $\delta^{13}C$ values for SOM in habitats A and D were intermediate (Fig. 2a). Seasonal variations of SOM $\delta^{13}C$ were less pronounced than those of SPOM and phytoplankton, but nitrogen isotope ratios varied markedly among the seasons. Apparently, lower SOM $\delta^{15}N$ occurred in fall and increased in winter, and then it remained fairly stable in spring and summer in all the habitats. It is noteworthy that in habitats A and D SOM $\delta^{15}N$ reached negative values of −4.2‰ and − 0.9‰, respectively, in fall.

Sokołowski et al. (2015) provide detailed data on species composition and the total biomass of benthic primary producers in different habitats of the Puck Lagoon. Primary producer $\delta^{13}C$ and $\delta^{15}N$ differed

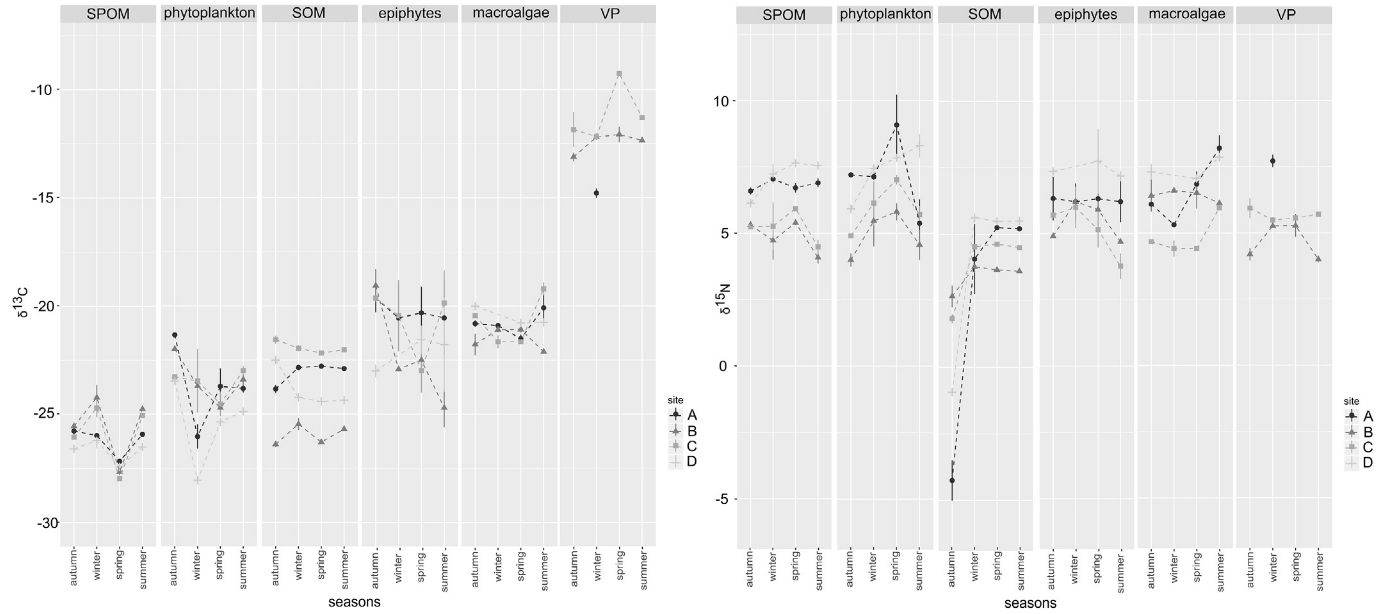

Fig. 2. Temporal variations of carbon (a) and nitrogen (b) isotope ratios (mean ± SD) of suspended organic matter (SPOM), phytoplankton, sediment organic matter/detritus (SOM), benthic primary producers (macroalgae, epiphytes, vascular plants) in four benthic habitats in the Puck Lagoon from fall 2010 to summer 2011.

statistically (one-way PERMANOVA, df = 3, Ms. = 831.99, Pseudo-F = 108.5, p < 0.001 for δ^{13}C and df = 3, Ms. = 66.20, Pseudo-F = 371.31, p < 0.001 for δ^{15}N), and vascular plants had the lowest δ^{15}N. Additionally, vascular plant δ^{13}C was lower than that of macroalgae and epiphytes, which reflected differences in their mode of C fixation and the use of different C sources (Marshall and Zhang, 1994). The biomass of sandy bottoms with little vegetation (habitats A and D) were mostly dominated by two species of macroalgae, *Cladophora glomerata* (habitat A) and *Pylaiella littoralis* (habitat D), while in habitats B and C the prevailing vascular plants were pondweed, *Stuckenia pectinata*, and eelgrass, *Z. marin*a, respectively. Macroalgal biomass in habitats A and D was substantially lower than in habitats B and C (Sokołowski et al., 2015). Macroalgal taxa showed apparent variations in δ^{13}C and δ^{15}N over time, but only δ^{15}N was statistically different among taxa and habitats (Table 3). Macroalgal δ^{15}N was the highest on sand with little vegetation, and temporal patterns were similar in habitats A and D. The isotopic ratios of epiphytes also varied among habitats and seasons with higher values of δ^{15}N noted during the vegetative season in habitats A and D. The seasonal variation of epiphyte δ^{13}C was similar to that of phytoplankton, but mean epiphyte δ^{13}C was much higher (Fig. 2a). The vascular plants that dominated the biomass structure in habitats B and C also occurred occasionally in winter in habitat A. Vascular plant δ^{13}C and δ^{15}N varied substantially in all seasons, and the interspecific differences in nitrogen isotope ratios were significant (Table 3). *Zostera marina* δ^{13}C was lower (−11.2‰ ± 1.3, *n* = 12) than that of *S. pectinata* (−12.4‰ ± 0.4, n = 12), whereas *Z. marina* δ^{15}N was slightly higher (5.7‰ ± 0.2, n = 12) than that of *S. pectinata* (4.7 ± 0.6, n = 12).

3.2. Contribution of organic matter sources to sediments

The SIAR results demonstrated that SOM in different habitats consisted of different sources and that SPOM and phytoplankton dominated in most cases (Fig. 3). Despite large biomass, vascular plants were of minor importance (< 20%) in habitats B and C, while macroalgae contributed considerably to SOM in all habitats (the maximum macroalgal contribution in spring was 43% in habitat A). A high percentage of macroalgae in SOM was observed mainly in habitats A and D in all seasons (except winter).

3.3. Spatial and temporal variations of consumer δ^{13}C and δ^{15}N

The benthic communities of the Puck Lagoon were composed of 29 macrofaunal species, one meiofaunal compartment (nematodes), two demersal fishes associated with seagrass beds (*Sygnathus typhle*, *Nerophis ophidion*), four demersal fishes (*Pomatoschistus minutus*, *Neogobius melanostomus*, *Gobius niger*, *Platichthys flesus*) and four benthopelagic fishes (*Pungitius pungitius*, *Gasterosteus aculeatus*, *Perca fluviatilis, Rutilus rutilus*). Consumers differed statistically in isotope carbon ratios spanning from −15.5‰ for *Palaemon adspersus* (habitat B) to −25.7‰ for *Mya arenaria* (habitat D) and in isotope nitrogen ratios spanning from 4.7‰ for *Gammarus* spp. (habitat C) to 14.9‰ for *P. flesus* (habitat D) (Fig. 4). The annual δ^{13}C mean (± SD) in habitat A ranged from −25.6‰ ± 0.7 (*n* = 4) for the cockle *Cerastoderma glaucum* to −17.3‰ ± 0.1 (*n* = 2) for the bryozoans *Einhornia crustulenta*. In habitat B, the pipefish *N. ophidion* had the lowest δ^{13}C (−24.1‰ ± 1.4, *n* = 3), whereas the prawn *P. adspersus* was the most ^{13}C-enriched (−15.5‰ ± 1.5, *n* = 2*)*. In habitat C, the range of consumer δ^{13}C was the widest (8.7‰) and varied from −25.2‰ ± 1.0 (n = 4) for *C. glaucum* to −16.7‰ ± 0.5 (*n* = 3) for *P. adspersus*. In habitat D, the lowest consumer δ^{13}C was noted in the clam *M. arenaria* (−25.7‰ ± 1.1, n = 4), while the highest was noted in the isopod *Lekanesphaera hookeri* (−17.6‰ ± 0.1, *n* = 1). The annual mean benthic consumer δ^{15}N in habitat A ranged from 6.8‰ ± 0.5 (n = 2) for *C. glaucum* to 14.1‰ ± 0.7 (n = 1) for the perch *P. fluviatilis*. In habitat D, the highest δ^{15}N value was measured for *P. flesus*

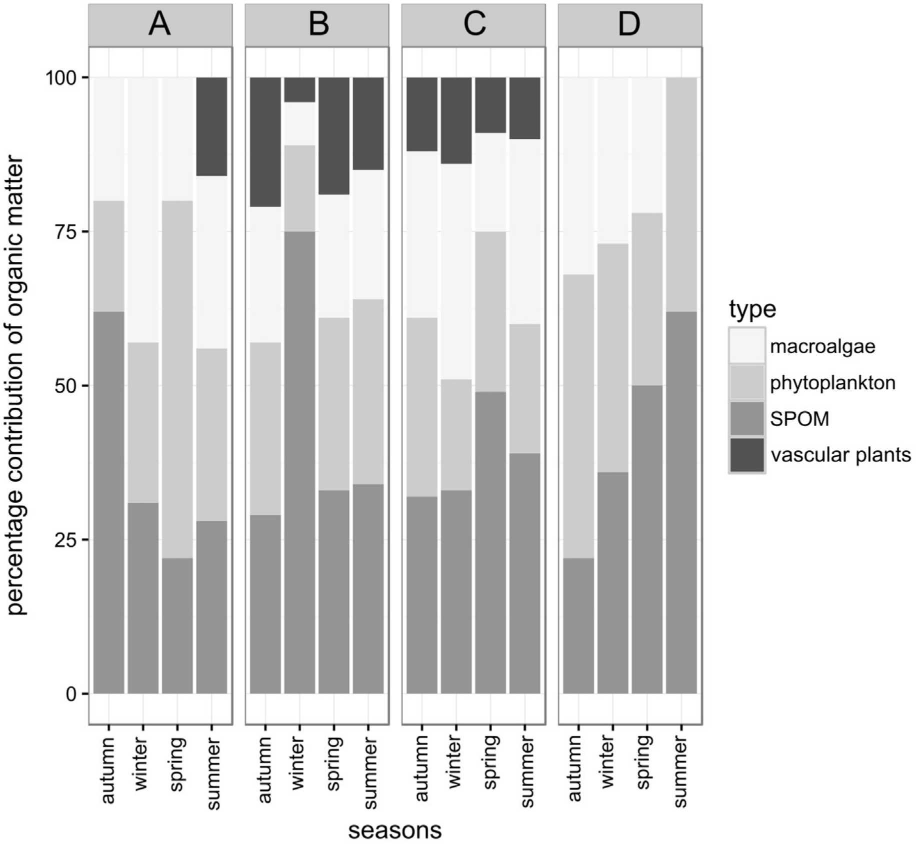

Fig. 3. Percentage contribution of different organic matter sources to SOM in benthic habitats in the Puck Lagoon in four seasons determined with SIAR.

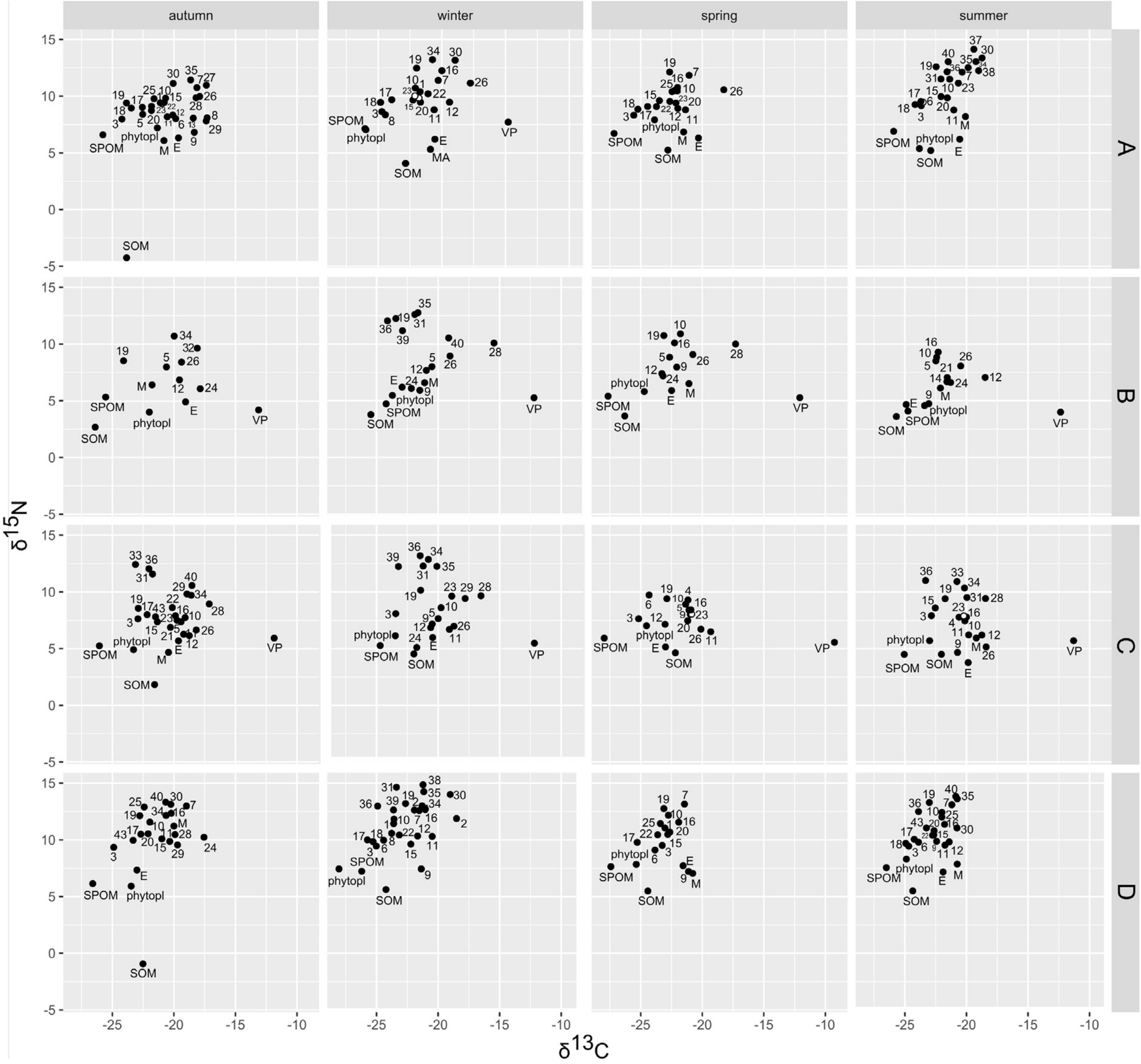

Fig. 4. Biplots of carbon and nitrogen stable isotope ratios of benthic consumers, fishes, and organic matter sources (SPOM, Phyt – phytoplankton, SOM, E – epiphytes, M – macroalgae, Vp – vascular plants) in different benthic habitats of the Puck Lagoon in four seasons (from fall 2010 to summer 2011). Each benthic consumer is denoted by a number: 1 - *Amphibalanus improvisus*, 2 - *Bathyporeia pilosa*, 3 - *Cerastoderma glaucum*, 4 - Chaoboridae, 5 - Chironomidae, 6 - *Corophium volutator*, 7 - *Cyathura carinata*, 8 - *Einhornia crustulenta*, 9 - *Gammarus* spp., 10 - *Hediste diversicolor*, 11 - *Peringia ulvae*, 12 - *Idotea chelipes*, 13- *Jaera* spp., 14 - *Lymnea peregra*, 15 - *Limecola balthica*, 16 - *Marenzelleria neglecta*, 17 - *Mya arenaria*, 18 - *Mytilus trossulus*, 19 - Nematoda, 20 - Oligochaeta, 21 - *Potamopyrgus antipodarum,* 22 - *Pygospio elegans*, 23 - *Rhithropanopeus harrisii*, 24 - *Lekanesphaera hookeri*, 25 - *Streblospio* spp., 26 - *Theodoxus fluviatilis*, 27- *Dendrocoelum lacteum*, 28 - *Palaemon adspersus*, 29 - *Palaemon elegans*, 30 - *Crangon crangon*, 31- *Pungitius pungitius*, 32 - *Rutilus rutilus*, 33 - *Sygnathus typhle*, 34 - *Pomatoschistus minutus*, 35 - *Neogobius melanostomus*, 36 - *Nerophis ophidion*, 37- *Perca fluviatilis*, 38 - *Platichthys flesus*, 39 - *Gasterosteus aculeatus*, 40 - *Gobius niger.*

(14.9‰ ± 0.1, n = 1), while the amphipods *Gammarus* spp. exhibited the lowest mean δ^{15}N (7.2‰ ± 0.5, n = 3). Benthic consumers associated with sandy bottoms with little vegetation (habitats A and D) demonstrated significantly higher mean δ^{15}N compared to those in habitats B and C, but their δ^{15}N range was much smaller (7.3‰ and 7.7‰, respectively). In habitat B, *Gammarus* spp. was the most ^{15}N-depleted (4.7‰ ± 1.4, n = 3), whereas the goby *N. melanostomus* had the highest δ^{15}N values (12.8‰ ± 1.4, n = 3). The widest range of mean δ^{15}N was observed in habitat C from 4.7‰ ± 1.4 (n = 3) for *Gammarus* spp. to 13.2‰ ± 0.8 (n = 3) for *N. ophidion*.

