Structure and functioning of the benthic communities associated with macrophytes meadows in the Gulf of Gdańsk

Struktura i funkcjonowanie zespołów bentosowych związanych z łąkami makrofitów w Zatoce Gdańskiej

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CONTENTS

Abstract

Seagrass meadows are among the most diverse and productive coastal ecosystems in the world. Seagrass plants are habitat builders by forming a dense three-dimensional structures and ecosystem engineers as they can modify the availability of resources for other organisms. Seagrass vegetated sediments often support enhanced biodiversity, biomass of benthic organisms and food webs fuelled by larger number of food sources, compared to the neighbouring unvegetated systems. Nowadays, in the era of global warming, seagrass meadows play an important function of the effective carbon storages ("blue carbon sinks").

The dissertation is based on studies conducted in the southern Baltic Sea (the Gulf of Gdańsk), where a dramatic reduction in *Zostera marina* meadows area occurred between 70s and 80s of the last century. Recently, a natural recovery of eelgrass habitats in this area is observed. The aim of the present dissertation is to investigate if and how the recovering eelgrass meadows affect the functioning of the benthic systems in the Gulf of Gdańsk. The seagrass meadows in the Gulf of Gdańsk remain at relatively low densities and biomass, whereas the benthic fauna communities are characterized by low biodiversity. Thus the Gulf of Gdańsk study gives the opportunity to compare the obtained results with those from stable seagrass systems with better developed vegetation and regions with higher diversity of benthic fauna. It will help to understand the effects of the meadow development on its ability to modify the functioning of the seabed in coastal areas.

The present dissertation includes the first assessment of the organic carbon stock and accumulation in the sediments covered by the eelgrass meadows in the southern Baltic Sea. Several descriptors of the organic matter quantity and quality were compared among sediment samples collected at the vegetated and unvegetated bottoms. Significantly higher concentrations of organic matter (POC) and photosynthetic pigments (chlorophyll *a*, pheopigments) in the sediments covered by seagrass meadows were noted. Higher concentrations of the organic carbon in the vegetated sediments were not accompanied by similar differences in the composition of carbon stable isotope (δ^{13}C). The model SIAR (Stable Isotopes in R) was used to estimate the relative contributions of the potential sources to organic matter pool on the basis of the carbon and nitrogen stable isotopes. The modelled contributions of organic matter derived from seagrass were significantly higher in

the vegetated (40-45%) than in the unvegetated sediments (5-21%). The total amount of organic carbon stored within seagrass meadows in the top layer of sediment (10 cm) ranged from 50.2 to 228.0 g m^{-2}, the rate of carbon accumulation varied from 0.84 to 3.85 g m^{-2} y^{-1}. The estimated organic carbon accumulation rates in the Gulf of Gdańsk seagrass meadows are lower than those reported from the warm water *Posidonia* dominated seagrass systems or better developed (i.e. with higher density and biomass of vegetation) *Z. marina* meadows. Results indicate that low density eelgrass meadows of the Gulf of Gdańsk can act as carbon sinks. However, the relatively low values of carbon accumulation rates suggest that present day global estimations of seagrass carbon sink (based mostly on data from *Posidonia* systems) should be reconsidered taking into account more local assessments representing different levels of vegetation development.

The present study was also focused on reconstructing food web structure (defined by the food sources contributions to the consumers diet) of benthic fauna associated with seagrass meadows and inhabiting the bare sandy bottom. The trophic connections were examined using biochemical markers (stable isotopes of carbon and nitrogen, fatty acids). Analysis included meio- and macrofauna consumers (identified to the species level) and all potential food sources (POM, SOM, epiphytes, microphytobenthos/bacteria, macrophytes) collected at the vegetated and unvegetated bottom. The samples were analyzed in terms of the total fatty acid composition and isotopic composition (δ^{13}C, δ^{15}N). Significantly higher amounts of the fatty acid bacterial marker (C18:1ω7) were observed in meiofauna (approximately 40%) than in macrofauna (1% on average), what suggests that the bacteria are an important part of meiofauna diet. The Bayesian mixing model (MixSIAR) based on markers of fatty acids and stable isotopes were used to estimate the relative contributions of food sources to the consumers diet. It indicated that both meio- and macrofauna consumers in the vegetated habitat utilized more food sources (epiphytes and some plants matter by meiofauna *T. discipes* and grazers), and omnivore organisms relied to a larger degree on an animal originated organic matter (meiofauna and macrofauna prey). The results underline the importance of seagrass meadows as habitats increasing the availability and variety of food for benthic consumers.

Results of the present study indicate that the recovering *Z. marina* meadows in the Puck Bay, despite the relatively weakly developed vegetation (low density and biomass of macrophytes) significantly impact the functioning of the benthic system.

Streszczenie

Trawy morskie należą do morskich roślin kwiatowych, które tworzą gęste łąki w strefach przybrzeżnych wszystkich kontynentów z wyjątkiem Antarktydy. Obecnie szacuje się, iż całkowita powierzchnia łąk traw morskich wynosi ok. 177 000 km^2, natomiast powierzchnia łąk podwodnych w obszarze Północnego Atlantyku oraz Morza Bałtyckiego stanowi co najmniej 1480 km^2. *Zostera marina* jest gatunkiem trawy morskiej najbardziej powszechnym i kosmopolitycznym oraz dominującym w strefie przybrzeżnej Północnego Atlantyku. *Z. marina* jest również jedynym gatunkiem trawy morskiej występującym w Morzu Bałtyckim.

Łąki trawy morskiej stanowią jedne z najbardziej różnorodnych i produktywnych ekosystemów przybrzeżnych. Pełnią funkcję "inżynierów ekosystemu", czyli organizmów, które bezpośrednio lub pośrednio zmieniają dostępność zasobów dla innych gatunków. Łąki trawy morskiej modyfikują przepływ wody (zmniejszenie siły fal i prądów) oraz sedymentację cząstek (zwiększona depozycja) i tym samym wpływają na ilość pokarmu dostępnego dla organizmów bentosowych, a siła tego oddziaływania zależy od charakterystyki danej łąki (zagęszczenie, długość liści) oraz od właściwego typu osadu, jak i od warunków hydrodynamicznych danego rejonu.

Dzięki zdolności 'zatrzymywania' większej ilości materii organicznej w porastanych osadach, łąki trawy morskiej są uznawane za skuteczne magazyny węgla w osadzie (tzw. ang. „blue carbon sinks"). Łąki podwodne pełnią też ważną rolę jako siedliska oraz są kluczowym elementem przybrzeżnych łańcuchów pokarmowych. Nie tylko sprzyjają zwiększonej ilości materii organicznej w osadzie, ale również zwiększają ilość dostępnych źródeł pokarmu (epifity, makroglony, glony nitkowate) jak i podtrzymują wysokie liczebności konsumentów (meiofauna, macrofauna, ryby).

W ciągu ostatnich dziesięcioleci, odnotowuje się ciągły spadek powierzchni trawy morskiej na świecie. W polskiej strefie Morza Bałtyckiego rozległe łąki trawy morskiej obejmowały sporą część Zatoki Puckiej, jednak w drugiej połowie XX wieku nastąpiła ich znaczna degradacja. W ostatnich latach, naturalna odbudowa łąk podwodnych zaczęła postępować w kilku miejscach w Zatoce Gdańskiej. Powierzchnia łąk podwodnych gwałtownie wzrosła natomiast zagęszczenie i biomasa trawy morskiej pozostała niska w porównaniu do innych łąk *Z. marina*. Naturalna odnowa łąk podmorskich może

w znaczący sposób wpływać na strukturę i funkcjonowanie systemu dna morskiego w obszarach przybrzeżnych Zatoki Gdańskiej, w tym na dostępność pokarmu dla konsumentów oraz ścieżki przepływu energii i materii.

Celem rozprawy doktorskiej było zbadanie wpływu odradzających się łąk traw morskich o niskim zagęszczeniu na funkcjonowanie systemów bentosowych na przykładzie Zatoki Gdańskiej. Zatoka Gdańska stanowi przykład systemu, gdzie odradzające się łąki pozostają na stosunkowo niskim poziomie zagęszczeń i biomasy, a faunę cechuje niska bioróżnorodność. Porównanie wyników badań z zatoki z wynikami z systemów łąk o dłuższej historii, stabilnej i dobrze rozwiniętej wegetacji pozwoliło na ocenę znaczenia stopnia rozwoju łąk podwodnych na zdolność do modyfikacji funkcjonowania systemów dna morskiego w obszarach przybrzeżnych.

