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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<sub>1</sub>) the  $\delta^{13}$ C and  $\delta^{15}$ N of basal resources differ among benthic habitats that are in close proximity to one another, (H<sub>2</sub>) consumer  $\delta^{13}$ C and  $\delta^{15}$ N vary among different habitat types, and (H<sub>3</sub>) 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<sup>2</sup> 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  $5\,\mathrm{dm^3}$  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  $\mu$ m) 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  $-20\,^\circ\text{C}$ .

Phytoplankton 25–100  $\mu m$  in size was collected vertically from above the bottom to the water surface with a WP2 net with 25  $\mu m$  mesh (diameter 57 cm). The material collected was then sieved gently through 1 mm and 125  $\mu m$  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  $\mu m$  and 100  $\mu m$  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<sup>2</sup>) 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

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