Consumer δ^{13}C and δ^{15}N varied significantly among habitats and seasons and the strongest effect on δ^{13}C and δ^{15}N was elucidated by habitat (Table 5). The pairwise t-test showed significant differences in consumer δ^{13}C among habitats in winter and summer (Table 4). Similarly to phytoplankton δ^{13}C, consumer δ^{13}C clearly separated habitats in the inner lagoon (B and C) from those in the outer lagoon (A and D).

Table 5
Results of two-way PERMANOVA tests for differences in δ^{13}C and δ^{15}N of all consumers among habitats and seasons (statistically significant values are in boldface type).

Factor	*df*	*MS*	*Pseudo-F*	*P*
δ^{13}C				
Habitat	3	94.78	32.02	**0.001**
Season	3	59.48	20.01	**0.001**
Habitat × season	9	3.55	1.21	0.030
δ^{15}N				
Habitat	3	319.84	110.37	**0.001**
Season	3	34.82	12.02	**0.001**
Habitat × season	9	22.82	7.88	**0.001**

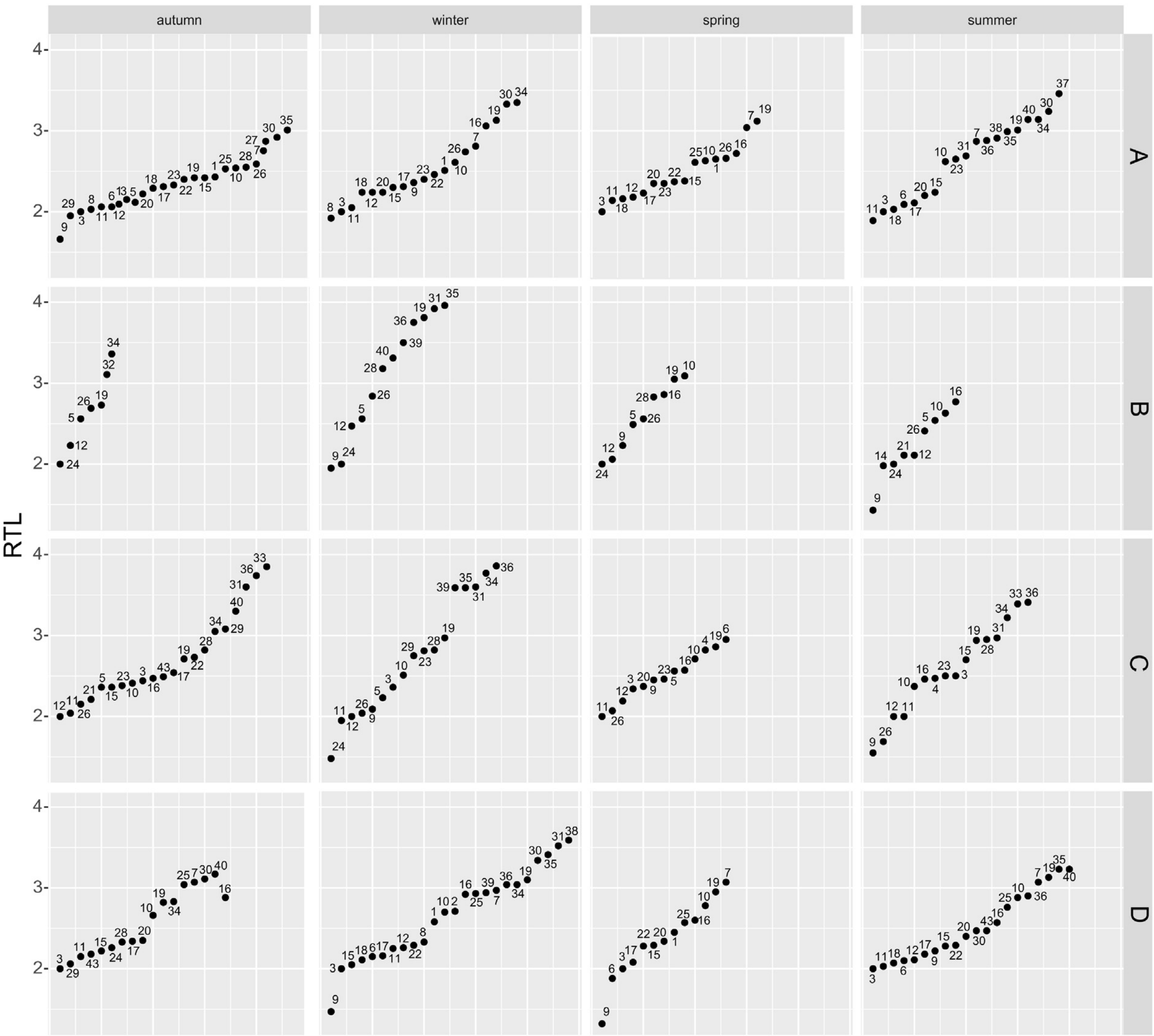

Fig. 5. Trophic position of consumers from different habitats in the Puck Lagoon. See Fig. 4 for abbreviations of species/groups.

For most taxa, the carbon isotope ratios in habitats B and C were higher than those in habitats A and D (Fig. 4). In contrast, benthic fauna δ^{15}N in habitats A and D had higher values than that in habitats B and C (Fig. 4). Similar patterns of δ^{13}C seasonal variation were detected for all habitats with lower values in winter and higher ones in summer. In addition, the broadest range of consumer δ^{13}C was observed in winter, while the narrowest was in the vegetative season (Fig. 4).

3.4. *Benthic community trophic structure and stability*

Three trophic levels were designated in the benthic communities of all the Puck Lagoon habitats (Fig. 5). The longest food chain (maximum RTL) was detected in habitat C and the shortest was in habitat A, while intermediate RTLs were noted in the faunal communities in habitats B and C (Fig. 5). Regardless of habitat, in most cases the lowest RTL was found (except habitat A) in spring and the highest was in winter. On sandy bottoms with little vegetation (habitats A and D), the highest trophic position was occupied by gobies, *N. melanostomus* and *G. niger*, brown shrimp, *Crangon crangon*, and *P. fluviatilis* (habitat A in summer) or *P. flesus* (habitat D in winter) (Fig. 5). *N. melanostomus* was also the top carnivore in habitat B in fall and winter, but the top consumers in habitat C included two pipefish species (*S. typhle* and *N. ophidion*) in all seasons. It is noteworthy that the number of primary consumers ($1 < \text{RTL} \leq 2$) in habitat B (12 taxa) was apparently lower than that in other habitats (from 16 to 24), and the habitat A benthic community contained the most numerous (nine taxa) secondary consumers ($2 < \text{RTL} \leq 3$). Macrobenthic communities from different habitats had different species richness and taxonomic composition (Sokołowski et al., 2015). No significant correlation was observed, however, between the number of species and FCL (correlation analysis).

3.5. *Contribution of organic matter sources to consumer diets*

Six organic matter sources (i.e., SPOM, phytoplankton, SOM, epiphytes, macroalgae, and vascular plants) likely support primary consumers in the Puck Lagoon. In order to determine the main trophic pathways, dominant primary consumers in terms of biomass were chosen in each habitat and season based on data presented in Sokołowski et al. (2015). The species selected constituted together > 95% of the total biomass of macrofaunal assemblages in a given habitat. Diet preferences of primary consumers were defined using literature data, and the contribution of different food sources to the diets of given species was assessed using SIAR. The model showed that the contribution of food sources differed among habitats and seasons for given species (Table 6). For example, on sandy bottoms with little vegetation (habitats A and D) *Peringia ulvae*, a typical grazer, fed mostly on macroalgae, while sediment was its prevailing organic matter source in habitat C in summer (41%) and fall (54%). Two other small

Table 6
Contribution of different organic matter sources (%) to the diets of dominant macrobenthic faunal taxa in different habitats of the Puck Lagoon in four seasons (results of the SIAR mixing model). Only taxa with biomass > 5% are presented. Phyt – phytoplankton, M – macroalgae, E – epiphytes, Vp – vascular plants.

Habitat		Autumn							Winter						
		SPOM	Phyt	SOM	M	E	Vp	fauna	SPOM	Phyt	SOM	M	E	Vp	fauna
A	*Cerastoderma glaucum*	74	26						45	55					
	Hediste diversicolor	13	24	8	22			33	19	17	18	20			26
	Peringia ulvae			6	78	16					35	31	20	14	
	Limecola balthica	15	79	6					21	19	60				
	Mya arenaria	38	62												
	Mytilus trossulus								60	40					
	Rhithropanopeus harrisii										22	19			59
B	*Chironomidae*			18	52	14	16				19	32	32	17	
	Theodoxus fluviatilis			15	37	26	22				16	28	24	32	
C	*Cerastoderma glaucum*	49	51						50	50					
	Hediste diversicolor	13	16	22	23			26	12	19	21	22			26
	Peringia ulvae			54	16	14	16				27	28	23	22	
	Idotea chelipes				43	37	20					51	38	11	
	Limecola balthica	45	43	12											
	Rhithropanopeus harrisii			17	29			54			27	33			40
	Gammarus spp.										34	29	29	8	
	Theodoxus fluviatilis										35	31	27	7	
D	*Cerastoderma glaucum*	76	24						88	12					
	Hediste diversicolor	20	24	19	37				19	15	24				42
	Peringia ulvae			18	65	17					100				
	Limecola balthica	28	42	30					40	28	32				
	Mya arenaria	35	65						60	40					
	Marenzelleria neglecta	29	38	33					33	28	39				

habitat		Spring							Summer						
		SPOM	Phyt	SOM	M	E	Vp	fauna	SPOM	Phyt	SOM	M	E	Vp	fauna
A	*Cerastoderma glaucum*	87	13						47	53					
	Hediste diversicolor	7	25	30	38				9	23	21	47			
	Peringia ulvae			33	46	21					24	49	27		
	Limecola balthica	28	43	29					14	53	33				
	Mya arenaria	54	46						41	59					
	Rhithropanopeus harrisii										27	73			
B	*Chironomidae*			41	29	24	6				28	32	31	9	
	Theodoxus fluviatilis			40	29	23	8				20	29	25	26	
	Lymnea peregra										62	6	6	26	
	Gammarus spp.			30	34	28	8				40	24	30	6	
	Idotea chelipes				41	27	32								
	Lekanesphaera hookeri				43	48	9								
	Hediste diversicolor	9	17	11	33			30							
	Marenzelleria neglecta	26	50	24											
C	*Cerastoderma glaucum*	50	50						28	72					
	Hediste diversicolor	12	19	21	22			26							
	Peringia ulvae			27	28	23	22				41	21	28	10	
	Idotea chelipes				51	38	11					57	34	9	
	Limecola balthica								27	40	33				
	Rhithropanopeus harrisii			29	33			38			62	15			23
	Gammarus spp.			33	30	30	7				63	15	15	7	
	Marenzelleria neglecta	26	50	24											
	Mya arenaria								16	84					
D	*Cerastoderma glaucum*								56	44					
	Hediste diversicolor	9	16	17	34			24	12	17	16	32			23
	Peringia ulvae			15	47	38					32	52	16		
	Limecola balthica	26	37	37					26	47	27				
	Mya arenaria	47	53						23	77					
	Marenzelleria neglecta	29	37	34					29	39	32				

herbivorous grazers (*I. chelipes* and L. *hookeri*), which were found in habitats B and C in spring and summer, consumed mainly macroalgae and epiphytes. Suspension feeding bivalves (*C. glaucum, M. arenaria, M. trossulus*) assimilated primarily SPOM and phytoplankton, and their relative contribution differed among seasons, but not among habitats (Table 6). The overall utilization of phytoplankton was much lower in winter when suspension feeders consumed mostly SPOM (e.g., 88% of the *C. glaucum* diet in habitat D) or SOM (e.g., 60% of the L. *balthica* diet in habitat A). Omnivorous species such as *H. diversicolor* fed mainly on small invertebrates like Chironomidae and *Corophium volutator* in fall and winter, whereas its diet was based on macroalgae in the vegetative season. Another omnivorous species, the crab *R. harrisii*, consumed small invertebrates (*Gammarus* spp., *T. fluviatlis*) throughout most of the year, but it switched to a diet based on SOM (habitat C) and one based on macroalgae (habitat A) in summer.

3.6. Trophic pathways in benthic communities in different habitats

Combining the biomass of dominant macrofaunal taxa with their carbon and nitrogen isotopic ratios revealed the main trophic pathways within benthic communities in each habitat. On sandy bottoms with little vegetation (habitats A and D), a large part of the biomass was accumulated in suspension feeders (*C. glaucum* and *M. arenaria*), which were the main primary consumers on the first trophic pathway and suspension/deposit feeders (*L. balthica*), which, together with the omnivorous *H. diversicolor* and the herbivorous *P. ulvae*, were the second pathway of energy transfer. SPOM and phytoplankton were the dominant basal organic carbon resources for benthic fauna, while macroalgae and epiphytes supported the food webs only in the vegetative season (Fig. 7). SOM was utilized mainly in spring (up to 32% of the *H. diversicolor*, *P. ulvae*, *L. balthica*, *Marenzelleria neglecta* diets in habitat D) and in winter (up to 26% in habitat A). Macroalgae were of minor importance although their overall percentage contribution to the benthic fauna diet increased in summer up to 27% and 17% in habitats A and D, respectively. On sediments with a large benthic vegetation biomass (habitats B and C), benthic communities utilized basal resources differently. Although habitat B was characterized by high *S. pectinata* biomass and benthic fauna was composed mainly of omnivores (Chironomidae larvae) and herbivores (*T. fluviatilis, L. peregra*), the main food sources were SOM and macroalgae throughout the year. Benthic primary production was transferred to the first trophic level mainly by small grazers (*P. ulvae*, *T. fluviatlis*, *I. chelipes*), which consumed macroalgae and some vascular plants and epiphytes. The gastropods *T. fluviatilis and* L. *peregra* utilized mainly vascular plants in fall and summer (19% and 20%, respectively), and epiphyte consumption was the highest in spring (12%) and summer (10%) when L. *hookeri* and *T. fluviatilis* occurred abundantly. In habitat C, different basal resources were utilized more evenly. The biomass of typical grazers (*P. ulvae*, *T. fluviatilis*, *Gammarus* spp., *I. chelipes)* was similar to that of suspension and suspension/deposit feeders (*C. glaucum*, *L. balthica*, *M. arenaria*) indicating that the contribution of plant material and SPOM/SOM to the first trophic level was similar and that there were two different trophic pathways. These two energy transfer pathways combined at the third trophic level at which the omnivores *R. harrisii* and *H. diversicolor* dominated the secondary consumers (Fig. 6c).