W ramach rozprawy przeprowadzono ocenę zdolności łąk Zatoki Gdańskiej do akumulowania węgla w osadzie (jest to pierwsza tego typu analiza przeprowadzona w rejonie południowego Bałtyku). Próbki osadu (górne 2 i 10 cm), a także potencjalnych źródeł materii organicznej (POM, epifity, makrofity) zostały pobrane przez płetwonurków latem 2012 oraz 2013 roku, w trzech rejonach o różnych warunkach środowiskowych (osłonięta, wewnętrzna część zatoki (Inner), otwarta zewnętrzna część zatoki (Outer, GS)) na dnie porośniętym i nieporośniętym trawą morską. Dodatkowo na stacjach porośniętych trawą morską, pobrane zostały rdzenie o średnicy 15 cm w celu wyznaczenia zagęszczenia oraz biomasy makrofitów, które wykazały zróżnicowanie łąk pomiędzy trzema lokalizacjami (najwyższe zagęszczenie trawy morskiej w rejonie GS wynoszące 84.9 roślin na m^{-2}, najniższe zagęszczenie w rejonie Outer wynoszące 46.9 roślin na m^{-2}). W celu określenia tempa sedymentacji pobrano cztery rdzenie o długości około 70 cm w wewnętrznej części Zatoki Puckiej (na wysokości Kuźnicy – miejsce o udokumentowanym występowaniu łąk *Z. marina* w ciągu ostatnich 30 lat). Próbki osadu zostały zanalizowane pod kątem zawartości materii organicznej, barwników fotosyntetycznych, uziarnienia osadu oraz składu izotopów stabilnych węgla i azotu, natomiast różnice w tych wskaźnikach pomiędzy dnem porośniętym a nieporośniętym były testowane za pomocą dwuczynnikowego testu PERMANOVA. Stwierdzono wyższe zawartości węgla organicznego i barwników fotosyntetycznych w osadach z dna porośniętego oraz brak różnic w składzie izotopów węgla $\delta^{13}C$ w osadach pobranych

w dwóch siedliskach. Model SIAR (Stable Isotopes in R) został wykorzystany dla określenia względnych udziałów źródeł materii organicznej w osadzie w oparciu o dane składu izotopowego azotu i węgla. Wyniki modelowania wskazują, iż ilość materii organicznej pochodzącej z trawy morskiej jest znacznie wyższa na dnie porośniętym roślinnością (40-45 %) w porównaniu do osadów dna nieporośniętego (4,5-21 %). Średnia zawartość węgla w górnej warstwie osadu (10 cm) porastanego przez trawę morską w Zatoce Gdańskiej wynosi od 50,2 do 228,0 g m^{-2}, natomiast akumulacja węgla w tych osadach od 0,84 do 3,85 g m^{-2} y $^{-1}$ (w zależności od rejonu). Efektywność łąk traw morskich do gromadzenia węgla w osadzie zależy od lokalizacji i panujących w niej warunków środowiskowych, najwyższa zawartość węgla organicznego została odnotowana w rejonie osłoniętej części zatoki (Inner). W przypadku dwóch lokalizacji w części zewnętrznej (Outer, GS) większa zawartość węgla organicznego notowana była w miejscu o wyższym zagęszczeniu roślin. Wartości węgla 'zmagazynowanego' w osadach stosunkowo słabo rozwiniętych łąki Z. *marina* Zatoki Gdańskiej zawierają się w przedziale wartości zanotowanych dla zdegradowanych łąk *Zostera* z wschodniego Atlantyku, natomiast tempo akumulacji węgla jest najniższe z jak dotąd odnotowanych. Uzyskane wartości gromadzenia oraz akumulacji węgla są znacznie niższe niż te odnotowane dla osadów porastanych przez gatunek *Posidonia* w cieplejszych ekosystemach. Uzyskane wyniki wskazują na znaczące różnice w gromadzeniu węgla pomiędzy gatunkami traw morskich z różnych rejonów świata i potrzebę uwzględnienia danych z rejonów reprezentujących różne strefy klimatyczne oraz łąki o różnym składzie gatunkowym, stopniu rozwoju roślinności w globalnych szacunkach potencjału traw jako magazynów węgla (takie szacunki jak dotąd oparte były przede wszystkim o dane z ciepłowodnych łąk zdominowanych przez *Posidonia*).

Celem rozprawy było również porównanie struktury bentosowej sieci troficznej (zdefiniowanej poprzez źródła pokarmu konsumentów) w systemach łąk podwodnych i dna nieporośniętego makrofitami. Badania prowadzone były przy wykorzystaniu markerów biochemicznych (izotopów stabilnych węgla i azotu oraz kwasów tłuszczowych). Próbki konsumentów (meiofauna – dwa gatunki copepoda *Paraleptastacus spinicauda, Tachidius discipes*; makrofauna - 22 gatunków, ryby – 3 gatunki wspólnie repezentujące 4 typy troficzne: organizmy odżywiające się zawiesiną oraz detrytusem (ang. *suspension/ detritus*

feeders), organizmy odżywiające się pokarmem pochodzenia roślinnego (ang. *grazers*), wszystkożercy (ang. *omnivores*), a także potencjalnych źródeł pokarmu (POM, SSOM, epifity, mikrofitobentos, makrofity) zostały pobrane przez płetwonurków latem 2014 roku, w zewnętrznej Zatoce Puckiej (w okolicach Jastarnii) na dnie porośniętym i nieporośniętym trawą morską. Próbki zanalizowano pod względem całkowitego składu kwasów tłuszczowych oraz składu izotopowego (δ^{13}C, δ^{15}N). 19 kwasów tłuszczowych zostało zidentyfikowanych w źródłach pokarmu oraz konsumentach. Skład dominujących kwasów tłuszczowych oraz skład izotopów stabilnych różnił się istotnie pomiędzy źródłami pokarmu. W makrofitach przeważały markery roślin naczyniowych (18:2ω6, 18:3ω3), w epifitach oraz glonach nitkowatych markery okrzemkowe (16:0, 20:5ω3), w mikrofitobentosie marker bakteryjny (18:1ω7, co wskazuje na wysoki udział bakterii w tym źródle), w SSOM marker bakteryjny (18:1ω7) oraz marker detrytusu (18:1ω9), natomiast POM zawierał największy udział markeru wiciowców spośród wszystkich źródeł (22:6ω3). Wartości izotopu węgla wynosiły od -23.5‰ (POM) do -10.6‰ (makrofity), natomiast izotopu azotu od 1.0‰ (SSOM) do 6.4‰ (glony nitkowate). Dość wysoką zawartość kwasu tłuszczowego uznawanego za marker bakteryjny (18: 1ω7) odnotowano dla meiofauny (średnio 40%), co sugeruje aktywną konsumpcję bakterii przez tą grupę (w makrofaunie udziały tego kwasu to jedynie 1%). W przypadku makrofauny, wysoką zawartość kwasu tłuszczowego uznawanego za marker wiciowców (22:6ω3) odnotowano w organizmach odżywiających się zawiesiną oraz detrytusem, w porównaniu do dwóch pozostałych grup konsumentów. Organizmy odżywiające się pokarmem pochodzenia roślinnego cechowały się wyższą zawartością kwasów markerów okrzemkowych (16:0, 20:5ω3) oraz roślin naczyniowych (18:2ω6, 18:3ω3), a wszystkożercy wyższą zawartością markera odpowiedzialnego za drapieżnictwo (18:1ω9). Najniższe wartości składu izotopowego azotu odnotowane zostały dla meiofauny (3.3‰) co wskazuje, że organizmy te znajdują się u podstawy sieci troficznej, natomiast najwyższe dla wszystkożerców (8.9‰), co wskazuje na znaczący udział drapieżnictwa w sposobach odżywiania tej grupy. Najniższe wartości składu izotopowego węgla (-20.4‰) odnotowano dla fauny odżywiającej się zawiesiną oraz detrytusem z dna nieporośniętego makrofitami, natomiast najwyższe dla organizmów odżywiających się pokarmem pochodzenia roślinnego z dna porośniętego (-17.1‰). W celu określenia udziałów poszczególnych

źródeł pokarmu w diecie konsumentów wykorzystano modelowanie w ujęciu bayesowskim MixSIAR z użyciem danych o składzie izotopów stabilnych i zawartości wybranych markerów kwasów tłuszczowych. Wyniki modelu wskazały, iż meiofauna konsumuje głównie SSOM oraz mikrofitobentos, natomiast dodatkowe źródło pokarmu dla meiofauny zamieszkującej dno porośnięte makrofitami stanowią epifity. Zaobserwowano brak różnic w diecie fauny odżywiającej się zawiesiną oraz detrytusem zamieszkujących dwa siedliska. Przedstawiciele tych dwu grup odżywiali się mieszaniną POM/SSOM, epifitów i mikrofitobentosu, z różnymi udziałami poszczególnych źródeł zależnymi od gatunku. Fauna odżywiająca się pokarmem pochodzenia roślinnego z siedliska traw morskich konsumowała więcej źródeł w porównaniu do tych z dna nieporośniętego (brak epifitów oraz roślin w diecie). Wszystkożercy na dnie porośniętym bazowali głównie na pokarmie pochodzenia zwierzęcego (meiofanie i makrofaunie), a na dnie nieporośniętym na SSOM. Różnice w strukturze sieci troficznej pomiędzy siedliskami obejmowały: większą liczbę źródeł pokarmu konsumowanych przez faunę łąki trawy morskiej (dodatkowym, istotnym źródłem pokarmu w diecie zarówno meiofauny (copepoda *T. dispices*) i makrofauny (odżywiającej się pokarmem pochodzenia roślinnego) były epifity) oraz większe drapieżnictwo wśród fauny z dna porośniętego (wyższe udziały źródeł pochodzenia zwierzęcego w diecie). Wyższe udziały meiofauny w diecie wszystkożerców z systemu łąk podwodnych w zestawieniu z wysoką zawartością markerów bakteryjnych w tkankach meiofauny wskazują na silniejszy przepływ węgla bakteryjnego w sieci troficznej systemu dna porośniętego przez makrofity.