4. Discussion

4.1. Organic matter sources

The carbon isotope ratios of SPOM in four benthic habitats of the Puck Lagoon were similar to those described in other studies for the same area (Jankowska et al., 2016; Jędruch et al., 2017) and lower than those observed in other regions of the Baltic Sea (e.g., Rolff, 2000; Nordström et al., 2009), but the temporal pattern exhibited a similar bimodal distribution with two minima, one in fall and one in spring. Lower SPOM δ^{13}C in the lagoon reflected the large input of allochthonous organic matter from rivers and anthropogenic sources, including local villages, agriculture, and terrestrial vegetation (Sokołowski, 2009). Despite the close geographical proximity of the habitats studied (from 2 to 12 km), habitat-related differences in stable carbon and nitrogen isotope ratios of potential food sources were apparent. Interestingly, in habitats B and C, which were located in the northwestern part of the inner lagoon, SPOM was of more marine origin presumably because of the horizontal transport of suspended marine organic matter from the open Gulf of Gdansk (Sokołowski, 2009). In contrast, habitats A and D in the deeper outer region, which is influenced by the Reda River, had more terrestrial SPOM δ^{13}C, particularly in spring when increased freshwater discharge accounted for more negative SPOM δ^{13}C in this area (from −27.2‰ to −27.9‰). Because of hydrodynamics (waves and currents) are not intense here and water column vertical mixing is limited, the SPOM deposition rate is higher in the Puck Lagoon (Uścinowicz, 2011; Jędruch et al., 2015), which strongly affects sediment isotopic ratios. The SOM δ^{13}C in the Puck Lagoon was much lower than typical values for estuarine sediments (Thornton and McManus, 1994; Cifuentes et al., 1996). Both carbon and nitrogen stable isotope ratios in the sediments varied spatially among the habitats and over time. SOM in the lagoon was composed of a mixture of SPOM and phytoplankton in different proportions with substantial contributions of benthic macroalgae and vascular plants locally. Microphytobenthos was not included in the analyses of SOM composition or of the macrofaunal diet because of its low biomass on sandy sediments (Sokołowski, unpublished data). The recent study by Jankowska (2017) on microphytobenthos in the Puck Lagoon using SIA and fatty acid (FA) techniques demonstrates that local microphytobenthic communities were poor and composed mainly of the bacterial fraction with MUFA 18:1ω7.

For example, ^{13}C-enriched SOM was found in the *Chara/Cladophora* dominated sediment (habitat C) suggesting that plant tissues were an important component of the sediment detrital pool (up to 20%). The significant input of plant organic matter to sediments was also observed in the *Z. marina* meadows in the Danish coastal zone by Thormar et al. (2016). Additionally, SOM consisted of high quality organic matter (low C/N ratio) in habitat C, so macrophytes probably enhanced the sedimentation of fine organic-rich particles (Benoy and Kalff, 1999; Gacia et al., 2002). A large percentage contribution of benthic plants to SOM (max. 19%) was also noted in *Stuckenia*-dominated sediment (habitat B), but SOM δ^{13}C was much lower there than could be expected. The low δ^{13}C and the poor SOM quality in this area likely resulted from terrestrial organic matter input from the Płutnica River. The SOM of sandy bottoms with little vegetation (habitats A and D) had intermediate δ^{13}C values, but δ^{15}N was clearly higher than it was in other habitats, which was probably caused by higher SPOM δ^{15}N and by decomposing floating macroalgae that entered the sediment pool (Dubois et al., 2012). Algal decomposition is faster than vascular plant degradation mainly due to their higher metabolic rates (Salovius and Bonsdorff, 2004) and more rapid bacterial development in thalli that stimulates organic matter transformation inducing increased SOM δ^{15}N (Schaal et al., 2008). SOM δ^{15}N variation was also highly seasonal, and negative values were noted in habitats A and D in fall. A shift of the nitrogen isotope ratios of organic matter in the sediments toward lower (even negative) values in autumn could be related to the recycling of ammonium and the utilization by bacteria of isotopically light $NH4+$; these processes have been described well in sestonic organic matter (Checkley Jr. and Entzeroth, 1985). Isotopic impoverishment in sediments can also indicate the bacterial decay of organic matter due to preferential degradation of ^{15}N-enriched amino acids (Wakeham et al., 1997; Böttcher et al., 1998).

4.2. Consumer utilization of food sources

Previous studies showed that benthic vegetation type (Bouillon et al., 2004; Richoux and Froneman, 2007) and hydrogeomorphology (Hoeinghaus et al., 2011) can be an important factor determining benthic consumer food source utilization in coastal areas. In our studies, consumer isotopic ratios varied among taxa and habitats suggesting that different carbon sources supported local food webs. Benthic invertebrates in the Puck Lagoon assimilated carbon mainly from their habitats as evidenced by the similar δ^{13}C values of consumers and available food sources in given habitats. Additionally, comparisons of the δ^{13}C and δ^{15}N of consumers from different habitats revealed species-specific stable isotope ratios. For example, in habitat C the typical grazing gastropod *P. ulvae* had very high δ^{13}C values and low δ^{15}N values, which mirrored the increased SOM δ^{13}C and decreased δ^{15}N in this habitat. In contrast, the low *P. ulvae* δ^{13}C values in habitats A and D were consistent with those of the benthic macroalgae and epiphytes in the vegetative season. This gastropod is characterized by trophic plasticity and derives energy mostly from green macroalgae detritus and the total SOM pool in sandy sediments (Riera, 2009). Omnivorous species such as *H. diversicolor* and *R. harrisii* also exhibited shifts in δ^{13}C and δ^{15}N among habitats. Although no clear differences in diet composition were found across habitats, the lower δ^{13}C of the ragworm *H.*

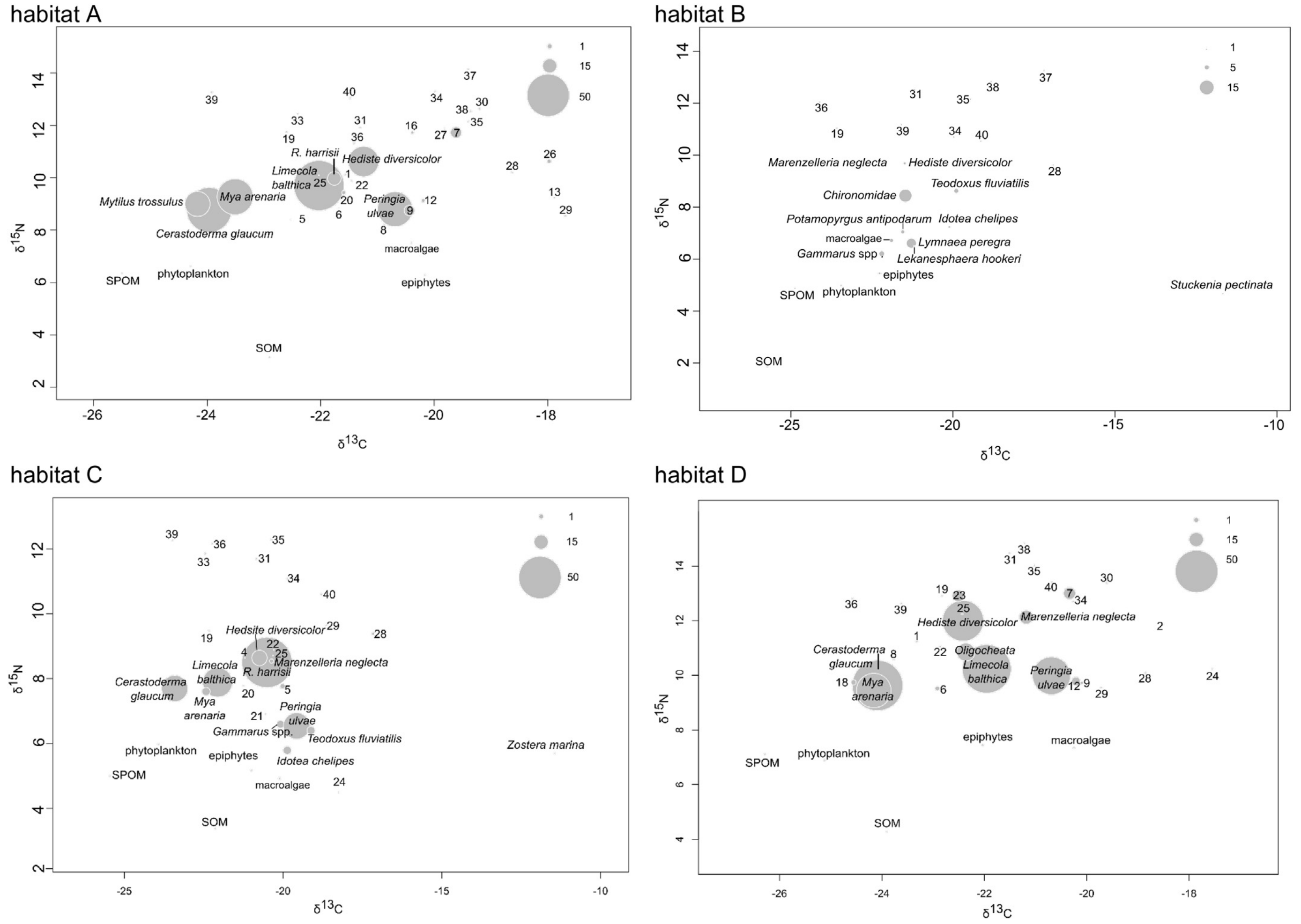

Fig. 6. $\delta^{13}C$ vs. $\delta^{15}N$ biplot of dominant species collected in different habitats (A, B, C, D) in the Puck Lagoon. Bubble values represent the relative contribution of each species to the total biomass of the macrofaunal assemblages in each habitat. Primary consumers that contributed > 95% of the total biomass are labeled.

diversicolor in habitats A and D (Fig. 4) implies the assimilation of ^{13}C-depleted SPOM and phytoplankton, while the increased $\delta^{13}C$ of the American crab *R. harrisii* in habitat C reflects the dietary contribution of ^{13}C-enriched organic matter from sediments. In the southern Baltic Sea, *R. harrisii* feeds on detritus and animal and plant matter, and the food it ingests varies with benthic habitats (Hegele-Drywa and Normant, 2009). Habit-specific utilization of food resources was also evident in suspension feeders. The relatively low *C. glaucum* $\delta^{13}C$ value and the important contribution of suspended organic matter in its diet in habitat A indicated the preferential assimilation of the more depleted SPOM in this area. In contrast, *L. balthica* $\delta^{13}C$ was fairly similar in three different habitats (A, C, D), and no clear spatial variability in the carbon isotope ratios of this suspension/deposit feeder was detected. It is noteworthy that the L. *balthica* $\delta^{13}C$ value exceeded markedly that of other bivalve species (*C. glaucum*, *M. arenaria*, *M. trossulus*) suggesting the importance of isotopically heavier sources such as SOM in its diet. *L. balthica* exhibits a highly flexible feeding strategy and consumes both SPOM and deposited organic matter depending on food availability and season (Riisgård and Kamermans, 2001; Törnroos et al., 2015). Indeed, the results of SIAR revealed that, in habitat A, *L. balthica* preferred phytoplankton as its major food source from spring through to fall, while SOM was its main diet item in winter when phytoplanktonic food was limited.

4.3. Food web structure vs. biodiversity and consequences in trophic pathways

Sandy bottoms with little vegetation (habitats A and D) hosted richer and more productive (Sokołowski et al., 2015) benthic communities of similar taxonomic and biomass structures with the prevalence of suspension feeders (*C. glaucum*, *M. arenaria*), facultative deposit feeders (*L. balthica*), omnivores (*H. diversicolor*), and grazers (*P. ulvae*). Differences among habitats in mean FCL were small, and there were few differences in the composition of community food web structure (Fig. 4), which was dominated by functionally similar species. While the high species richness of macrofaunal communities in sandy habitats with little vegetation does not result in higher FCL, it likely increases community stability and productivity by creating additional trophic links (Worm and Duffy, 2003). Both of the communities in habitats A and D were dominated, however, by suspension feeders that relied on suspended and/or resuspended organic matter from the water column and formed the main trophic pathway. This trophic structure was probably driven by increased SPOM concentrations originating from intense local planktonic production and the additional input of suspended material transported by sea currents from the open Gulf of Gdańsk. Secondary consumers were represented here by predatory fishes (e.g., *P. minutus*, *N. melanostomus*) and shrimp (*C. crangon*). In habitat D, high deposit feeder (oligochetes, *M. neglecta, H. diversicolor*) biomass was observed; however, this probably resulted from the shallow water depth, the sheltered environment, and increased sedimentation in the vicinity of the Reda River that supported the

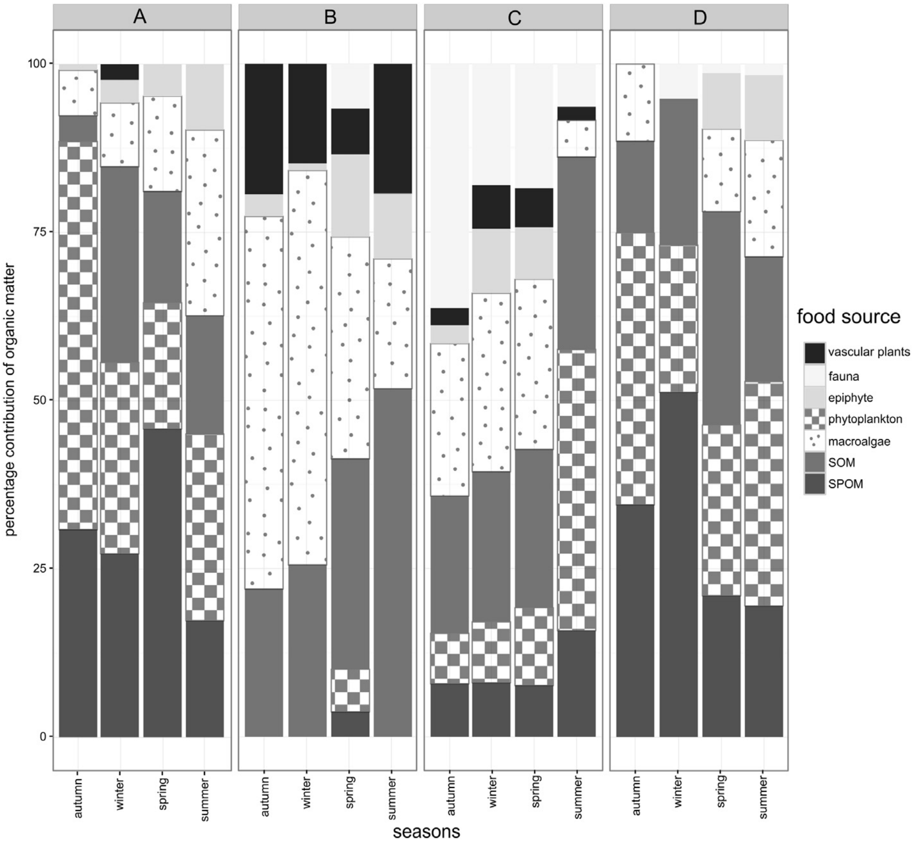

Fig. 7. Results of the isotopic mixing model determined with SIAR showing mean percentage contributions of different organic matter sources to primary consumer diets in the benthic habitats of the Puck Lagoon and in four seasons.

development of the deposit feeding community. This is common in stable marine and coastal environments where resources are limited (Levinton and Kelaher, 2004). Slow flow velocities in habitat D promoted the deposition of low quality organic matter (Dyer et al., 2002) and an increase in δ^{15}N in the food web (Carlier et al., 2008; McClelland et al., 1997, Quillien et al., 2016). Macroalgae and epiphytes were mostly utilized by *P. ulvae* and *H. diversicolor* (46% and 38% of their diets, respectively) during the vegetative season. *Peringia ulvae* formed assemblages of relatively high biomass in both habitats and was a key species that fed on plant material in the outer Puck Lagoon.