Podsumowując, wyniki rozprawy wskazują, iż łąki *Z. marina*, pomimo niskiego stopnia rozwoju (niskich zagęszczeń i biomasy makrofitów), wpływają na funkcjonowanie systemu dna morskiego Zatoki Gdańskiej. Zaobserwowane efekty występowania zarośli makrofitów to:

− zwiększona zawartość węgla organicznego oraz pigmentów fotosyntetycznych w osadzie,

− istotne udziały tkanek trawy morskiej w puli źródeł materii organicznej w osadzie (40% w osadach porośniętych, 14 % w osadach nieporośniętych),

− modyfikacja struktury sieci troficznej poprzez większą liczbę dostępnych i konsumowanych źródeł (epifity jako istotne źródło w diecie meiofauny i makrofauny

dna porośniętego), wyższy stopień drapieżnictwa wśród organizmów wszystkożernych (prawdopodobnie dzięki większej dostępności pokarmu zwierzęcego) i zwiększony przepływ materii organicznej pochodzenia bakteryjnego w systemie dna porośniętego.

1. Introduction

1.1. Aims of the thesis

Seagrasses belong to marine flowering plants that form dense meadows in the coastal zone of all continents except Antarctica (Green and Short 2003). The most recent estimations of worldwide areal distribution of seagrasses excess 177. 000 km^2 (Spalding et al. 2003), with only the North Atlantic and the Baltic Sea seagrasses area representing minimum of 1480 km^2 (Boström et al. 2014). Seagrass meadows are among the most diverse and highly productive coastal ecosystems in the world providing many goods and services (Hemminga and Duarte 2000). Due to the effects of reducing water velocity and trapping particles, seagrass meadows may be the effective carbon sinks (recent worldwide estimations report 19. 900 Tg of sequestrated carbon, Fourqurean et al. 2012), reduce coastal erosion and increase water transparency (Boström and Bonsdorff 2000). Moreover, they play an important role of habitat-forming species by creating three-dimensional structures (leaves, rhizomes, roots). Hence, they increase the complexity of the seabed architecture and provide shelter and numerous niches for other organisms (Gartner et al. 2013). What is more, seagrasses and associated macrophytes, especially epiphytes, can be direct food sources for faunal consumers, thus they sustain populations of commercially important vertebrate and invertebrate species (Hemminga and Duarte 2000).

Seagrasses are regarded as 'ecosystem engineering organisms' as defined by Jones et al. (1994) as 'organisms that directly or indirectly modify the availability of resources to other species, by causing changes in physical state of biotic or abiotic materials'. Seagrass meadows act as engineering organisms because they modify water flow regimes and sedimentation of particles and thus influence organic and inorganic matter availability to benthic organisms (Hemminga and Duarte 2000). Many studies reported increased amounts of fine particles in the sediments covered with seagrass as compared to the bare sea bottoms (e.g. Herkul and Kotta 2009, van Katwijk et al. 2010, Jankowska et al. 2014). However, the seagrass engineering effects depend on the characteristics of the seagrass vegetation, original sediment characteristics, and the hydrodynamic regimes of a given locality (van Katwijk et al. 2010). For example, the effects of slowing down the current velocities and trapping fine particles by seagrass meadows were correlated to plant canopy heights (Gacia

et al. 1999) or shoot density (Webster et al. 1998, van Katwijk et al. 2010). In highly dynamic systems sparse vegetation did not influence fine particles trapping (van Katwijk et al. 2010). Hence, ecosystem engineering effects can largely vary among different coastal localities, meadows dominated by different seagrass species and with different levels of the vegetation development (Bos et al. 2007, Herkul and Kotta 2009).

Over the past decades, the significant decrease in seagrass abundance and aerial cover have been recorded worldwide (Watcott et al. 2009). It is linked to many possible causes including eutrophication (Hauxwell et al. 2001), sediment resuspension and deposition (Frederiksen et al. 2004), sea level rise (Glenmarec et al. 1997), extreme weather (Reusch et al. 2005, Birch and Birch 1984), coastal development (Orth et al. 2006), thermal pollution (Zeimen and Wood 1975) and dredging (Gordon et al. 1994). In the southern Baltic Sea, extensive eelgrass meadows were covering considerable part of the Puck Bay. However, the severe decline of the meadows was observed in the second half of the last century (Kruk-Dowigałło 1991). Recently, the natural recovery of eelgrass-dominated underwater meadows has begun in several places in the Gulf of Gdańsk. The areal coverage of the seagrass beds increased rapidly, but the density and biomass of the plant tissues remains low compared to the other European *Z. marina* meadows (Jankowska et al. 2014).

The aim of the present dissertation is to investigate if and how the recovering eelgrass meadows affect the functioning of the benthic systems in the Gulf of Gdańsk (southern Baltic Sea). The Gulf of Gdańsk serves as an example of the system characterized by both the low level of vegetation development (low density and biomass of macrophytes) and low faunal diversity defined by the Baltic Sea species pool. The study focus on two aspects of possible effects of macrophyte vegetation: carbon storage in sediments and benthic food web structure defined by the consumers diets.

The hypothesis of the thesis is:

The recovering low-density *Z. marina* meadows significantly modify the seabed system functioning, particularly

1) enhance the carbon storage in sediments,

2) increase the number of food sources in diets of benthic consumers.

The dissertation presents the first assessment of seagrass sediment carbon storage in the low-density temperate *Z. marina* beds in the southern Baltic Sea. The seagrass ability to store organic carbon depends on the meadows characteristics (macrophyte species and density), while most assessments of seagrass meadows capacity to store carbon were performed in warm water meadows dominated by *Posidonia oceanica* (a large plant forming a very dense vegetation) or well established meadows with dense vegetation of temperate *Zostera* species. The study in the Gulf of Gdańsk can show if the effects documented in the meadows with better developed vegetation can be also observed in a locality representing the low-end of vegetation density and biomass. It will be also an important complementation of the present-day global scale seagrass carbon storage assessments (Fourqurean et al. 2012) that are based mostly on information from *Posidonia* systems and do not consider the low-density cases as the Baltic Sea eelgrass meadows.

Also, the food web part of the dissertation is aimed to explore if the effects reported from the better developed meadows and more diverse benthic communities can be observed in a case of the recovering vegetation and the impoverished Baltic Sea fauna. The information on various aspects of the underwater meadows food web structure is increasing but it is often fragmentary and scattered across a number of scientific publications (e.g. the majority of publications focus only on one group of consumers or do not include all possible sources) that used different methodology (only stable isotopes, both stable isotopes and fatty acids) and rarely implemented Bayesian mixing models. Thus the present study reveal a comprehensive view of the benthic food web structure in two habitats: vegetated sediments and bare sands. It includes all major possible food sources (bacteria/microphytobenthos, epiphytes, macroalgae, seagrass, POM, SSOM) and most consumers identified to species level (meiofauna copepods, macrofauna and fish). The species diet is estimated using biochemical markers (fatty acids, stable isotopes) and Bayesian mixing models. Benefits of using combined approach of stable isotopes and fatty acids in seagrass systems have been recently demonstrated by Leduc et al. 2006, Jaschinski et al. 2008, Lebreton et al. 2011. Isotopic mixing models has been often used to convert the isotopic data into estimates of food sources contributions to animal's diet and more recently mixing models based on Bayesian statistics that incorporate uncertainty are widely applied (Phillips et al. 2014). In the last three years some studies using fatty acids data in mixing

models in a quantitative manner have been published (Galloway et al. 2014, Galloway et al. 2015, Neubauer and Jensen 2015). The number of publications using Bayesian mixing models inference is rapidly growing (Phillips et al. 2014) and this method has been considered as accurately estimating sources contribution to animal's diet (Moore and Semmens 2008). Despite the fact that stable isotopes or fatty acids based Bayesian mixing models can serve as useful tools in determining species diet, they have been rarely applied in seagrass studies (Lebreton et al. 2011, Vafeiadou et al. 2013, 2014, Mittermayr et al. 2014, Michel et al. 2014). The present study is the first field study integrating all components of benthic system and using stable isotopes and fatty acids in a Bayesian mixing models, to get the best estimations of trophic links in complex seagrass food webs.

1.2. Seagrass and its significance for coastal ecosystems

1.2.1. Seagrass origin and distribution

Seagrasses are flowering angiosperms that colonized the marine environment about 100 million years ago (Hemminga and Duarte 2000). Most probably they evolved from freshwater macrophytes to grow in brackish and marine environments (Hemminga and Duarte 2000, Green and Short 2003). During the evolution, seagrasses have developed key adaptations to marine environment: a) blade or subulate leafs with sheaths needed in high-energy environments, b) hydrophilous pollination, c) lacunar systems allowing the internal gas flow needed to maintain the oxygen supply required by their belowground parts, d) anchoring system (Hemminga and Duarte 2000, Green and Short 2003). Seagrasses are clonal plants that are interconnected via belowground stems called rhizomes (Hemminga and Duarte 2000). The aboveground part called a shoot, consists of a bundle of leaves attached to the rhizome. The final component is the root system, which is responsible for anchoring of the plant and nutrient uptake from the sediment (Kuo and den Hartog 2006). The plants reproduce both sexually and vegetatively, and due to rarely occurring sexual reproduction and limited spatial dispersion via hydrophilous pollination, their genetic diversity is lower compared to their terrestrial equivalents. Seagrasses are assigned to two families (Potamogetonaceae and Hydrocharitaceae) which encompass 12 genera containing about 55 species. Three of the genera (*Halophila, Zostera, Posidonia*) comprise most of the

species (55%, Hemminga and Duarte 2000). Two other aquatic plants families, Ruppiaceae and Zannichelliaceae also occur in brackish or marine habitats, however, it is still debated whether those families should be considered as seagrasses (Spalding et al. 2003). Seagrasses occur all around the world in shallow subtidal or intertidal areas including estuaries, brackish and fully marine seas (Hemminga and Duarte 2000) with depth limits set by the light availability that ranges from 1 m in turbid systems to over 50 m in very clear waters (Duarte 1991). Most of seagrass meadows are monospecific, however, meadows containing more seagrass species occur in the southeast Asia, Japan/Republic of Korea and southwestern Australia (Spalding et al. 2003, Short et al. 2007, Fig. 1). Often seagrass creates mixed meadows with other macrophytes, macroalgae or epiphytes.
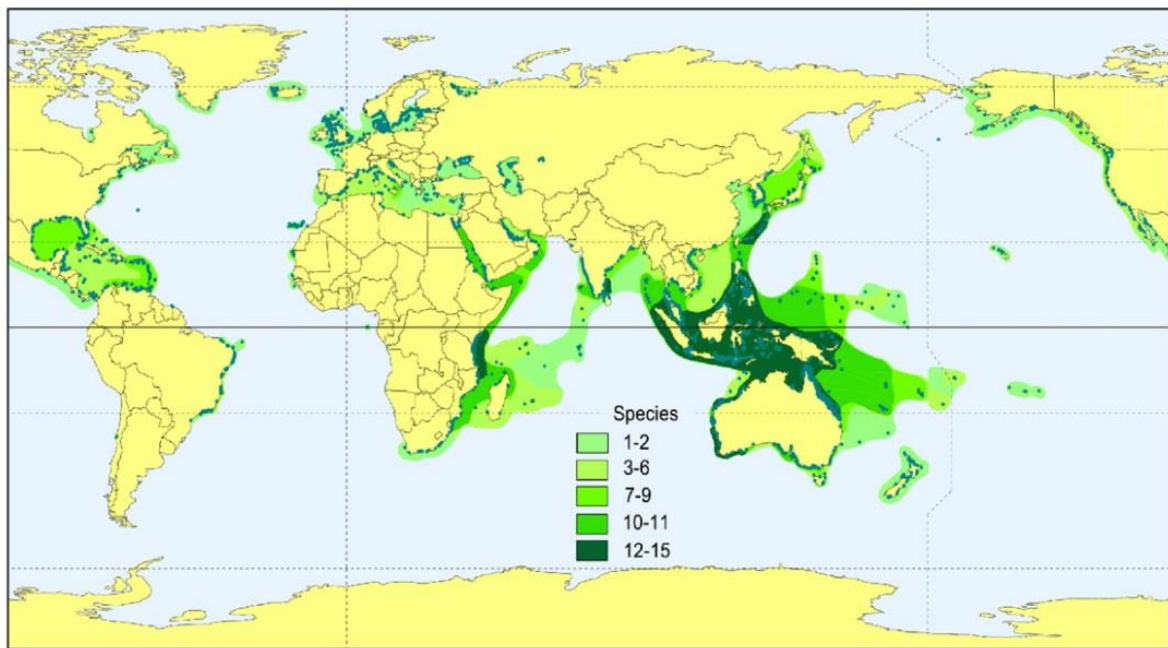
Fig. 1   Global seagrass diversity and distribution. Shades of green indicate numbers of seagrass or macrophytes species reported for an area where seagrass occurrence is documented (after Short et al. 2007)

The *Zostera* genus contains nine species (Moore and Short 2006). *Zostera marina* called 'eelgrass' has the most cosmopolitan distribution (Moore and Short 2006). It has been observed in tropical and temperate climate zones, in both hemispheres and reported to occur even north of the Arctic Circle (Spalding et al. 2003). Eelgrass is a dominant species

in the temperate North Atlantic and the only species inhabiting the Baltic Sea (Boström et al. 2003, Fig. 2).
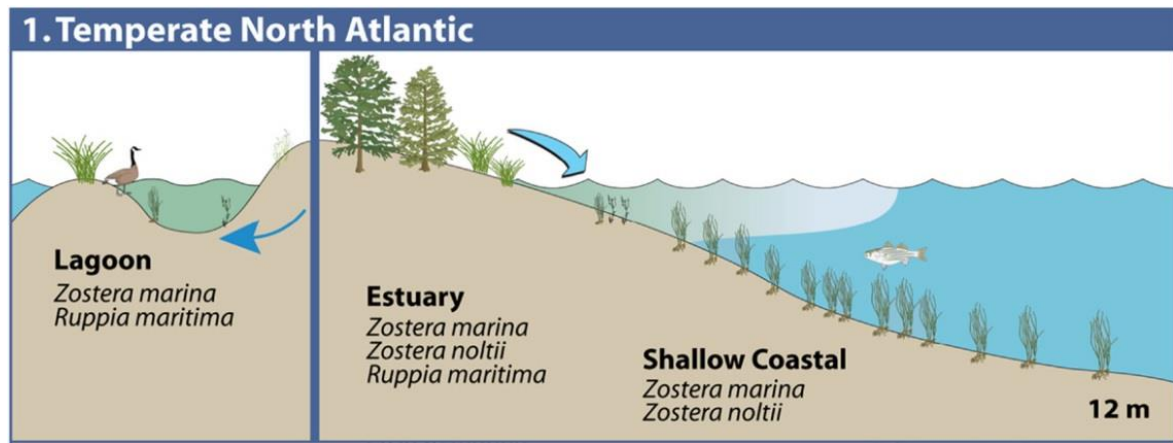
Fig. 2   Scheme of seagrass occurrence in the temperate North Atlantic coastal zone (after Short et al. 2007)

In the Proper Baltic, eelgrass occurs in the coastal waters of Sweden (total meadows area of Sweden is 60-130 km^2), southwest Finland (30 km^2), Estonian coast (155 km^2) and Polish coast (48 km^2, Boström et al. 2014). This seagrass species is characterized by flat, elongated leaves that can widely range in length (from 10 to 60 cm) depending on the environmental conditions. In temperate seas, due to changes in hydrodynamic regimes, temperature and solar irradiance, the variation in eelgrass biomass and productivity over annual cycle can be substantial (Caulsen et al. 2014). Most temperate seagrass plants loses considerable part of the aboveground biomass in autumn, and survive the winter with the energy (carbohydrates) stored in its rhizomes (Moore and Short 2006).

1.2.2. Seagrass as an ecosystem engineer

The concept of ecosystem engineers was first introduced by Jones et al. (1994), as 'an organism that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials' (Jones et al. 1994). There are two types of ecosystem engineering effects changing the accessibility of the resources to other organisms: a) a direct consequence of the structure created by them (autogenic engineers), b) the modulation of biotic or abiotic

forces by its structure or their biological activity (allogenic engineers) (Jones et al. 1994, Gutiérrez et al. 2010). Coastal vegetation, such as kelp forest, mangroves, marsh plants and seagrasses, are known as the autogenic ecosystem engineers, as they reduce water flow within their canopy or root system, promoting sedimentation within the vegetation and provide substrate for both sessile and mobile organisms (Bos et al. 2007, Bouma et al. 2009). Several studies reported that seagrass meadows acted as ecosystem engineers as they could modify the water flow regimes and sedimentation rates and hence changed the sedimentary settings and/or increased food supplies for benthic organisms.

Terrados and Duarte (2000) provided evidence that eelgrass canopies were able to reduce particle resuspension from the seabed sediments. Bos et al. (2007) reported that the transplantation of seagrass resulted in an increase of silt fraction and accretion of 7 mm of sediment. A two-fold increase in organic matter in the sediments covered by the *Zostera noltii* from the Mauritanian coast was observed within the 10 cm sediment cores compared to those collected in the bare bottoms (Boer 2007). However, sediment modification effects are dependent on the characteristics of the vegetation, the original sediment characteristics and the hydrodynamic regimes of a given locality (van Katwijk et al. 2010). For example, Gacia et al. (1999) showed that slowing down of current velocities was proportional to the canopy height of the *P. oceanica* (the Mediterranean Sea) plants as well as Webster et al. (1998) stated that the effects of eelgrass on sediment characteristics was dependent on shoot density (south-west United Kingdom coast). The seasonal study in the Puck Bay (southern Baltic Sea) noted increased organic matter and fine sand content in the vegetated sediments, however the magnitude of the documented effects differed seasonally and followed the seasonal changes in the structure of the seagrass vegetation (Jankowska et al. 2014).