Sediments dominated by *Stuckenia* (habitat B) and *Chara/Cladophora* (habitat C) hosted highly different benthic communities despite similar vegetation biomass and vascular plant dominance. The benthic fauna in habitat B was characterized by a low number of taxa and the lowest biomass with few primary consumers, which could have resulted from the low resource availability and low quality SOM in this habitat (high C/N ratio; Sokołowski et al., 2015). The SOM in this habitat was mainly composed of riverine decaying SPOM (up to 60% in spring), which decreased the quality of organic matter deposited on the seafloor and highlighted the important role of terrigenous input. Habitat B was inhabited mostly by opportunistic deposit feeding Chironomidae larvae and grazing gastropods (*T. fluviatilis*, *L. peregra*) that fed on SOM (microbiologically degraded detritus) and algal material (macroalgae and epiphytes; Hemminga and Duarte, 2000). Vascular plant utilization was limited (Table 6), and that which was used was likely only in the form of dead material deposited on the seafloor. The preferential consumption of macroalgae over vascular plants stems from the lower digestibility of plant tissues because of the increased protein content associated with the microflora on their surfaces (Kornijow et al., 1995). In contrast, the high vegetation biomass and high SOM quality (Sokołowski et al., 2015) supported a more diverse benthic community with a longer mean FCL on *Chara/Cladophora* sediment than on those dominated by *Stuckenia* (habitat B). The primary consumers in habitat C were dominated by grazers and suspension/deposit feeders, while the omnivorous *R. harrisii* and the benthic fishes *S. typhle* and *N. ophidion* prevailed in higher trophic levels. The similar contribution of vascular plants to the SOM pool in habitats B and C indicated that the higher SOM quality in the latter was related to the limited inflow of terrestrial suspended organic matter with riverine water. Because habitat C is more distant from the Reda River mouth, the SPOM there contained much less degraded terrigenous material. Consumers utilized different basal resources more evenly, and none of the food types was dominant (except in summer when phytoplankton was a large share of consumer diets). *Zostera marina* did not appear to be a dominant carbon source for benthic fauna, but its leaves provided suitable substrata for numerous epiphytes, and macroalgae (e.g., *C. glomerata*) developed on its blades and roots. Macroalgae and epiphytes were actively consumed by grazers (*I. chelipes*, *P. ulvae*, *Gammarus* spp., *T. fluviatilis*) that can control algal biomass development and assist macrophytes by preventing them from becoming overgrown by microalgae (Valentine and Duffy, 2006).

5. Conclusions

Our results provided evidence of spatial and temporal variations of food web structure in geographically close benthic habitats in the Puck Lagoon. Habitat attributes such as the type and biomass of vegetation, the quality of SOM, and the presence of riverine discharge were key factors that accounted for local differences in basal resources and trophic links. The organic matter pool available for benthic animals included, to varying degrees, SPOM, phytoplankton (in the vegetative season), and SOM, which contained substantial amounts of vascular plants and macroalgae in areas with high vegetative biomass. Benthic invertebrates fed mostly on the carbon sources available in their habitats and showed species-specific stable carbon and nitrogen isotope ratios. Two main trophic pathways were designated on sediments with little vegetation in the outer lagoon: (1) SPOM and phytoplankton supported suspension feeders in the area located further from the river mouth, and (2) SOM provided the main organic matter source for deposit feeders and omnivores in the sheltered environment influenced by riverine discharge. Free-floating macroalgae and their epiphytes, which developed massively in warm seasons, were of minor importance. On *Stuckenia*-dominated sediments, SOM and macroalgae fueled the benthic food web in which opportunistic and tolerant omnivores and herbivores prevailed probably because of the high load of low quality terrigenous organic matter from riverine waters. In contrast, the large biomass of benthic vegetation and the high SOM quality promoted trophic diversity in the benthic community on *Chara/Cladophora* sediments. SPOM and phytoplankton supported suspension feeders that formed one trophic pathway, and macroalgae and epiphytes promoted grazers and omnivores that formed a parallel trophic pathway. Despite their large biomass, vascular plants appeared not to be consumed by benthic invertebrates or fishes, but they provided suitable substrata for the macroalgae that developed on their blades and roots.

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9.1. Author contribution statement

Author contribution statement

We hereby confirm, that the specific contributions to the publication:

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were as follows:

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Chapter 10. Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics

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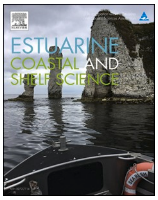

Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics

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ABSTRACT

Recognition of spatial and temporal variations of food webs is of fundamental importance for understanding ecological processes and biodiversity management. Changes in trophic organization alter routing patterns and dynamics of energy fluxes among ecosystem compartments and ultimately affect the ecosystem functioning. In this study, stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were employed to define trophic niche and diversity as well as redundancy of four macrofaunal benthic communities in a low diversity, brackish system of the Puck Lagoon (southern Baltic Sea). The Bayesian mixing models were used to delineate community-wide metrics at different trophic levels. Benthic macrovegetation appeared to facilitate directly and indirectly development of different trophic niches for consumers by diversification of basic carbon resources and providing habitat structure. In habitat with dense vegetation, diverse food sources supported benthic fauna of different feeding modes. Communities from sandy bottom with low biomass of macrophytes showed compact food webs of lower trophic diversity. Reliance on one dominant resource (suspended particulate organic matter-SPOM, and phytoplankton) resulted here in simplification of food web structure with a large proportion of species with one feeding mode (suspension feeders). Widening of $\delta^{13}C$ range (CR) and $\delta^{15}N$ range (NR) in the cold season was related to the extended carbon isotope ratios of organic matter sources and the presence of omnivorous and carnivorous fish that migrated towards the shoreline. A decreased trophic diversity during a vegetative season (spring-summer) was attributed to a narrowed isotopic range of primary producers that incorporated isotopically similar biogenic substances. Geographical and seasonal differences of trophic structure highlighted important natural variation of benthic communities which can benefit ecological restoration programmes and biodiversity management of coastal and marine areas.

1. Introduction

Food webs and trophic dynamics have been a subject of broad scientific interest as they incorporate information on ecosystem ecology (fluxes of energy and nutrients) and community ecology (population dynamics). Food webs provide a natural framework for understanding species ecological functions and ecosystem processes (Thompson et al., 2012; Catry et al., 2015; Rodil et al., 2020). Studies of trophic links in coastal systems focus primarily on benthic fauna as this ecological group plays a key role in benthic-pelagic coupling including geochemical processes at sediment-water interface, cross-boundary organic matter transport, elemental cycling and transfer to higher trophic levels (Layman et al., 2012). Basic taxonomic attributes of faunal communities (such as composition, richness and abundance) and their functional traits (such as feeding mode and tolerance) can be used to describe functional relationship among species or trophic units and in combination with carbon and nitrogen stable isotope measurements allow inferring trophic relationship and energy links (Layman et al., 2012). Carbon and nitrogen isotopic composition in a $\delta^{13}C$-$\delta^{15}N$–biplot defines isotopic niche of the community and is employed as a descriptor of the resource use and trophic links of that community (Newsome et al., 2007). In addition, isotopic ratios of biological compartments were employed to create community-wide metrics as a tool to trophic diversity and redundancy (Layman et al., 2007; Abrantes et al., 2014; hereafter Layman's metrics). Quantifying isotopic niche size of species has become a proxy for assessing amount of energy and elemental space

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occupied by species in food web of different trophic levels (e.g., Bocher et al., 2014; Catry et al., 2015).

Owing to omnivorous mode or overlapping diet preferences (so called resource partitioning), multiple species can perform similar trophic functions sharing the same trophic niche so, the species are ecologically redundant (Westerbom et al., 2018). In ecosystems of high trophic diversity and redundancy, one species can be compensated by another species of similar ecological niche, buffering potential losses in terms of overall ecosystem functioning (Lawton and Brown, 1993; Ojwang et al., 2010). Such redundant species contribute essentially to maintaining certain ecosystem functions such as stabilizing effects of species diversity and prevention of species loss (Rosenfeld, 2002). On the other hand, species of narrow diet spectrum (small trophic profile) can be considered extraneous, particularly in systems of high species richness and taxonomic biodiversity (Chapin et al., 1992; West, 1993; Bowman, 1994; Cowling et al., 1994; Kennedy and Smith, 1995). Trophic redundancy can vary strongly with physico-chemical variables and species' ecological importance can alter under different environmental conditions, even among habitats within a small but heterogeneous environment (Wellnitz and Poff, 2001). Investigations of the effect of abiotic parameters on the structure of food webs and ecosystem resilience are therefore required, in particular in areas of specific environmental and ecological conditions such as the Baltic Sea (Tomczak et al., 2013; Smit et al., 2021). Due to natural variation of resource availability and feeding interactions in an ecosystem over time, food web structure and trophic diversity of faunal assemblages can be expected to change also seasonally (Pool et al., 2017). While most empirical marine and coastal food-web studies focus on short-time resolution (e.g., Liu Yi et al., 2020) or single sampling (e.g., Pasotti et al., 2015; Kahma et al., 2021) the variation in dynamics over the course of a year remains a significant gap in the understanding of food webs (Blackman et al., 2022). The importance of seasonal variation on the structure and functioning of trophic links has been addressed so far only in few field studies (e.g., Nagata et al., 2015; Antit et al., 2016) and the general mechanisms through which seasonality could impact trophic niches of fauna are therefore poorly known. To this end, one of the specific objectives of this work was to assess seasonal patterns of trophic diversity and food-web characteristics of macrofaunal communities in the southern Baltic.

Shallow and sheltered lagoons, bays and inlets of the Baltic Sea are characterised by a high variety of benthic habitats which reflects heterogenous geomorphological, bathymetric and hydrological features as well as different anthropogenic pressures (Boström and Bonsdorff, 1997). A good example of such areas is the Puck Lagoon in the western part of the Gulf of Gdańsk (southern Baltic Sea) which represents an exceptionally diverse environment covering a range of benthic habitats i.e., bare sands, filamentous macroalgae dominated sands, *Zostera* beds, *Chara* meadows and deep muddy depressions (Gic-Grusza et al., 2009; Sokołowski et al., 2015, 2021). The bay also provides a clear zonation of soft-bottom macrofaunal assemblages whose structure and biomass are driven primarily by biomass and taxonomic structure of benthic macrophyte, and surface sediment organic matter (C/N ratio) quality (Sokołowski et al., 2015). The resident benthic fauna uses various food sources highlighting spatial variation of the system functions (Ziółkowska et al., 2018). The lagoon has been designated as a Special Protection Area (PLB 220005) and Special Area of Conservation (PHL 220032) as described in the EU wide network of nature protection areas Natura 2000 (Sokołowski et al., 2015) and is considered the most valuable part of the Polish Marine Areas (Węsławski et al., 2009). The bay offers thus a good environment in which to study small-scale system response to changing environmental conditions and to make predictions on natural or human-induced impacts.

The aim of this work was to define and compare the structure of food webs using community-wide metrics that were based on measurements of carbon and nitrogen stable isotope ratios in macrobenthic fauna in four different habitats in a low diversity system of the Puck Lagoon over four seasons. By combining indices of community structure and trophic ecology of animals the study also assessed contribution of different food sources to the diets of dominant macrofaunal species. This work employed the Bayesian stable isotope mixing models and community-wide metrics to verify the following specific hypotheses: 1) trophic diversity and trophic redundancy vary among macrofaunal communities which are fuelled by different organic matter sources; 2) benthic communities vary in niche space of functional trophic groups in space and over time and 3) metrics of the faunal communities are related to their taxonomic diversity. Although the study has a localised perspective, it will provide novel empirical information on spatio-temporal changes of trophic diversity and trophic redundancy of benthic communities and their relationship with taxonomic diversity and habitat characteristics. The resultant data might be therefore of importance for better understanding mechanisms that drive spatial and seasonal variations of faunal assemblages and can contribute to development of conservation programmes of coastal biodiversity and restoration of degraded ecosystems (Piacenza et al., 2015).

2. Material and methods

2.1. Habitat description

The Puck Lagoon (southern Baltic Sea) is a non-tidal semi-enclosed lagoon of a total surface area 104.8 km^2 where four different benthic habitats (A, B, C and D) were distinguished based on the quality of the surface sediment organic matter (measured as C/N_{sed} ratio), water depth, the presence of riverine discharge, benthic macrophyte composition and biomass: sand with little mixed vegetation (habitat A), *Stuckenia*-dominated sediment (habitat B), *Chara*/*Cladophora* sediment (habitat C) and sand with little *Pylaiella* (habitat D) (Fig. 1) (Sokołowski et al., 2015). Sandy sediments (A, D) located in the outer part of the lagoon offer good nutritional conditions for long-lived deposit and suspension feeders (bivalves) which account primarily for elevated macrofaunal biomass. Moreover, benthic communities from sandy habitat

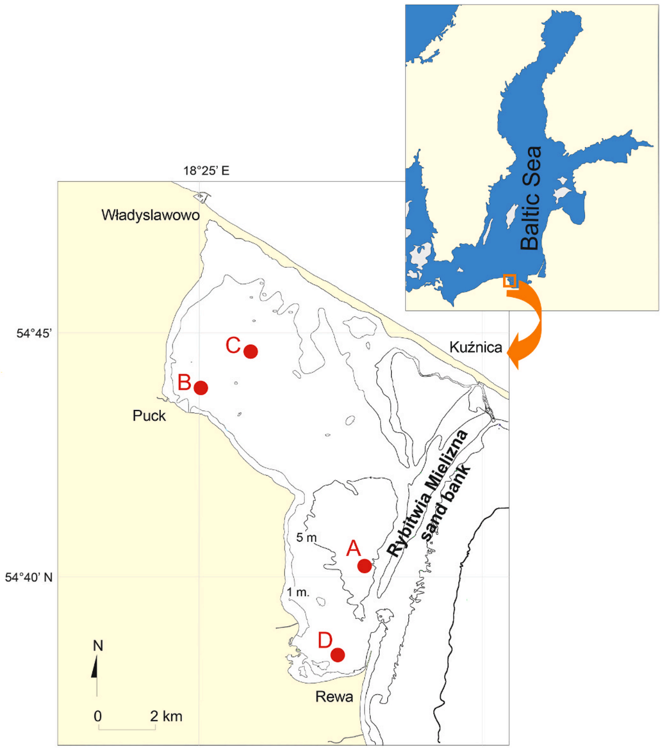

Fig. 1. Location of benthic habitats (communities) in the Puck Lagoon (southern Baltic Sea).

with low biomass of macrophytes rely mainly on SPOM and phytoplankton (suspension feeders in the area located further from river mouth (habitat A) and SOM (deposit feeders and omnivores in sheltered environment under influence of riverine discharge (habitat D). In the inner part, *Stuckenia*-dominated sediments (habitat B) together with the low quality of organic matter from the river support faunal assemblages of low taxonomic diversity. However, the second habitat located in the inner part of the lagoon, *Chara/Cladophora* sediment (habitat C) of high SOM quality, promotes taxonomic and trophic diversity of the resident benthic community. The main basal resources in habitat C include SPOM and phytoplankton, which fuel suspension feeder-based trophic pathways, and macroalgae with epiphytes which support a separate trophic chain of grazers and omnivores. For the purpose of this study, macrofaunal communities resident in each benthic habitat were named following the nomenclature of the habitats i.e., community A, B, C and D (Sokołowski et al., 2015; Ziółkowska et al., 2018).

2.2. *Sampling procedure and isotope analyses*

The dataset originates from Ziółkowska et al. (2018) who reconstructed the food webs and examined how basal organic carbon resources vary geographically and over time.

Macrobenthic organisms were sampled simultaneously from each habitat in four consecutive seasons (autumn – October 2010, winter – February/March 2011, spring – May 2011 and summer – July 2011). Macrofauna (>1 mm size) were collected in triplicate with a Van Veen grab (catch area 0.1 m^2). Sediments from the grab were gently sieved through a 1 mm mesh net to sort out the macrobenthic animals which were then placed in a container with aerated sea water taken *in situ* and transported cool to laboratory. Benthic macrofauna was kept alive overnight at temperature and salinity corresponding to the ambient environmental situation to depurate. The animals were sorted using binocular microscopes and identified to species level except for *Streblospio* spp., *Gammarus* spp., Chaoboridae, Chironomidae larvae and Oligochaeta. Animals with exoskeletons, such as bivalves, gastropods and barnacles, were dissected and a section of white muscle from the caudal region or the abdomen was collected from the larger fish and crustacean specimens. Samples of whole individuals or individual soft tissues were then frozen at – 20 °C until stable isotope analysis (Mateo et al., 2008). Description of sampling procedure of basal resources was presented in detail in Sokołowski et al. (2015) and Ziółkowska et al. (2018). The samples were freeze-dried and ground to a fine homogenous powder using a mixer Mill Retsch MM 200. The stable isotope ratios of C and N were measured using an Isoprime Micromass IRMS-EA (MicroMass CHN analyser coupled with MICROMASS mass spectrometer) that provides simultaneous data on carbon and nitrogen content. Isotope composition was expressed in the standard δ units (‰) as the relative differences (in part per thousand) between the sample and conventional standards (atmospheric N_2 for N; PD-belemnite [PDB] carbonate for C) in accordance with the formula δ R (‰) = $[(R_{sample} - R_{standard})/R$ standard$]*10^3$ (Ponsard and Arditi, 2000) where R is the heavy-to-light isotope ratio of the element (R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Replicate analyses of standards allowed calculating precision (analytical error; SD) of the overall procedure (i.e., sample preparation and analysis) that was ±0.1‰ for carbon and ±0.2‰ for nitrogen, respectively.

2.3. *Data analysis*

Community-wide metrics were employed to assess isotopic niche of benthic communities based on biplots of mean macrofaunal isotopic values of multiple individuals for each species in a food web (Layman et al., 2007; Jackson et al., 2011). Although the Layman's concept has been applied to many ecological studies in different freshwater (e.g., Dalu et al., 2017), brackish (e.g., Szczepanek et al., 2021) and marine systems (e.g., Shipley et al., 2019) interpretation of the resultant data requires caution due to its limitations (Hoeinghaus and Zeug, 2008). Several authors have pointed out that the measures of isotopic functional richness (CR and NR) can be sensitive to isotopic baselines (i.e., isotopic values of basal sources) that show high temporal and spatial variabilities (Belle and Cabana, 2020; Jabot et al., 2017). According to Hoeinghaus and Zeug (2008) the metrics based on Euclidean distances (CD, MNND, and SDNND) might be in turn affected by isotopic ratios of nitrogen and carbon (as demonstrated by different variances of CR and NR in the biplot, respectively). In this study the Layman metrics were intended to compare food web structure associated with different benthic habitats within the Puck Lagoon. Isotopic diversity indices were calculated for each benthic community and season to investigate spatial and temporal variations of the food webs analysed. The following Bayesian indices were computed using the packages SIAR (Stable Isotope Analysis in R, Parnell and Jackson, 2008; Parnell et al., 2010): $\delta^{13}C$ range (CR), $\delta^{15}N$ range (NR), mean distance to centroid (CD), mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND). The first three indices provide information on the trophic diversity within a food web measuring the spacing of different components in the $\delta^{13}C$ - $\delta^{15}N$ space. The $\delta^{13}C$ range metric (CR) shows the diversity of the base of the community food web and is the difference between maximum $\delta^{13}C$ and the minimum $\delta^{13}C$ value. The $\delta^{15}N$ range metric (NR) determines the trophic length of the food web and is computed as the difference between maximum $\delta^{15}N$ and the minimum $\delta^{15}N$ value. CR and NR are greater when benthic community is supported by multiple resources or consumers belong to more than one trophic level. CD is the average Euclidian distance of each community component to the centroid, giving indication of the average trophic diversity. The mean nearest neighbour distance to centroid (MNND) is the mean Euclidean distance of each data point to the centroid and is considered a measure of trophic diversity within a food web. The indices MNND and SDNND specify trophic redundancy of the community. When MNND is small the trophic niches of communities are similar and dominated by species of the same trophic level. The descriptor SDNNR shows how evenly trophic diversity is distributed among consumers within a community (Jackson et al., 2011). In order to calculate niche space, the standard ellipse area (SEAc), which contains around 40% of the isotopic data (Batschelet, 1981), was used. The standard ellipse area is considered a measure of the isotopic niche utilised by each individual and gives similar results to the univariate SD while is less sensitive to sample size than total area (Layman et al., 2007). Moreover, SEAc provides a better and more comparable description of the isotopic niche of community and is not affected by bias associated with the number of groups therefore allowing comparisons between communities with different number of components to be made (Jackson et al., 2011). Overlap in SEAc among benthic communities was calculated after 16 000 iterations (approach detailed in Jackson et al. (2011) for each habitat and season (‰^{2}). Trophic groups were not restricted to a specific taxonomic group of similar morphologies and their presumed trophic roles were not derived from phenotypic characteristics (e.g., Winemiller, 1991) but were based on a representation of realized trophic niches (*sensu* Post, 2002) by quantified position of species in isotopic space (Ziółkowska et al., 2018).

Normality of data (the Kolmogorov-Smirnov test for goodness of fit) and homogeneity of their variances (the Levene's test) were checked as prerequisites to further statistical analyses. Most indices fulfilled assumptions of parametric approach, exception was MNND the data of which had not normal distribution. The functional relation between a number of species and community metrics was described with Pearson correlation analysis and with Spearman's correlation analysis in case of MNND in Statistica 13.1.

3. Results

3.1. *Spatial and temporal variations of community-wide metrics*

Differences were found in the Layman metrics among the macrobenthic faunal communities and over time in the Puck Lagoon (Fig. 2). The lowest δ^{13}C range and δ^{15}N range were observed in the community B (mean value for four seasons; 3.0 n = 4 and 3.2 n = 4, respectively) whereas the highest CR and NR occurred in the community C (4.3 n = 4 and 4.3 n = 4, respectively) indicating the widest diversification of basal resources and the longest trophic chain. Moreover, CR and NR were highest in winter in all communities (except the community D). The mean distance to centroid was higher in the community B and C (both 2.01 n = 4) suggesting higher trophic diversity especially in winter (Fig. 2) Furthermore, communities in habitats with low biomass vegetation (A, D) showed lower CD (mean value for four seasons; 1.41 n = 4 and 1.52 n = 4, respectively) during all seasons than other two communities. The lowest values of CD were observed in spring for the community A (1.08) and in summer for the community D (1.28). The mean nearest neighbour distance to centroid (MNND), an indicator of trophic redundancy, was highest in communities of high biomass vegetation suggesting that the structure of these food webs is composed mainly of species representing similar trophic ecologies (higher trophic redundancy). SDNND showed that evenness of species packing within food web was generally lowest in the community B (mean value for four seasons; 0.46 n = 4) and highest in the community C (0.80 n = 4).

3.2. Spatial and temporal variations of SEAc

The isotopic niche measured as standard ellipse area of four macrobenthic communities differed clearly among habitat types and seasons (Figs. 2 and 3). The lowest SEAc was observed in the community A (mean for all seasons; 6.82‰^{2} n = 4) and highest in the community B (10.22‰^{2} n = 4). The communities showed also apparent variation in SEAc over time, individual values ranged from 4.37‰^{2} in the community D in summer to 21.14‰^{2} in the community B in winter. Except the community B, all communities showed reduced SEAc in a vegetative season (spring-summer period) and a substantial increase of SEAc in cold period (autumn-winter). The minimal SEAc was calculated in summer in the community D (4.37‰^{2}) and in spring in the community C (4.76‰^{2}) to reach the maximum value in winter in both communities (15.68‰^{2} and 21.14‰^{2}, respectively). Moreover, important differences were also noticed in shape and location of standard ellipses in the δ^{13}C *vs* δ^{15}N space (Fig. 3). In most cases, ellipses of the communities with high biomass vegetation (B and C) were located in the bottom right corner of the δ^{13}C/δ^{15}N plot that resulted from higher δ^{13}C and lower δ^{15}N isotopic composition of the resident species. The communities from habitats with low biomass vegetation showed much higher values of δ^{15}N and lower δ^{13}C so, the ellipses were located in upper part of the plots in all cases.

There was more overlap between different SEAc's in cold period (autumn-winter) than during a vegetative period (spring-summer) (Table 1). The highest niche overlap (0.74) was observed between communities B and C in winter and the lowest (0.23) between communities B and D in summer. In addition, location of standard ellipses in summer clearly separated communities into two groups: *i*) communities B and C from habitats with high biomass vegetation in the inner part of the lagoon and *ii*) communities A and D from habitats with low biomass vegetation in the outer part. Both groups (B - C and A - D) showed relatively large isotopic overlap i.e., 0.59 and 0.53, respectively. The degree of trophic niche overlap between seasons was relatively low, a total number of pair-wise overlaps of SEAc for all communities in the ranges <0.45, 0.45–0.60 and > 0.60 was 12 (50% of all cases), 7 (29%) and 5 (21%), respectively (Table 1).

3.3. Trophic niche comparison among functional groups

The size of trophic niche of various functional groups differed among the communities studied (Table 2). The Bayesian ellipse areas of trophic groups in the community A varied over time with clear dominance of omnivores in autumn (8.12‰^{2}), grazers in winter (4.45‰^{2}) and carnivores in summer (4.65‰^{2}). In spring, SEAc's of functional groups in the community A were low and similar across different seasons. In the community B, grazers formed the most important group over most year with SEAc ranging from 1.98‰^{2} in winter to 5.41‰^{2} in summer. The only exception was winter when the largest SEAc was observed for carnivores (4.83‰^{2}). The other two functional groups, omnivores and suspension deposit feeders, were present in spring and summer but did not demonstrate large sizes of isotopic niche. The community C showed the largest isotopic niche for carnivores in all seasons (from 2.41‰^{2}–4.94‰^{2}). Grazers constituted here the second most important functional group with the largest size of isotopic niche (from 2.10‰^{2}–2.96‰^{2}) but in autumn and winter high SEAc also exhibited omnivores (2.29‰^{2}–3.43‰^{2}, respectively). The SEAc of grazers in the communities with high biomass vegetation (B and C) were stable throughout a year and exceeded markedly those in the communities with low biomass vegetation (A and D). The size of the trophic niches of different functional groups varied most in the community D: in autumn omnivores showed the largest SEAc (5.98‰^{2}), in winter and summer carnivores exhibited the largest niche width (7.48‰^{2} and 5.08‰^{2}, respectively) and in spring suspension deposit feeder prevailed (3.11‰^{2}). Generally, suspension feeders and suspension deposit feeders in the habitats with low biomass vegetation (communities A and D) had the largest isotopic niches; SEAc of suspension feeders ranged from 5.07‰^{2} in the community A in autumn to 0.6‰^{2} in the community D in summer whereas SEAc of suspension deposit feeders varied from 6.25‰^{2} in winter to 0.79‰^{2} in summer in the community D.

3.4. Correlation between community metrics and biodiversity (species richness)

Correlation analyses between community-wide metrics and species richness, which was obtained for the same communities from Sokołowski et al. (2015), provided information of potential relation between taxonomic diversity and trophic diversity, and between biodiversity and redundancy. When all data for communities and seasons were incorporated in the calculations, the number of species was positively correlated with CR ($R = 0.55$ $p = 0.018$ $n = 16$) and NR ($R = 0.58$ $p = 0.027$ $n = 16$) whereas correlation to MNND ($R = -0.85$ $p = 0.0001$ $n = 4$) and SDNNR ($R = -0.64$ $p = 0.007$ $n = 4$) was negative. Interestingly, the correlation between a number of species and SEAc (as a proxy of trophic diversity within food web) and CD (average degree of trophic diversity) was not found.

4. Discussion

Employment of community-wide metrics based on stable isotopes of carbon and nitrogen allowed detecting spatial and temporal variations of trophic diversity and redundancy of four macrofaunal communities which differ in taxonomic composition, the use of basal resources and food web structure. Clear geographical and seasons patterns in trophic structure and the trophic niche variations were distinguished across closely located but heterogenous communities inhabiting a low diversity system of the shallow and semi-enclosed Puck Lagoon (southern Baltic Sea).

4.1. Isotopic diversity indices in different habitats

Macrobenthic vegetation appeared an important factor for the isotopic niche width and food web structure of the resident fauna. The community C, which occupied the habitat with dense macrophytal biomass and good quality of sediment organic matter, had the widest average isotope niche and higher trophic diversity than other communities. In contrast, the communities A and D, which inhabited sandy bottom with little and species-poor vegetation, demonstrated much smaller niche widths and simplified tropic links. Abundant primary producers in the community C (mainly macroalgae and vascular plants

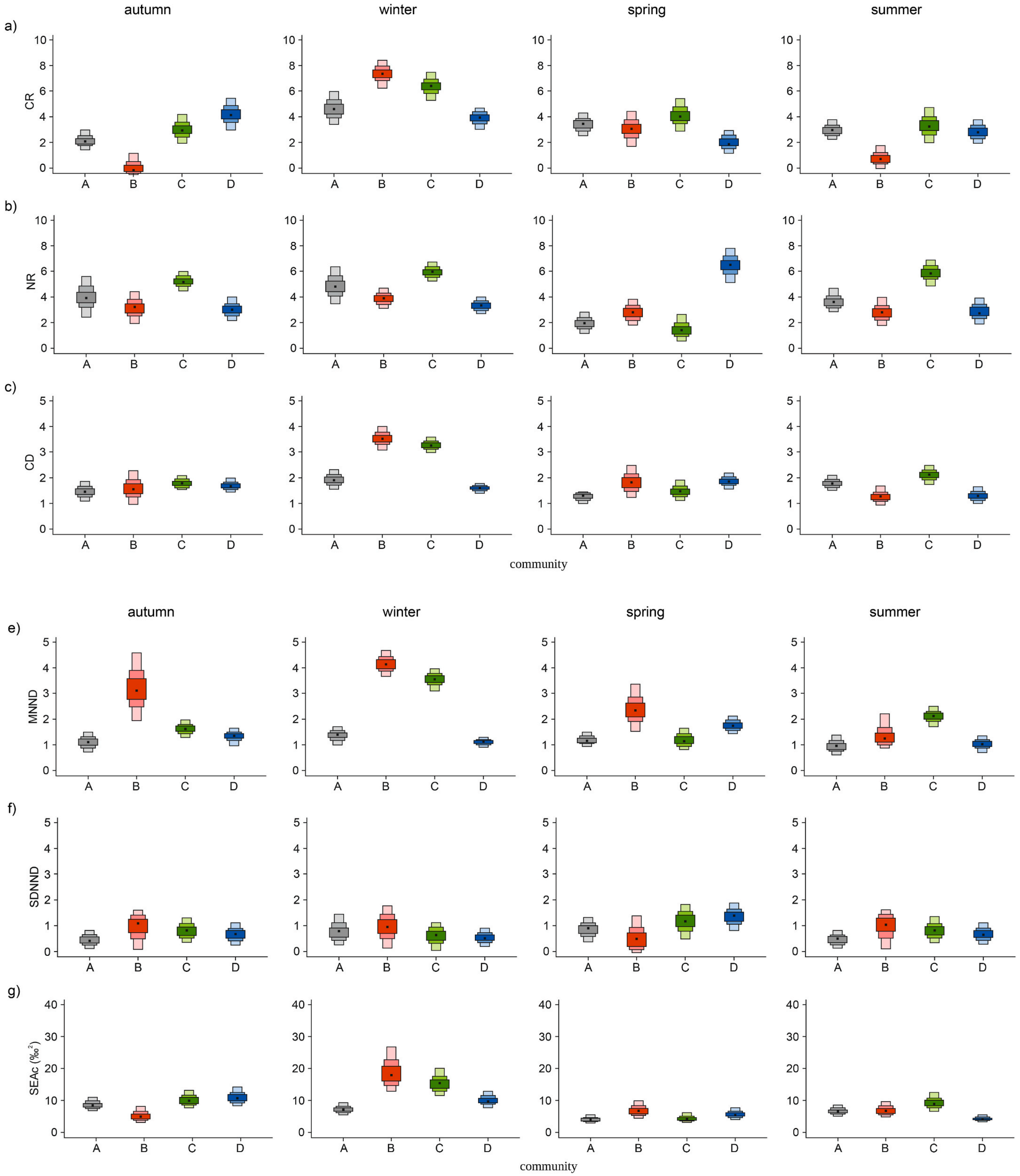

Fig. 2. Bayesian results for community-wide metrics that provide information on trophic diversity within a food web: a) CR, b) NR, c) CD, d) MNND, e) SDNND and f) SEAc. Black dots are the mode (‰) and boxes indicate the 50%, 75% and 95% credibility intervals in four benthic macrofaunal communities (A, B, C and D) over four seasons.