1.2.3. Seagrass goods and services

Seagrasses are of a great ecological importance and provide many goods and services. They are among the most productive ecosystems worldwide and harbor a high biodiversity of marine animal species (Duarte 2002, Green and Short 2003, Larkum et al. 2006, Orth et al. 2006). Underwater meadows serve as nursery grounds for the juveniles (Orth et al. 2006) and change the food web structure. Seagrass based food webs usually

comprise the vast number of components because the plants increase number of primary producers and are a direct food source for grazers such as sea urchins, turtles, manatees, dugongs, migrating birds and fish, thus play important role for sustaining commercially important species (Valentine and Heck 1999, Hemminga and Duarte 2000, Larkum et al. 2006). The effects of seagrass on the food web functioning can result not only from the modification of the food source composition but also from the altered composition, diversity and standing stocks of consumers (Gilles et al. 2012).

Seagrass meadows are also regarded as "blue carbon sinks" (Nellemann et al. 2009). This term refers to natural marine habitats that are able to capture and store carbon for long time periods (centuries or millennia, Murray et al. 2011). In seagrass beds mineral carbon is photosynthetically fixed as an organic matter in plant tissues and part of it is allocated to the belowground tissues (roots and rhizomes). Particulate organic carbon suspended in the water can also be trapped by seagrass and buried into the sediments due to vegetation-induced reductions in water flow and wave action (Koch et al. 2006). Then, it can remain stored in the seagrass meadow sediments over millenary time scales (Mateo et al. 1997). The global seagrass meadows carbon storage is estimated to be 19. 900 Tg (Fourqurean et al. 2012). Whereas annual rate of carbon accumulation in seagrass meadows provided by other global studies exceeds 83 g C m^{-2} y^{-1} (average value for seagrass meadows worldwide, Duarte et al. 2005) or 27– 44 Tg C y^{-1} (total global accumulation, Kennedy et al. 2010).

Additionally, seagrasses also play role in shoreline protection by reducing impact of currents and waves (Gambi et al. 1990, Fonseca and Cahalan 1992, Duarte 2002) and in purifying the water column by trapping nutrients and sediment particles (Granata et al. 2001, Agawin and Duarte 2002).

All these functions and services of seagrass meadows combined together result in a high economic value of the seagrasses that represent one of the most valuable coastal habitat with global annual value of US$3.8 trillion (calculated for global seagrass area of 2 million km^2, value derived only from nutrient cycling, Costanza et al. 1997).

1.2.4. Threats to the seagrass meadows

Due to the fact the seagrass meadows occupy the coastal zone they are often threatened by many stressors of natural and human origins. Seagrass decreases in temperate regions were caused by a combination of many factors. Seagrass require good light conditions, therefore eutrophication (Hauxwell et al. 2001), sediment resuspension and turbidity (Frederiksen et al. 2004) considerably affect their growth. Due to climate change and its various effects seagrasses face a number of challenges significantly reducing their abundance (thermal pollution, pH decreas, increased storm frequency, sea level rise, Orth et al. 2006). Thermal pollution and sea level rise cause reduce the amount of solar radiation that reach the sea bottom, acidification affects physiology of seagrass and numerous storms mechanically destroy underground meadows structures (Orth et al. 2006). Apart from these factors, the wasting disease epidemic of the 1930s, caused by the protist *Labyrinthula zosterae* (Muehlstein et al. 1988, Vergeer et al. 1995), also considerably reduced the most common temperate seagrass species (*Z. marina*) from the North Atlantic region (den Hartog 1987, Vergeer and den Hartog 1994). Therefore, over the past three decades, accelerating loss of seagrass area has been noted worldwide (Waycott et al. 2009). Only in the Baltic Sea, large scale losses of 60 to 100% eelgrass area have been recorded in Denmark, Sweden and Poland between 1900s and the mid-1980s, caused mostly by eutrophication, seabed dredging and costal construction (Boström et al. 2014, Fig. 3).
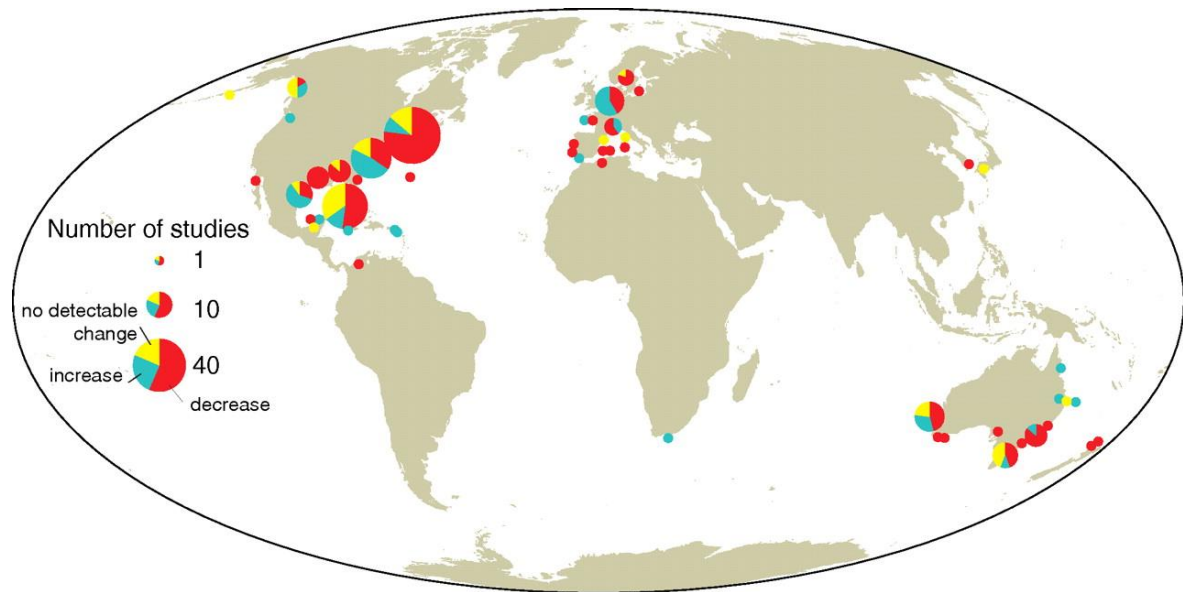
Fig. 3   Global map of changes in seagrass coverage noted between 1879 and 2006. Changes in seagrass areal extent at each site are defined as declining (red) or increasing (green) when areal extent changed by >10%, or no detectable change (yellow) when final area was within ±10% of the initial area (Waycott et al. 2009). The assessment is based on 131 sites in the North America, 34 sites in the Europe, and 40 sites in the Australia (after Waycott et al. 2009)

2. Materials and methods

2.1. Study area

The study took place in the Gulf of Gdańsk, located in the southern Baltic Sea. The Baltic Sea is a semi-enclosed shallow body of brackish water, consisting of several sub-basins, with an approximate surface area of 4 x 105 km^2. Large quantities of freshwater from discharging rivers mix with sea water entering the basin through the Sound (Öresund) and the Danish Belts (Ojaveer et al. 2010). The salinity gradient runs from the more saline (around 10) southwestern region, through medium saline main basin (7) to the freshwater-like (about 2) conditions in the north.

The Gulf of Gdańsk is located in the southern Baltic Sea off the Polish coast where salinity reach around 8 (Nowacki 1993). A considerable part of the gulf is made by the Puck Bay, separated from the open sea by the Hel Peninsula. The Ryf Mew sandbank (8 km long) divides the bay into two parts: the notably deeper outer Puck Bay (with an average depth of 20 m), and the shallower inner part called the Puck Lagoon (3 m on average). The sandbank forms a shallow dam of average depth 1 m with only two deeper channels (up to 7 meters deep) and causes significant reduction of water exchange between inner part of the bay and open waters of the outer bay. The water exchange takes place during only 17% days of a year (Nowacki 1993). The Ryf Mew shallows protect the inner part of the bay from the impact of open sea storms. The average wave height is greatly higher for the outer and shallow area of the Gulf of Gdańsk (from 0.2 to 4 m, depending on the wind direction), than the inner Bay (from 0.1 to 1.5 m, Jarosz and Kowalewski 1993). The sediment characteristics of the Gulf of Gdańsk are shaped by bathymetric patterns of hydrodynamic pressures and muddy sediment are noted mostly in deeper parts (above 10 meters) whereas shallows consists of sand of medium grain size or even gravel in some areas (Jankowska and Łęczyński 1993). There are few rivers entering the Gulf of Gdańsk including the Vistula river – the longest river of Poland with water masses inflow of 1047 m^3 s^{-1} (IMGW 2011). Few small rivers mouths are entering directly to the Puck Bay – Gizdebka, Płutnica, Reda, Zagórska Struga, Kacza.