with their epiphytes) provide a variety of potential carbon forms. The resident macrofauna is supported by different food sources (Ziółkowska et al., 2018) and shows an even distribution of trophic diversity among consumers. The effect of benthic macrophytes on community structure has been widely documented for a range of organisms going from micro- and macroinvertebrates (Bergström et al., 2000; Theel et al., 2008;

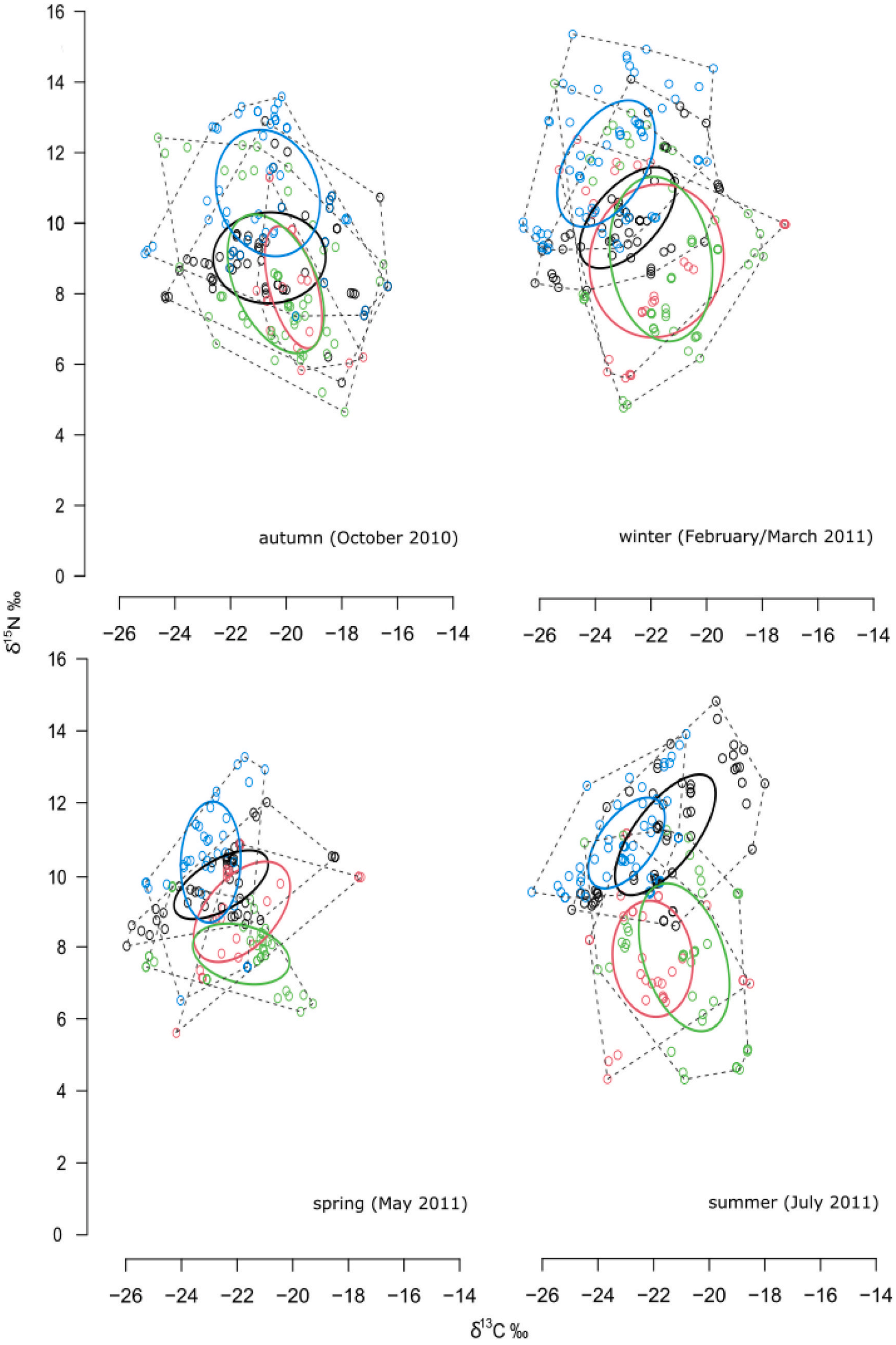

Fig. 3. Mean stable isotope composition (‰) of four macrobenthic faunal communities (invertebrates and fish) in the Puck Lagoon in four seasons. Solid lines enclose the standard ellipses area (SEAc), containing c. 40% of data showing isotopic niche of communities. Each ellipses indicate the standard ellipse areas: black (community A), red (community B), green (community C), blue (community D). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Overlaps in small size-corrected standard ellipse areas (SEAc, ‰^{2}) between pairs of communities for the same season (a) and between pairs of seasons for the same community (b).

a)

community	Season											
	Autumn			winter			spring			summer		
	B	C	D	B	C	D	B	C	D	B	C	D
A	0.42	0.59	0.53	0.35	0.42	0.46	0.50	0.26	0.42	0.29	0.31	0.53
B		0.52	0.31		0.74	0.40		0.45	0.40		0.59	0.23
C			0.47			0.36			0.29			0.24

b)

	Community											
	A			B			C			D		
Season	winter	Spring	summer	winter	spring	Summer	winter	spring	summer	winter	spring	summer
Autumn	0.48	0.40	0.38	0.26	0.33	0.34	0.63	0.33	0.74	0.60	0.46	0.44
Winter		0.57	0.69		0.35	0.34		0.28	0.55		0.47	0.42
Spring			0.51			0.54			0.38			0.58

Table 2
Small size-corrected standard ellipse areas (SEAc; ‰^{2}) of different functional groups of macrobenthic fauna in four communities of the Puck Lagoon (southern Baltic Sea) in four seasons. Empty cells indicate the lack of given guilds within community.

Community season	Functional groups					
	Grazer	omnivore	suspension feeder	suspension-deposit feeder	deposit feeder	carnivore
A						
Autumn	7.38	8.13	5.07	1.50	0.94	5.74
Winter	4.46	1.52	2.38	0.38	0.38	1.41
Spring	1.11	0.67	1.14	0.26	1.06	
Summer	0.11	0.64	0.15	0.20	0.01	4.66
B						
Autumn	3.37					0.08
Winter	1.98	0.00				4.84
Spring	2.21	0.07				
Summer	5.41	0.45				
C						
Autumn	2.18	3.43	1.51	0.38	0.00	4.94
Winter	2.84	2.29	0.01			3.57
Spring	2.96	0.43	0.05	0.76	0.01	
Summer	2.10	0.82	0.17	0.27		2.41
D						
Autumn	0.16	5.98	1.05	0.50	0.44	1.25
Winter	1.61	0.80	2.07	6.25	0.42	7.48
Spring	0.10	0.80	2.77	3.11	0.79	
Summer	0.27	0.60	0.39	0.79	0.94	5.09

Sokołowski et al., 2015) to coastal fish (e.g., Diehl, 1992; Diehl and Kornijów, 1998; Choi and Kim, 2020) and waterbirds (e.g., Klaassen and Nolet, 2007). Macrophytes have been shown to serve as an important habitat structurer, influencing composition of the associated fauna and its interspecific relationships (Thomaz and da Cunha, 2010). Abrantes et al. (2014) and Liu Yi et al. (2020) highlighted also ecological significance of bottom macrovegetation for the structure of food web. In this study, wide trophic niche of whole community (SEAc) along with broad δ^{13}C range metric suggest that the presence of macrophytes of a relatively enriched δ^{13}C ratio enhances trophic diversity at the base of the food web. Diversification of basic resources is not, however, directly connected with nutritional value of benthic vegetation but with its role as physical structure that increases habitat complexity and microniche heterogeneity (Levin et al., 2006; Harley and O'Riley, 2011; Alsaffar et al., 2020). This is consistent with other isotope studies in estuarine and coastal systems which revealed that macrophytes are consumed by primary consumers to a much smaller extent than free-living and attached algae (Mann, 1988). It can be therefore concluded that in habitat of the community C, macrophytes together with macroalgae and epiphytes facilitate directly and indirectly development of diversified space and trophic niches for consumers. In addition, these complex niches serve locally as shelter and as spawning and nursery grounds for many benthic invertebrates and fish (Sabo et al., 2009; Sokołowski et al., 2021). The stable isotope mixing models confirmed that no single food dominates the diet of consumers in this community (Ziółkowska et al., 2018). Diversified organic matter sources resulted also in high variation of primary (small mobile invertebrates, particularly crustaceans and gastropods) and secondary consumers (larger crustaceans and benthic fishes) in this community. The community C encompasses thus species representing different feeding modes with the largest resource-use areas being occupied by grazers, omnivores and carnivores (Table 2). While grazers utilise preferentially microphytobenthos and epiphytes (Ziółkowska et al., 2018; Voigt and Hovel, 2019), omnivorous animals are able to consume many types of carbon resources and change the resource channels depending on food availability and quality. Increased SEAc of omnivores suggests that they can exert a stabilizing effect on the food webs (Lawler and Morin, 1993; Fagan, 1997; Holyoak and Sachdev, 1998; Lalonde et al., 1999) as together with grazers omnivores form one energy pathways which fuel secondary consumers (Ziółkowska et al., 2018). Due to the fact that omnivores have a large plasticity of food preferences, omnivorous links in food webs are intimately associated with weak species interactions (McCann and Hastings, 1997; McCann et al., 1998; Neutel et al., 2002). What is more, high whole-community SEAc was accompanied by increased NR which indicates that predatory invertebrates and fishes were common in the community C in the inner Puck Lagoon (pers. obs.) explaining a longer trophic chain and a greater degree of vertical trophic diversity. Longer trophic chain and higher trophic diversity of the community C induce more complex trophic links which utilise the available resources more effectively (Power et al., 1996; Duffy, 2009; McHugh et al., 2010; Cardinale et al., 2011; Naeem et al., 2012; Ortega-Cisneros et al., 2017).

Another community (B) with massive but species-poor vegetation and located in the inner part of the lagoon demonstrated different taxonomic composition and lower species diversity of macrobenthic fauna than those of the community C (Sokołowski et al., 2015). A smaller number of taxa has been reflected in the narrower δ^{13}C and δ^{15}N ranges indicative of lower niche diversification at the base of the food web and shorter trophic length, respectively. The resident animals utilise similar organic matter sources which are dominated by allochthonous organic particles from the local Płutnica River, peat outcroppings and decaying plant material (Sokołowski et al., 2015). The local animal assemblage consists primarily of organic matter-resistant but numerous small-bodied infauna such as Chironomidae larvae and herbivores such as the isopod *Lekanesphaera hookeri* and the gastropod *Theodoxus fluviatilis* (Sokołowski et al., 2015). Benthic fauna in this habitat relies thus on homogenous resources and represents little variation of diet composition and more even distribution of species. Food links among different community components build here less complex web of low connectance and redundancy (Abrantes et al., 2014). In contrast to the trophically diverse community C, the largest resource-use area in the community B has a single trophic guild-grazers that exploit preferentially macroalgae, epiphytes and sediment organic matter (Ziółkowska et al., 2018). Interestingly, the width of the resource-use areas (SEAc) did not vary between the community B and the community C, and the whole isotope niches of the two communities represent high overlap (Table 1) so, the consumers exploit isotopically similar resources. Both food webs were clearly increased in δ^{13}C (Ziółkowska et al., 2018) indicating utilisation of isotopically enriched organic matter of autochthonous (marine) origin.

Benthic communities from sandy habitats with low biomass of macrophytes (A and D) in the external part of the Puck Lagoon had smaller SEAc's and CDs suggesting more compact food webs of lower trophic diversity. This results from less diversified organic matter sources and limited availability of macrobenthic vegetation that develops only in warm seasons (Sokołowski et al., 2015). Food webs of the communities A and D exploit primarily suspended particulate matter (SPOM, phytoplankton and resuspended sediment particles) that occurs abundantly in the water column and supports preferentially two trophic groups: suspension- and suspension-deposit-feeders. They include typical filter-feeders such as infaunal (*Macoma balthica* and *Mya arenaria*) and epifaunal bivalves (*Cerastoderma glaucum*) which inhabit numerously the seafloor in this area and dominate the local macrozoobenthic biomass (Sokołowski et al., 2015; Ziółkowska et al., 2018). Suspension- and suspension-deposit feeders demonstrated a relatively small size of their trophic niches while carnivores had large SEAc's reflecting the presence of predatory benthic fish (e.g., the perch *Perca fluviatilis* and the European flounder *Platichthys flesus*) that utilise local food sources. Due to the fact that suspended particulate matter occurs in high concentration over most a year but particularly during intense planktonic production in a vegetative season (Sokołowski et al., 2015), suspension feeders are not limited by food availability and form the main energy pathway to secondary consumers. Reliance on one dominant basal resource implies, however, simplification of trophic structure in these communities with a large proportion of species characterized by one feeding mode i.e., more redundant. Trophic redundancy is a significant feature to develop more resilient food web in which the effects of species loss on the population functional dynamics are compensated by other species that have links to the same sources (Borrvall et al., 2000). According to Sanders et al. (2018) trophic redundancy rather than species richness is a factor that protects communities from biodiversity loss in response to habitat modifications or environmental disturbances so, greater trophic redundancy can buffer against the effects of species loss.

Our findings, that species-rich benthic vegetation facilitates development of different trophic niches for consumers and thus increases taxonomic and functional diversity of the resident invertebrates and fish, has direct implications for biodiversity conservation programmes. Sustainable management of the coastal zone, which aims at protection of valuable areas or restoration of degraded habitats, should account for spatial diversity of benthic habitats and faunal communities even at a small geographical scale. Multi-species assemblages of benthic vegetation in the Puck Lagoon favours trophic diversity and different functional guilds whereas massive but taxonomically homogenous benthic plants and habitats of little vegetation support simple food webs of low connectance.

4.2. Seasonal variation in food web structure

For all macrobenthic faunal communities in the Puck Lagoon, the dissimilarities in mode values of the different community-wide metrics and relatively low overlaps (Table 1) (Abrantes et al., 2014; García et al., 2020) evidenced seasonal variation in trophic structure. Geographical similarities in the metrics have been reflected somehow in patterns of temporal changes of the Bayesian indices analysed. For majority of the indices, the communities C and B followed similar patterns that were distinct from those observed for the communities A and D. Temporal variation of trophic diversity as manifested by seasonally changing isotopic space was linked primarily to the availability and heterogeneity of basal carbon resources.