The trajectory of eelgrass meadows extent in the southern Baltic Sea of the Polish coast has shown dramatic changes over the past 60 years. Before 1950s, most of the

seafloor of the Inner Puck Bay was covered by the meadows. A significant decrease (caused most probably by eutrophication and massive growth of filamentous algae) of *Z. marina* occurrence in the area has been observed in 1987 – when eelgrass area declined to only 16 km^2 (Kruk-Dowgiałło 1991, Fig. 4).
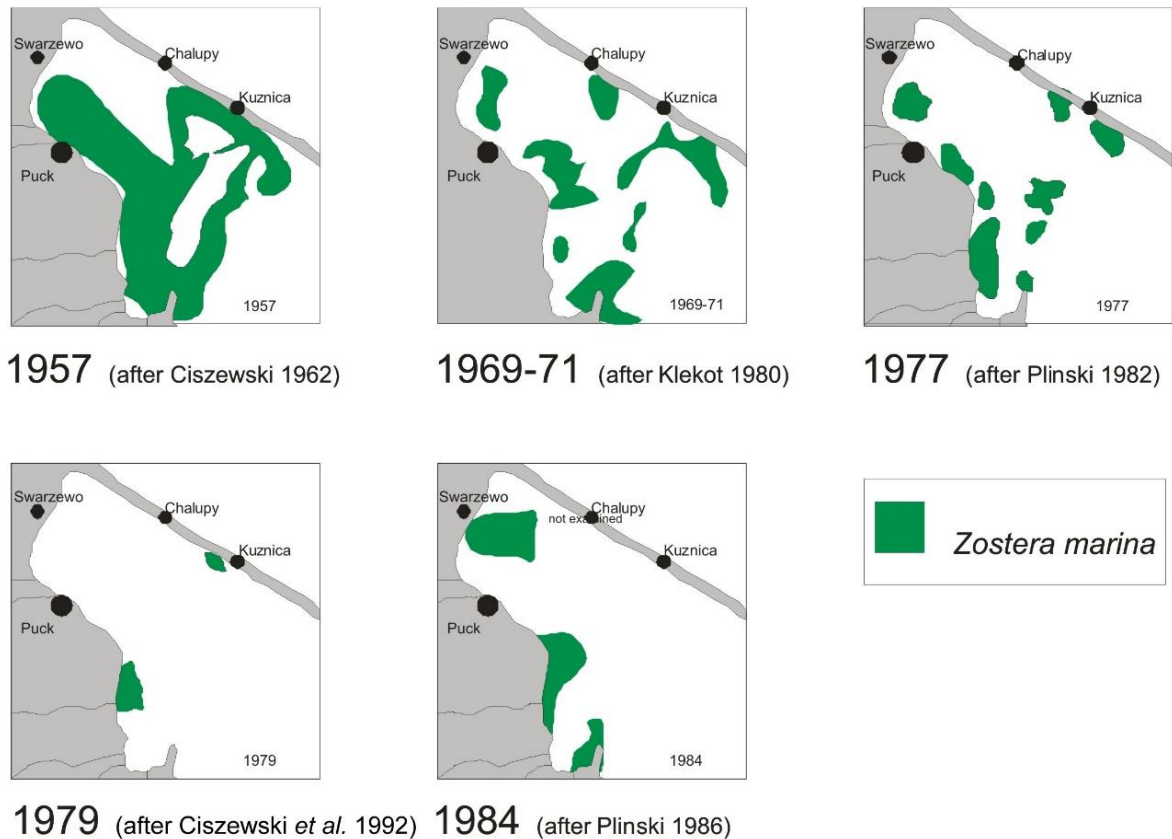
Fig. 4 Long term changes in eelgrass distribution in the inner Puck Bay (http://www.IO PAN.gda.pl/projects/Zostera/history.html, after Ciszewski 1962, Klekot 1980, Pliński 1982, Pliński 1990, Ciszewski 1992)

A recent inventory of the seabed habitats in the Polish Exclusive Economic Zone documented that areas covered by *Z. marina* meadows are rapidly growing in size. Areal distribution of eelgrass beds estimated in 2009, amounted 48 km^2 only for the inner Puck Bay (Węsławski et al. 2013). At the moment, the actual eelgrass-covered area may be even higher, as new locations of seagrass occurrence in the Gulf of Gdańsk have been observed during sampling campaigns in 2012-2014 (Jankowska, personal observations).

The seasonal study of seagrass vegetation biometrics showed that shoots of eelgrass in the Puck Bay persisted throughout the year despite of hard winter conditions (heavy storms, freezing temperatures, ice cover) (Jankowska et al. 2014). Meadows density ranged from 50 shoots m^{-2} in March to 202 shoots m^{-2} in July, the highest mean leaf length reached 25 cm in July, the biomass ranged from 9 g dw m^{-2} (March) to 40 g dw m^{-2} (July, Fig. 5).
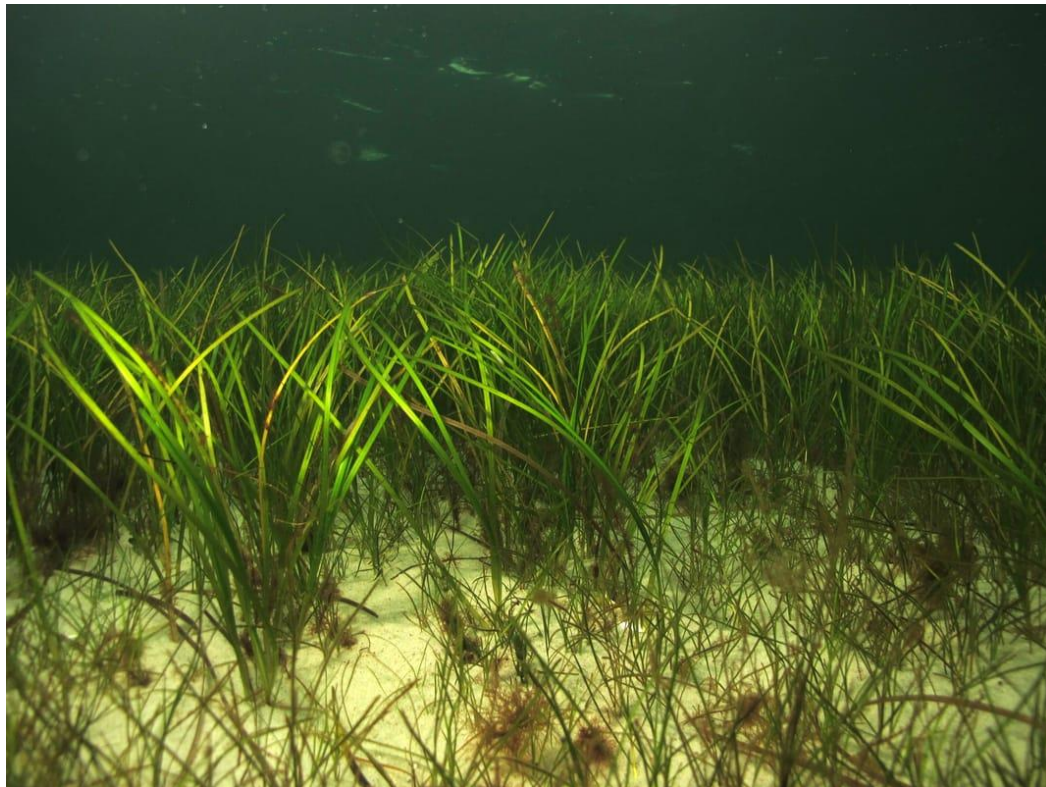
Fig. 5 Eelgrass meadows at the outer Puck Bay in summer season (July) photographed by Piotr Bałazy

The number of macrophyte species associated with the seagrass meadow dropped from summer (five macrophyte species, including *Z. marina*, *Ruppia maritima*, *Pylaiella littoralis, Chara baltica, Ceramiun rubrum, Furcellaria fastigiata*) to winter (only eelgrass, Jankowska et al. 2014). The Puck Bay seagrass meadows supported higher densities, biomass and diversity of macrobenthic fauna than the neighboring bare sands, however the presence and magnitude of these effects was also season dependent (Włodarska-Kowalczuk et al. 2015).

Density and biomass of *Z. marina* in the Gulf of Gdańsk was low compared to other temperate eelgrass meadows of Northern hemisphere, thus represents low density meadows (Fig.6, Jankowska et al. 2014).
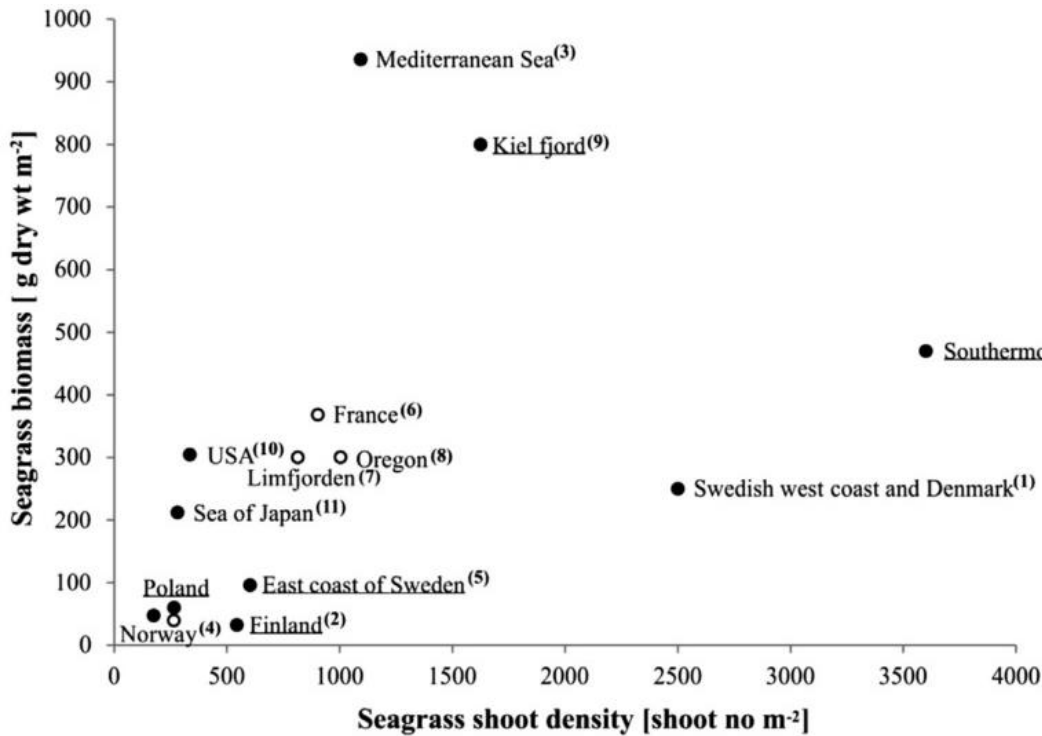
Fig. 6   The biomass and shoot density of *Z. marina* meadows noted worldwide. The Baltic Sea sites are underlined (after Jankowska et al. 2014)

2.2 Sampling

2.2.1. Seagrass vegetation and sediment characteristics

The study was conducted at three locations that are characterized by different environment characteristics: sheltered inner Puck Bay (Inner, samples collected in a depth ranging from 1.5 to 2 meters), exposed outer Puck Bay (Outer, samples collected in a depth ranging from 1.5 to 2 meters) and exposed shallows near shore area (close to the Gdynia - Sopot agglomeration, samples collected in a depth ranging from 2.5 to 3.5 meters) in the main basin of the gulf (GS) (Fig. 7).
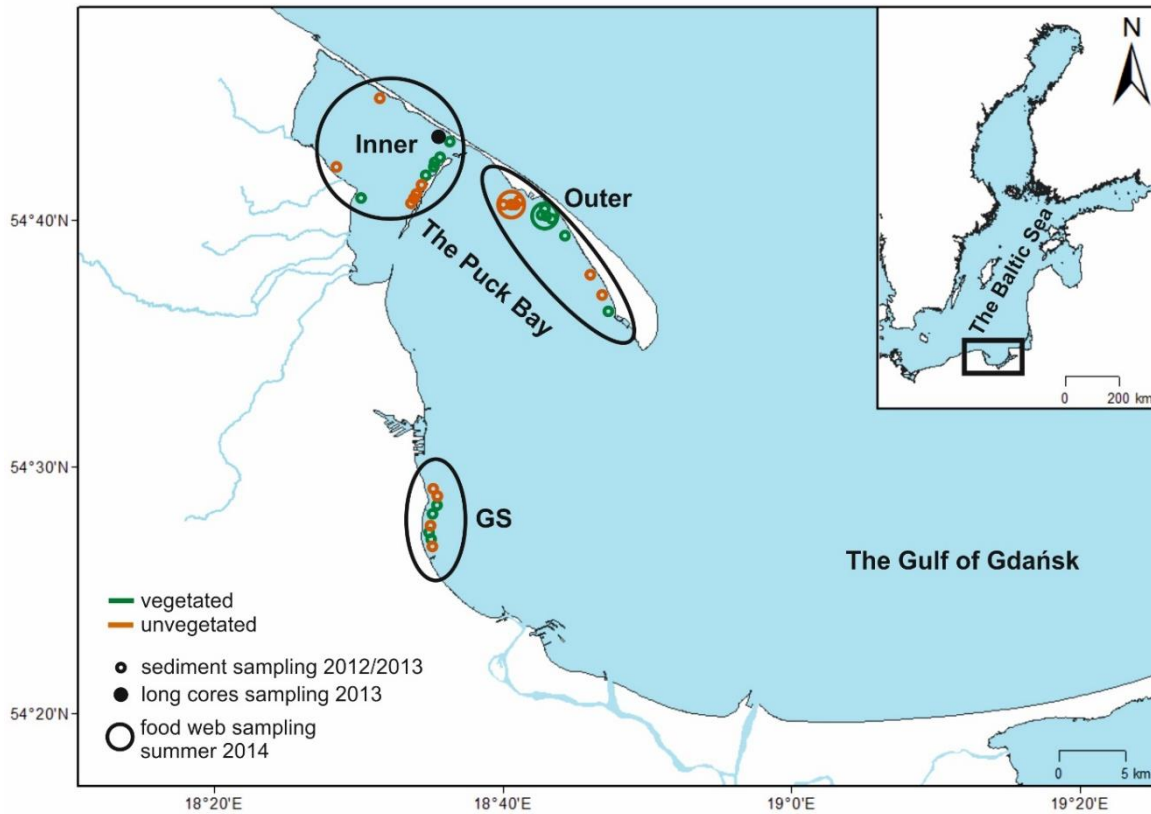
Fig. 7 Study area with indication of the sampling points. Map was made using the ArcMap 10.4 software by ESRI (WGS1984 coordinate system). The spatial data have been provided courtesy of the GIS Center, University of Gdańsk

Sampling took place in the summer (the season of maximum seagrass vegetation development in the Gulf of Gdańsk, Jankowska et al. 2014), in July 2012 and 2013. At each location, the water temperature and salinity were measured (using a Mettler-Toledo sensor). 6 liters of suspended POM (Particulate Organic Matter, used in a study as a proxy of phytoplankton), benthic macrophytes and epiphytes were sampled as possible organic matter sources at each locality for stable isotope analysis. Sediment samples were collected at 96 stations: 24 stations at the GS location 36 stations at Inner and 36 stations at Outer. At each location, half of the stations were located on the vegetated bottoms and the other half on the bare sands. Each vegetated station was placed in the center of a meadow, each bare sand station was placed at least 50 m away from the nearest meadow's edge. A set of samples collected by a SCUBA diver at each station included sediment samples (collected with use of 2 cm ⌀ core) for the photosynthetic pigments concentration (upper 2 cm),

particulate organic carbon (POC [%]), total nitrogen (TN [%]), carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios (upper 2 cm) and grain size analysis (upper 10 cm). At vegetated stations samples of macrophytes (collected with use of 15 cm ø core) for vegetation cover characteristics were also collected.

Moreover, at four stations in each location (2 randomly selected stations in each habitat: vegetated and unvegetated), 10 cm long cores were collected and sliced every 2 cm to explore the vertical variability in the sediment characteristics.

Four 60 cm long sediment cores (5 cm ø) were collected for ^{210}Pb dating and organic matter description (POC, TN, δ^{13}C, δ^{15}N) at the Inner location. This location was chosen as the best locality for accumulation rate assessment because of well recorded historical seagrass presence in that area (near Kuźnica, Fig. 7). The cores were sliced into 2 cm layers. The samples from the four long cores were combined to provide satisfactory (0.2 g) amounts of pelite fractions (>0.063 mm), which were needed for effective ^{210}Pb dating.

The sediment samples were preserved at -20°C, except for the samples for the photosynthetic pigments analyses, which were stored at -80°C; the macrophytes were fixed and preserved in 4% formaldehyde.

2.2.2. Benthic food web structure

The materials for benthic food web study were collected in the outer Puck Bay, close to Jastarnia port, in an area characterized by well-developed eelgrass vegetation (in terms of density and biomass, Jankowska et al. 2014) and high diversity in the seagrass associated benthic community (Jankowska et al. 2014, Włodarska-Kowalczuk et al. 2014). Two sampling stations (Fig. 7) were selected – one within the extensive eelgrass meadows (54o41'20.84N, 18o41'19.73E) and one in the neighboring large unvegetated area (54o41'19.88N, 18o38'34.37E), both stations were located at similar depths (1.5–2 m), around 2.3 km from each other.

Sampling took place in the summer (18-24 August 2014) when seagrass vegetation development is maximal in the Gulf of Gdańsk (Jankowska et al. 2014). At each station a set of samples was collected by a SCUBA diver. A set of samples included:

a. samples of potential food sources:

- − six cores of upper sediment for SSOM (surface sediment organic matter),

- − six liters of water for POM (as a proxy of phytoplankton),

- − the most upper sediment layer collected with a use of syringe for microphytobenthos,

- − filamentous algae (*Pylaiella litoralis*),

- − benthic macrophytes including eelgrass below- and above-ground structures and epiphytes (on the surface of the eelgrass leaves);

b. samples of consumers:

- − meiofauna (taxa associated with the seagrass leaves collected with a 42 µm mesh size net, benthic taxa by collecting the upper 2 cm of sediments),

- − macrofauna and fish (collected with a sediment corer and a small dredge).