For the communities C and B, widening of CR and NR in winter (Fig. 3) was related primarily to the presence of benthic fish that feed on variety of food sources of broad δ^{13}C and δ^{15}N range (Sokołowski, 2009; Ziółkowska et al., 2018). The appearance of these secondary consumers, that show omnivorous (e.g., three-spined stickleback *Gasterosteus aculeatus*) and carnivorous feeding modes (e.g., the straightnose pipefish *Nerophis ophidion*, nine-spined stickleback *Pungitius pungitius* and the round goby *Neogobius melanostomus*) (Arciszewski et al., 2016), increased temporarily local trophic diversity. It is also possible that some fish did not utilise local food sources but might have been migrants from other coastal areas and/or the adjacent Płutnica River. For example, the carbon stable isotope ratios of five fish species were impoverished on average by ca. 3.6‰ and by 2.2‰ relative to other omnivorous/carnivorous invertebrates in the communities B and C, respectively in cold season (Ziółkowska et al., 2018). The widening effect of benthic fish on NR and to a limited extent on SEAc was also observed in the community C in summer when, after a spring reduction, δ^{15}N range increased substantially. In contrast, diversity at the base of food web (CR) in the communities B and C, and food chain length in the community B decreased during a vegetative season (spring-summer) and were accompanied by a decrease in trophic diversity. This was due to narrowed isotopic range of primary producers i.e., phytoplankton and macroalgae, which incorporated from the water biogenic substances of similar carbon and nitrogen isotopic ratios. The exception was the community B where δ^{15}N range tended to rise over a warm season to reach maximum in summer. High NR of this community derived presumably from the presence of diazotrophic ^{15}N depleted nitrogen during the summer cyanobacteria bloom which has been shown to affect δ^{15}N of benthic consumers such as bivalve *Macoma balthica* and polychaete *Marenzelleria* cf. arctia in the Baltic Sea (Karlson et al., 2015). Another plausible explanation of lowered community-wide metrics in the summer months provides a decrease in diversity of the main resources i.e., phytoplankton, sediment organic matter and macroalgae.

Similar to the communities B and C but less pronounced patterns of seasonal variations of community-wide metrices (CR, NR, CD and MNND) were observed for the community A inhabiting sandy area with few macrophytes of mixed species composition. Increased δ^{13}C range in winter was associated with extended range of isotope ratios of organic matter sources and preferential utilisation of ^{13}C-impoverished SOM and SPOM by primary consumers (Ziółkowska et al., 2018). δ^{15}N range of this community remained at a similar level throughout a year with an apparent decrease in spring likely due to lowered nitrogen range of food resources (mainly macroalgae with a dominant role of ^{15}N-depleted *Pylaiella littoralis*) and the absence of carnivorous benthic fish and mobile crustaceans such as the common shrimp *Crangon crangon*. Carnivores occurred in high numbers in warm summer months contributing to higher trophic diversity in this period. The trophic links were based then, however, on single connections and thus did not increase trophic redundancy of the community, the similar phenomenon being observed already in the community C in summer.

Trophic structure of the community D, an assemblage on sandy bottom with little *Pylaiella* vegetation, followed a distinct pattern of seasonal variation. Contrary to other communities, trophic length of the food web, trophic diversity and variation of trophic ecologies were highest in spring when consumers of diversified food preferences (herbivores, suspension- and deposit-feeders, carnivores) feed on a mix of different resources (Ziółkowska et al., 2018). The faunal community was then supported in similar parts by phytoplankton, SPOM, SOM and macroalgae which all showed wide δ^{15}N range. The increased NR value can be explained mostly by elevated δ^{15}N of phytoplankton (on average 8.4‰) that incorporated inorganic nitrogen supplied with a large riverine run-off after winter. Suspended particulate pool in this zone might have thus contained also large amounts of terrigenous organic matter (e.g., freshwater phytoplankton) of enriched δ^{15}N (Sokołowski, 2009). Interestingly, the resident taxa showed clustered isotope values and formed weak trophic links of low redundancy.

4.3. *Linking taxonomical diversity with food web structure*

Sokołowski et al. (2015) have provided data on taxonomic diversity of the same macrofaunal communities in the Puck Lagoon over the same period of time. These data can be therefore related to the community-wide metrics that were calculated in this study. The relationships have been able to identify association between species richness and the Bayesian indices, predicting a link between biodiversity and food web structure. Positive correlation of a number of species (S) with CR and NR provides support to the hypothesis that the species-rich food webs utilise more diversified organic matter resources and have longer food chains. Such communities generate more trophic links and more links per species (linkage density; Yen et al., 2016), and are thus less vulnerable to disturbance (Calizza et al., 2019). Higher resilience to disturbance, including species loss, of taxonomically diverse communities indicates their higher redundancy. In the faunal assemblages containing taxa of different feeding strategies and food preferences (i.e., of high trophic diversity), large proportion of species shares similar trophic ecologies, increasing stability of trophic links. High diversity of benthic food web structures in a relatively small and shallow coastal water basin of low overall taxonomic diversity as the Puck Lagoon, underlines its exceptional biological value and call for protection and sustainable management.

5. Conclusions

The Bayesian stable isotope mixing model provided time-averaged information that incorporates spatio-temporal scales which are often not considered in food web studies based solely on the species feeding preferences or community composition. Macrobenthic faunal communities inhabiting closely located but heterogenous habitats in the shallow brackish Puck Lagoon (southern Baltic Sea) demonstrated clear spatial and seasonal patterns in trophic structure. The observed geographical variation in the food web structure were primarily driven by the availability and diversity of the basal food resources. Benthic macroalgae and vascular plants appeared to facilitate directly and indirectly development of different trophic niches for consumers by diversification of basic carbon resources. Massive macrovegetation supports benthic consumers of different feeding modes and various trophic positions and increases trophic niche size of the whole community. Faunal communities from sandy bottom with low biomass of macrophytes showed compact food webs of lower trophic diversity. Reliance of benthic animals on one dominant resource resulted in simplification of food web structure with a large proportion of species with one feeding mode (suspension feeders). At temporal scale, communities occupying habitats with high biomass vegetation had higher trophic diversity in winter and lower in spring-summer whereas communities from sandy habitats were more diverse in autumn. Widening of CR and NR in cold season was related to the extended isotope composition of organic matter sources and the presence of omnivorous and carnivorous fish which migrated towards the shoreline. A decreased trophic diversity during a vegetative season (spring-summer) could be attributed to a narrowed isotopic range of primary producers which incorporated biogenic substances of similar carbon and nitrogen isotopic ratios. Our findings provided support to the ecological restoration and biodiversity management of the coastal zone that needs to account for spatial diversity of faunal communities and their trophic structure.

CRediT authorship contribution statement

Marcelina Ziółkowska: Writing – original draft, Visualization, Software, Methodology, Data curation, Conceptualization. **Adam Sokołowski:** Writing – review & editing, Supervision, Funding acquisition.

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

Table A
Macrobenthic faunal taxa, their carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios (mean ± SD) and the assigned trophic group in four habitats in the Puck Lagoon (southern Baltic Sea) over four seasons. Empty cells - taxon was not present.

Habitat A (sand with little mixed vegetation)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/ March 2011)		spring (May 2011)		summer (July 2011)	
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
suspension feeder	*Amphibalanus improvisus*	−20.8 ± 0.0	9.4 ± 0.1	−21.7 ± 0.2	10.4 ± 0.1	−22.2 ± 0.1	10.5 ± 0.1		
	Cerastoderma glaucum	−24.2 ± 0.1	8.0 ± 0.0	−24.7 ± 0.1	8.6 ± 0.1	−25.6 ± 0.4	8.3 ± 0.2	−23.7 ± 0.1	9.2 ± 0.0
	Einhornia crustulenta	−17.2 ± 0.0	8.1 ± 0.0	−24.4 ± 1.1	8.4 ± 0.1				
	Mya arenaria	−22.6 ± 0.2	9.0 ± 0.1	−23.9 ± 0.3	9.7 ± 0.1	−24.4 ± 0.3	9.1 ± 0.5	−23.7 ± 0.2	9.5 ± 0.0
	Mytilus trossulus	−23.5 ± 0.2	8.9 ± 0.1	−24.8 ± 0.4	9.4 ± 0.1	−25.2 ± 0.4	8.9 ± 0.2	−24.2 ± 0.2	9.3 ± 0.2
suspension-deposit feeder	*Macoma balthica*	−21.1 ± 0.4	9.4 ± 0.4	−22.3 ± 0.1	9.7 ± 0.0	−23.5 ± 0.1	9.6 ± 0.0	−22.1 ± 0.3	10.0 ± 0.1
	Marenzelleria neglecta	−19.7 ± 0.1	12.7 ± 0.3	−20.0 ± 0.1	12.2 ± 0.0	−22.0 ± 0.2	10.7 ± 0.2		
omnivore	*Chironomidae*	−22.6 ± 0.0	8.5 ± 0.0						
	Gammarus spp.	−18.4 ± 0.7	7.1 ± 1.6	−21.8 ± 1.0	9.9 ± 0.5				
	Hediste diversicolor	−20.7 ± 0.6	9.8 ± 0.6	−22.1 ± 0.1	10.7 ± 0.1	−22.0 ± 0.0	10.5 ± 0.1	−21.4 ± 0.2	11.3 ± 0.1
	Nematoda	−23.9 ± 1.1	9.4 ± 1.6	−21.6 ± 0.1	12.6 ± 0.1	−22.7 ± 0.4	12.1 ± 0.4	−22.5 ± 0.2	12.6 ± 0.0
	Rhithropanopeus harrisii	−21.8 ± 0.1	9.1 ± 0.2	−22.1 ± 0.5	10.0 ± 0.1	−22.5 ± 0.5	9.5 ± 0.5	−20.8 ± 0.4	11.4 ± 0.4
	Palaemon adspersus	−18.2 ± 1.7	9.9 ± 1.4						
	Palaemon elegans	−17.4 ± 0.7	7.8 ± 0.4						
grazer	*Corophium volutator*	−19.8 ± 0.0	8.2 ± 0.0					−23.5 ± 0.0	9.5 ± 0.0
	Peringia ulvae	−20.5 ± 0.0	8.2 ± 0.1	−20.6 ± 0.0	8.8 ± 0.1	−21.4 ± 0.3	8.8 ± 0.1	−21.0 ± 0.2	8.8 ± 0.2
	Idotea chelipes	−20.1 ± 0.0	8.3 ± 0.0	−19.2 ± 0.9	9.5 ± 0.1	−22.0 ± 0.1	8.9 ± 0.0		
	Theodoxus fluviatilis	−17.9 ± 0.0	10.0 ± 0.0	−17.7 ± 0.0	11.1 ± 0.0	−18.3 ± 0.0	10.6 ± 0.0		
deposit feeder	Oligochaeta	−21.9 ± 0.6	8.7 ± 0.2	−21.7 ± 0.4	9.5 ± 0.2	−21.7 ± 0.1	9.5 ± 0.2	−21.6 ± 0.0	9.8 ± 0.0
	Pygospio elegans	−21.0 ± 0.3	9.3 ± 0.3	−21.1 ± 0.0	10.2 ± 0.0	−23.0 ± 0.6	9.6 ± 0.3		
	Streblospio spp.	−21.6 ± 0.0	9.7 ± 0.0			−22.3 ± 0.0	10.4 ± 0.1		
carnivore	*Cyathura carinata*	−18.1 ± 0.0	10.8 ± 0.1	−20.3 ± 0.5	11.4 ± 0.1	−21.1 ± 0.2	11.8 ± 0.2	−20.3 ± 0.0	12.1 ± 0.3
	Crangon crangon	−20.0 ± 0.2	12.3 ± 0.1	−19.0 ± 0.5	13.2 ± 0.2			−18.7 ± 0.1	13.4 ± 0.3
	Sygnathus typhle	−23.2 ± 0.0	12.6 ± 0.0					−21.6 ± 0.0	12.3 ± 0.0
	Neogobius melanostomus	−18.6 ± 1.8	11.4 ± 1.2					−19.9 ± 0.9	12.5 ± 0.1
Habitat B (*Stuckenia*-dominated sediment)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/March 2011)		spring (May 2011)		summer (July 2011)	
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
suspension -deposit feeder	*Marenzelleria neglecta*					−22.3 ± 0.0	10.0 ± 0.0	−22.3 ± 0.3	9.4 ± 1.7
omnivore	*Chironomidae*	−20.6 ± 0.2	8.0 ± 0.1	−20.5 ± 0.0	8.0 ± 0.1	−22.6 ± 0.1	8.8 ± 0.0	−22.5 ± 0.3	8.5 ± 0.9
	Hediste diversicolor					−21.8 ± 0.0	10.9 ± 0.0	−22.6 ± 1.2	8.8 ± 0.6
	Nematoda	−24.1 ± 0.0	8.6 ± 0.0			−23.1 ± 0.2	12.8 ± 0.5		

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Table A (*continued*)

Habitat A (sand with little mixed vegetation)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/ March 2011)		spring (May 2011)		summer (July 2011)	
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
	Palaemon adspersus			−15.0 ± 0.0	10.1 ± 0.0	−17.3 ± 0.0	10.0 ± 0.0		
grazer	*Gammarus* spp.			−21.5 ± 0.0	5.9 ± 0.0	−22.1 ± 0.3	8.0 ± 0.2	−23.1 ± 0.2	4.7 ± 0.3
	Idotea chelipes	−19.6 ± 0.6	6.8 ± 0.2	−20.9 ± 0.0	7.7 ± 0.0	−23.3 ± 0.9	7.4 ± 1.7	−18.6 ± 0.0	7.1 ± 0.0
	Peregriana peregra							−21.3 ± 0.0	6.7 ± 0.0
	Potamopyrgus antipodarum							−21.6 ± 0.2	7.1 ± 0.0
	Lekanesphaera hookeri	−18.1 ± 1.2	6.0 ± 0.2	−22.0 ± 0.3	6.1 ± 0.3	−23.2 ± 0.0	7.2 ± 0.0	−21.9 ± 0.0	6.5 ± 0.0
	Theodoxus fluviatilis	−19.4 ± 0.4	8.4 ± 0.1	−19.0 ± 0.2	9.0 ± 0.1	−20.8 ± 0.5	9.0 ± 0.8	−20.5 ± 0.5	8.1 ± 0.8
carnivore	*Pomatoschistus minutus*	−20.0 ± 0.4	10.7 ± 0.8						
	Platichthys flesus	−18.8 ± 0.2	12.8 ± 0.4						
	Gasterosteus aculeatus			−23.2 ± 0.1	10.7 ± 0.3				
Habitat C (*Chara/Cladophora* sediment)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/ March 2011)		spring (May 2011)		summer (July 2011)	
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
suspension feeder	*Cerastoderma glaucum*	−22.9 ± 0.6	7.6 ± 0.9	−23.5 ± 0.0	8.1 ± 0.1	−25.2 ± 0.1	7.6 ± 0.1	−22.8 ± 0.2	7.9 ± 0.3
	Corophium volutator					−24.3 ± 0.0	9.7 ± 0.0		
suspension- deposit feeder	*Macoma balthica*	−21.4 ± 0.0	7.5 ± 0.0					−22.5 ± 0.1	8.6 ± 0.2
	Marenzelleria neglecta	−19.6 ± 0.0	7.7 ± 0.0			−20.9 ± 0.1	8.4 ± 0.1	−20.6 ± 0.0	7.8 ± 0.0
	Mya arenaria	−22.2 ± 0.0	8.0 ± 0.0						
omnivore	*Chaoboridae*					−21.1 ± 0.1	9.3 ± 0.0	−20.0 ± 0.0	7.8 ± 0.0
	Chironomidae	−19.4 ± 0.4	7.4 ± 0.4	−20.0 ± 0.0	7.7 ± 0.1	−21.1 ± 0.5	8.4 ± 0.2		
	Hediste diversicolor	−19.4 ± 0.3	7.5 ± 0.2	−19.8 ± 0.0	8.6 ± 0.0	−21.3 ± 0.1	8.9 ± 0.5	−20.1 ± 0.3	7.4 ± 0.6
	Nematoda	−22.3 ± 0.1	9.3 ± 1.6	−20.4 ± 0.0	10.7 ± 0.0	−22.9 ± 0.9	9.4 ± 0.9	−21.7 ± 1.4	9.4 ± 0.2
	Rhithropanopeus harrisii	−19.3 ± 0.2	7.5 ± 0.3	−18.9 ± 0.0	9.6 ± 0.0	−20.7 ± 0.0	8.2 ± 0.0	−20.3 ± 0.0	7.9 ± 0.0
grazer	*Gammarus* spp.			−20.5 ± 0.0	7.2 ± 0.0	−21.0 ± 0.1	8.0 ± 0.1	−20.7 ± 0.2	4.7 ± 0.3
	Peringia ulvae	−19.2 ± 0.1	6.3 ± 0.1	−19.1 ± 0.5	6.7 ± 0.3	−19.3 ± 0.2	6.5 ± 0.2	−19.8 ± 0.2	6.2 ± 0.2
	Idotea chelipes	−18.9 ± 1.3	5.4 ± 0.7	−20.6 ± 0.0	7.6 ± 0.0	−23.0 ± 0.0	7.2 ± 0.0	−18.7 ± 0.0	4.6 ± 0.0
	Potamopyrgus antipodarum	−20.3 ± 0.0	6.9 ± 0.1						
	Lekanesphaera hookeri			−21.6 ± 0.0	5.1 ± 0.0				
	Theodoxus fluviatilis	−18.2 ± 0.1	6.6 ± 0.3	−18.7 ± 0.1	7.0 ± 0.0			−18.4 ± 0.0	5.2 ± 0.0
deposit feeder	Oligochaeta					−21 ± 0.2	7.7 ± 0.1		
	Pygospio elegans	−20.1 ± 0.0	8.6 ± 0.0						
carnivore	*Pungitius pungitius*	−21.7 ± 0.3	11.6 ± 0.1	−21.2 ± 1.1	12.2 ± 0.6			−20.0 ± 0.0	10.0 ± 0.0
	Sygnathus typhle	−23.1 ± 1.3	12.4 ± 0.1					−20.8 ± 0.4	10.9 ± 0.3
	Pomatoschistus minutus	−18.6 ± 0.2	9.7 ± 0.0	−20.8 ± 0.0	12.9 ± 0.0			−20.2 ± 0.2	10.4 ± 0.5

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Table A (*continued*)

Habitat A (sand with little mixed vegetation)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/ March 2011)		spring (May 2011)		summer (July 2011)	
		δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
	Neogobius melanostomus			−20.1 ± 0.0	12.3 ± 0.0				
	Nerophis ophidion	−22.0 ± 1.6	12.0 ± 0.3	−21.5 ± 1.6	12.1 ± 0.3			−23.3 ± 0.7	11.0 ± 0.1
	Gasterosteus aculeatus			−23.2 ± 1.0	12.4 ± 1.0				
	Gobius niger	−18.5 ± 1.7	10.6 ± 1.2						
Habitat D (sand with little *Pylaiella*)									
Trophic group	Taxon	Season							
		autumn (October 2010)		winter (February/ March 2011)		spring (May 2011)		summer (July 2011)	
		δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
suspension feeder	*Amphibalanus improvisus*			−23.6 ± 0.0	11.5 ± 0.0	−23.0 ± 0.1	11.1 ± 0.0		
	Cerastoderma glaucum	−24.9 ± 0.1	9.3 ± 0.1	−25.0 ± 0.1	9.5 ± 0.0	−23.3 ± 1.3	9.5 ± 0.3	−24.7 ± 0.1	9.4 ± 0.1
	Einhornia crustulenta			−25.2 ± 0.0	9.4 ± 0.0				
	Mya arenaria	−22.7 ± 0.0	10.8 ± 0.0	−25.6 ± 0.4	10.0 ± 0.2	−25.3 ± 0.0	9.8 ± 0.1	−24.2 ± 0.2	10.0 ± 0.1
	Mytilus trossulus			−25.3 ± 0.2	9.8 ± 0.1			−25.3 ± 0.4	9.6 ± 0.1
suspension- deposit feeder	*Macoma balthica*	−21.0 ± 0.2	10.1 ± 0.3	−22.2 ± 0.3	9.6 ± 0.2	−22.8 ± 0.3	10.5 ± 0.1	−22.8 ± 0.4	10.4 ± 0.4
	Marenzelleria neglecta	−20.2 ± 0.1	13.3 ± 0.3	−21.5 ± 0.7	12.6 ± 0.2	−21.9 ± 0.4	12.1 ± 0.5	−21.8 ± 0.1	11.5 ± 0.1
omnivore	*Hediste diversicolor*	−21.9 ± 0.3	11.6 ± 0.2	−23.6 ± 0.4	11.8 ± 0.2	−22.7 ± 0.1	12.2 ± 0.2	−22.0 ± 0.5	12.4 ± 0.3
	Nematoda	−22.7 ± 0.7	12.2 ± 1.3	−22.5 ± 0.2	13.6 ± 0.3	−23.1 ± 0.2	12.8 ± 0.5	−23.0 ± 0.0	13.3 ± 0.1
	Rhithropanopeus harrisii							−21.2 ± 0.0	12.1 ± 0.0
	Crangon crangon	−20.2 ± 0.4	13.1 ± 0.2	−18.3 ± 0.3	14.2 ± 0.3			−20.8 ± 0.0	11.5 ± 0.0
grazer	*Corophium volutator*			−23.6 ± 0.0	10.5 ± 0.0	−23.8 ± 0.2	9.1 ± 1.8	−23.9 ± 0.2	9.8 ± 0.5
	Gammarus spp.							−22.1 ± 0.3	10.2 ± 0.3
	Peringia ulvae	−20.3 ± 0.1	9.9 ± 0.0	−20.5 ± 0.1	10.3 ± 0.0			−21.8 ± 0.0	9.5 ± 0.0
	Idotea chelipes			−21.7 ± 0.1	10.4 ± 0.1			−21.4 ± 0.0	9.8 ± 0.0
	Lekanesphaera hookeri	−17.5 ± 0.0	10.3 ± 0.0					−22.7 ± 0.0	10.5 ± 0.0
deposit feeder	Oligochaeta	−22.1 ± 0.1	10.5 ± 0.4			−22.6 ± 0.2	10.7 ± 0.4	−22.6 ± 0.0	10.8 ± 0.0
	Pygospio elegans	−24.1 ± 0.0	14.9 ± 0.0	−23.1 ± 0.0	10.5 ± 0.0	−23.5 ± 0.4	10.5 ± 0.1		
	Streblospio spp.	−22.5 ± 0.0	12.9 ± 0.0	−21.9 ± 0.0	12.7 ± 0.0	−23.4 ± 0.0	11.5 ± 0.0	−22.9 ± 0.0	12.0 ± 0.0
carnivore	*Cyathura carinata*	−19.0 ± 0.4	13 .0 ± 0.1	−21.0 ± 0.0	12.8 ± 0.1	−21.4 ± 0.4	13.1 ± 0.1	−21.2 ± 0.1	13.1 ± 0.0
	Pomatoschistus minutus	−20.6 ± 0.7	12.2 ± 0.8						
	Neogobius melanostomus			−20.7 ± 0.6	13.8 ± 0.5			−20.8 ± 0.3	13.6 ± 0.3
	Nerophis ophidion			−24.9 ± 0.0	13.0 ± 0.0			−23.9 ± 0.0	12.5 ± 0.0
	Gasterosteus aculeatus			−23.6 ± 0.8	12.9 ± 1.1				
	Gobius niger	−20.7 ± 0.6	13.3 ± 0.5					−20.7 ± 0.0	13.6 ± 0.0

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10.1. Author contribution statement

Author contribution statement

We hereby confirm, that the specific contributions to the publication:

Ziółkowska, M., Sokołowski, A., 2022. Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics. Estuarine, Coastal and Shelf Science, 274, 107931. https://doi.org/10.1016/j.ecss.2022.107931.

were as follows:

Marcelina Maria Ziółkowska - 85 %

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conceptualization and design of the study, field sampling, laboratory work, statistical analyses and interpretation of the results, preparation of figures and tables, writing the manuscript, revision and editing, contribution to response to the reviews, correspondence with editor

....

Adam Sokołowski - 15 %

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conceptualization and design of the study, field and laboratory work, revision and commenting on manuscript, funding acquisition

....

Chapter 11. Funding

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CURRICULUM VITAE OF THE AUTHOR

EDUCATION

2009–2016	PhD studies , University of Gdańsk Faculty of Oceanography and Geography
2005–2009	MSc studies, University of Gdańsk, Faculty of Oceanography and Geography, speciality Marine Biology

PUBLICATIONS

Co-authorship of 10 scientific papers, including 9 published in journals indexed on JCR list

Ziółkowska, M., Sokołowski, A. (2022). Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics. *Estuarine, Coastal and Shelf Science*, 274, 107931.

Sokołowski, A., Świeżak, J., Hallmann, A., Olsen, A. J., Ziółkowska, M., Øverjordet, I. B., Nordtug, T., Altin, D., Krause, D.F., Salaberria, I., Smolarz, K. (2021). Cellular level response of the bivalve Limecola balthica to seawater acidification due to potential CO2 leakage from a sub-seabed storage site in the southern Baltic Sea: TiTank experiment at representative hydrostatic pressure. *Science of the Total Environment*, 794, 148593.

Jędruch, A., Bełdowska, M., Ziółkowska, M. (2019). The role of benthic macrofauna in the trophic transfer of mercury in a low-diversity temperate coastal ecosystem (Puck Lagoon, southern Baltic Sea). *Environmental Monitoring and Assessment*, 191, 1-25.

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Bełdowska, M., Jędruch, A., Zgrundo, A., Ziółkowska, M., Graca, B., & Gębka, K. (2016). The influence of cold season warming on the mercury pool in coastal benthic organisms. *Estuarine, Coastal and Shelf Science*, 171, 99-105.

Brulińska, D., Olenycz, M., Ziółkowska, M., Mudrak-Cegiołka, S., & Wołowicz, M. (2016). Moon jellyfish, Aurelia aurita, in the Gulf of Gdansk: threatening predator or not?, BOREAL ENVIRONMENT RESEARCH, 21, 528–540.

Sokołowski, A., Ziółkowska, M., Zgrundo, A. (2015). Habitat-related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea). *Journal of Sea Research*, 103, 93-102.

Latała A., Wołowicz M., Ziółkowska M., Fisiologia de organismos marinhos, Elabouoe e editou: Academia Maritima de Gdynia, Gdynia , Polonia

RESEARCH GRANTS

2021 – present	Transport via ocean currents of human pharmaceutical products and their impact on marine biota in the European Arctic, project under the Polish-Norwegian Research Fund, 2019/34/H/NZ8/00590, contactor
2014-2017	Impact of potential leakage from the sub-seabed CO2 storage site on marine environment at relevant hydrostatic pressure, project under the Polish-Norwegian Research Fund, Pol-Nor/201992/93/2014, contractor
2012	Dietary habits and response to antropogenic stress: marine bivalve as a bioindicators of hazardous conditions in oligotrophic waters and their usefulness in natural bioremediation process (Dietox), Association of European Marine Biological Laboratories (ASSEMBLE), Call 6 to the Interuniversity Institute for Marine Science, Eilat (IUI), Israel, contractor
2012	Rtęć w środowisku morskim na tle anomalii pogodowych, Research project from the Ministry of Science and Higher Education, 2011/01/B/ST10/07697, contractor
2012	Określenie obecności bakterii symbiotycznych u małży z gatunku Macoma balthica za pomocą pomiaru stabilnych izotopów węgla i azotu oraz metody histologicznej i cytologicznej, research project from University of Gdańsk, G010-620-796/2012, project menager
2011	Określenie współczynnika frakcjonowania troficznego na przykładzie organizmów filtrujących, research project from University of Gdańsk, 586-G245-0451-1, project menager
2009 -2012	Struktura i funkcjonowanie sieci troficznej w ekosystemie Zatoki Puckiej, Research project from the Ministry of Science and Higher Education, contractor

RESEARCH INTERNSHIP

2012	scientific and professional internship on the Santa Barbara vessel (Petrobalic Sp z o.o.) as part of the European project "Sub-seabed Co2 Storage: Impact on Marine Ecosystems (ECO2)"
2012	scientific internship at the Interuniversity Institute for Marine Science Eilat (UIU), Israel under the 7th Framework Program European Union
2011	scientific internship at the LIttoral ENvironnement et Sociétés department. University of La Rochelle, France
2010	scientific internship financed by the French Embassy LIttoral ENvironnement et Sociétés, University of La Rochelle, France
2008	scientific internship at the Department of Fisheries Oceanography and Marine Ecology, National Marine Fisheries Research Institute (analysis of macrozoobenthos samples from the Baltic Sea, conservation methods and data analysis)

CONFERENCES

Author and co-authorship of 3 oral presentation and 5 posters presented at scientific conferences

Hammer KM., Overjordet IB., Krause D., Salaverria-Zabalegui I., Ardelan M., Olsen AJ., Nordtung T., Smolarz K., Łukawska-Matuszewska K., Burska D., Pryputniewicz – Flis D., Hallmann A., Szymelfenig M., Kozłowska D., Ziółkowska M., Świeżak J., Sokołowski A., Impact of potential leakage from the sub-seabed CO2 storage site on marine environment at relevant hydrostatic pressure (CO2Marine), *18th Pollutant Responses In Marine Organisms (PRIMO)*, Trondheim, Norwegia (poster presentation)

Bełdowska M., Jędruch A., Zgrundo A., Ziółkowska M., Graca B., Gębka K., 2013, Mercury in the coastal zone of Southern Baltic Sea as a function of changing climate - preliminary results, *The 11th International Conference on Mercury as a Global Pollutant*, Edenburg, Szkocja (poster presentation)

Ziółkowska M., Sokołowski A., Richard P., 2012, Food webs in the Puck Lagoon (southern Baltic Sea)-stable isotopes analysis case study, *Marine Biological Association Postgraduated Conference*, Ireland (oral presentantion)

Ziółkowska M., Sokołowski A., Kuklinski, P., Bałazy P., 2011, Development of invertebrate assemblages on hard substrate in coastal region of the Gulf of Gdańsk, *ICES Annual Science Conference*, Gdańsk, Polska (poster presentation)

Sokołowski A., Ziółkowska M., Richard P., Wołowicz M., 2011, Trophic efficiency in benthic communities of the southern Baltic Sea (the Gulf of Gdańsk) as determined by dual stable isotope technique, *46th European Marine Biology Symposium*, Chorwacja (oral presentantion)

Zgrudno A., Ziółkowska M., 2011, Macrophytobenthos of the Puck Bay (southern Baltic Sea) and associated epiphytic diatoms – preliminary results of studies on the structure and functioning of the food web, *The British & Irish Diatom Meeting*, Norfolk, Wielka Brytania (poster presentation)

Kuklinski, P., Sokolowski, A., Ziolkowska, M., Balazy, P., Novosel, M., Barnes, D.K.A., 2010, Growth ratio of selected sheet-like bryozoan colonies along a latitudinal transect, 15th *Internacional Bryzoology Association Conference*, Kiel, Germany (poster presentation)

Ziółkowska M., 2009, Development of invertebrate assemblages on hard substrata in two region in the Gulf of Gdańsk, *Symposium of young oceanographers*, Gdynia, Polska (oral presentantion)

COURSES

2016	Stable Isotope Mixing Models (SIMMs) using SIAR, SIBER and MixSIAR, Glasgow, Wielka Brytania
2014	Środowisko R od podstaw: analiza i wizualizacja danych, Poznań, Polska
2014	Stable isotope: analysis and application in food web ecology, Ghent, Belgia
2013	Błękitna Biotechnologia, Instytut Oceanografii, Gdynia, Uniwersytet Gdański
2012	Sampling animal tissue for stable isotope analysis, Brest, Francja
2011	Ocena oddziaływania na środowisko ze szczególnym uwzględnieniem aspektów przyrodniczych, Gdańsk, Polska
2009	Zrównoważony rozwój regionu bałtyckiego, Baltic University, Arrupe Center Gdynia, Polska

TEACHING EXPERIENCE

2009-2016	Classes with students of Oceanography (University of Gdańsk): Marine Ekology and Specialized classes in the sea and coastal zone
2012-2013	Jean Monnet educational and research project "Children's University for Europe, Gdynia
2013	A series of lectures on marine ecology at the Experyment Science Center in Gdynia
2010-2012	Educational project financed by the European Union from the Human Capital Programme („Rozwój przez kompetencje”), conducting scientific lectures for students from the Pomeranian Voivodeship and conducting natural science workshops for young scientists at the Institute of Oceanography, Gdynia Jean Monnet educational and research project "Children's University for Europe, Gdynia