Six replicates for each source at each station (3 replicates for stable isotope analyses and 3 replicates for fatty acid analyses) were collected in summer. The same level of replication was aimed for the consumers (not achieved in case of rare taxa).

2.3. Laboratory analysis

2.3.1. Seagrass vegetation and sediment characteristics

Seagrass meadows vegetation biometrics

The macrophytes collected in the cores were identified to the lowest possible taxonomic level. Algae and plants were dried at 60˚C for 48 h and weighed. Seagrass shoots were counted, the leaf length was measured, and the dry mass of the above-ground and below-ground parts was determined. The term "shoot" was used for seagrass clusters of leaves supported by a single basal meristem (Olesen and Sand-Jensen 1993).

Grain size and photosynthetic pigments concentration in the sediments

To determine the grain size distribution, the sediment samples were dried (48 h, 60°C) and sieved through thirteen sieves at 0.5 phi size intervals from 0.063 to 2 mm (Folk and Ward 1957). To measure the chlorophyll *a* (Chl a) and pheopigments (Pheo) concentrations in the sediment samples, a fluorometric method was used. Freeze-dried sediments were used for pigments extraction in 90% acetone for 24 h at 4 °C (Evans et al. 1987). Measurement were performed with use of Perkin Elmer LS55 Fluorescence

Spectrometer, by measuring emissions at 671 nm and excitations at 431 nm, before and after sample acidification with 1 M HCl. Chl a and Pheo concentration in the sediment were calculated according to Evans and O'Reilly (1982) and expressed in μg per g of dry sediment.

POC, TN and stable isotope composition in the organic matter sources and the sediments

Samples of organic matter sources were processed in the laboratory immediately after sampling: water was pre-filtered on a 320 μm sieve to eliminate large zooplankton then filtered through GF/F Whatman glass fiber filters (0.7μm porosity). Macrophytes were identified, epiphytes were detached from the leaves by shaking using vortex mixer (10 min) and sonificating (2 x 60s, using Sonifier Tansonic Labor 2000) the seagrass leaves and macrophytes in a pre-filtered seawater. Then the water containing detached epiphytes was filtered through GF/F Whatman glass fiber filters (0.7μm porosity). Visual observation was done on seagrass leaves and macrophytes to ensure all epiphytes were detached.

The sediment samples included 96 samples of surface sediments (upper 2 cm), 120 samples from 10 cm-long sediment cores (divided into 2 cm sections) and 36 samples from (combined) four 60 cm long cores. They were freeze-dried and grounded.

All samples of sediment and possible organic matter sources were analyzed for POC [%], TN [%], δ^{13}C [‰] and δ^{15}N [‰] via continuous flow - elemental analysis - isotope ratio mass spectrometry (CF-EA- IRMS) at the University of Liège using a Vario Micro Cube elemental analyzer (Elementar Analysen systeme GmBH, Hanau, Germany) coupled to an Isoprime 100 mass spectrometer (Isoprime, Cheadle, United Kingdom). The freeze-dried, grounded samples were packed into tin capsules and weighed to the nearest 10 μg. Prior to the analyses, to remove inorganic carbon for the measurements, the sediment samples were acidified with direct addition of HCl (Hedges and Stern 1984) and then dried again at 60°C for 24 h. The measurements were performed on both acidified and non-acidified samples. Sucrose (IAEA-C6, δ^{13}C = -10.8 ± 0.5‰, mean ± st.dev.) and ammonium sulfate (IAEA-N$_2$, δ^{15}N = 20.3 ± 0.2‰, mean ± st.dev.) were used as certified reference materials (CRM). Both CRMs are calibrated against international isotopic references, i.e., the Vienna Pee Dee Belemnite (VPBD) for carbon and Atmospheric Air for nitrogen. The standard deviations of the multi-batch replicate measurements of the lab

standards (amphipod crustaceans) interspersed among the samples were 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$. Glycine (Merck, Darmstadt, Germany) was used as a standard for the elemental content measurements. The analytical precision was 2% of the relative content of the samples (i.e., 0.04% for a sample containing 2% of a given element).

Isotopic ratios were expressed using the δ notation (Coplen 2011). The delta value (δ) is calculated as follows:

$$\delta^H X = [(R_{sample}/R_{standard}-1)]*1000,$$

where:

X – is an element

H – is a heave isotope mass of the element

R_{sample} – is a ratio of heavy isotope to the light isotope for the element measured in the sample

$R_{standard}$ – is a ratio of heavy isotope to the light isotope for the element measured in the standard, (Fry 2008).

The multiplication by 1000, gives δ expressed in per-mills [‰] (Fry 2008). The stable isotope ratio is further referred to as "SI". In reporting stable isotope results, the recommendations of Bond and Hobson (2012) are followed, for example $\delta^{13}C$, $\delta^{15}N$ are referred to as isotope composition or isotope ratio.

Measurements of ^{210}PB

The ^{210}Pb dating method introduced by Goldberg (1963) was applied at the Biogeochemistry Department in the Institute of Oceanology Polish Academy of Sciences. The sediment samples (particular layers of 60 cm long cores) intended for ^{210}Pb dating were freeze-dried and grounded in the laboratory. The sediment moisture and porosity were calculated. Because most of the sediment consisted of sandy fraction, the sediments were sieved through a 0.063 mm sieve so only fine, pelite fraction material was used for ^{210}Pb activity concentration analyses (Duarte et al. 2010). The ^{210}Pb activity concentration was measured indirectly by alpha spectrometry counting its daughter nuclide, ^{210}Po. Since ^{210}Po may be more efficiently absorbed by organic matter than ^{210}Pb, measurements were performed almost a year after the sampling (when the eventual excess ^{210}Po in the surface sediment layers decayed). Radiochemical separation of ^{210}Po was performed by the method

presented in Zaborska et al. (2007). Briefly, the sediment samples were spiked with ^{209}Po (chemical yield tracer) and digested in 130°C using HClO$_3$, HF and HNO$_3$. Polonium isotopes were then spontaneously deposited onto silver discs. The discs were analyzed for ^{210}Po and ^{209}Po activity concentrations in a multi-channel analyzer (Canberra) equipped with Si/Li detectors. The samples were counted 1 day. The activity concentration of ^{210}Po in the sample was determined based on chemical recovery by comparing the measured and spiked activity concentrations of ^{209}Po. Reference materials (e.g., IAEA-326) were measured to verify the efficiency of the separation procedure and detection. One blank sample (without sediment) was measured for every 7 sediment samples. The analytical procedure background was negligible.

The remaining subsamples of the pelite fraction was used for the POC, TN, δ^{13}C, and δ^{15}N analysis (as described above).

2.3.2. Benthic food web structure

Samples preparation

Samples of potential food sources were prepared as described in subchapter 2.3.1. Additionally, fresh microphytobenthos was collected by transferring the upper 1 cm of the sediment to plastic boxes. Then the sediment was covered with 100 x 150 mm Whatman lens cleaning tissue and cover glass, and exposed to artificial white light source, to enable diatom migration. After 24 h, microphytobenthos were scraped off the cover slides and transferred to vials with pre-filtered seawater. However, fatty acids analyses indicated that those samples contained large quantities of bacteria, so they are treated as a mixture of bacteria and microphytobenthos.

For the meiofauna only two harpacticoid copepod species *Paraleptastacus spinicauda* of family Leptastacidae and *Tachidius discipes* of family Tachidiidae. were chosen for analysis since they were abundant enough to collect a sufficient number of individuals. Adult individuals were extracted alive from the sediment using decantation and attraction of positive photoactic copepods with artificial a white light. Copepods were placed alive in a petri dish in a pre-filtered seawater for few hours to allow gut clearance. Afterwards individuals of the two species, were picked with a pipet under the stereomicroscope to make several replicate samples, each replicate sample consisting of

200 adults. Macrofauna and fish were kept for 24 h in pre-filtered sea water to purge their gut content. Then, they were identified to the species level. When the individuals were too small to provide enough tissue for one sample several individuals (from 1 to 60, detailed information presented in Table 1) were pooled to obtain large enough sample. Samples of fish consisted of parts of muscles (each sample representing one individual). All samples were placed in a glass vials and frozen at -80°C. Afterwards the samples (of food sources and consumers) were freeze-dried and grounded for further analysis. Grounded samples for fatty acids analysis were kept in -80°C.

Table 1 Samples collected for SI and FA analyses

species/ sources type sources	source type/ feeding group	habitat	replicates for FA	replicates for SI	ind. per replicate
Chara baltica, A.Bruzelius, 1824	plants	veg	1	3	
Myriophyllum sp., Les, 2009	plants	veg	2	3	
Potamogeton pectinatus, (L.) Börner, 1912	plants	veg	2	3	
Zannichellia palustris, Linnaeus, 1753	plants	veg	1	1	
Zostera marina leaves, Linnaeus, 1753	plants	veg	3	3	
Zostera marina roots, Linnaeus, 1754	plants	veg	3	3	
Pylaiella littoralis, (Linnaeus) Kjellman, 1872	filamentous algae	veg/unveg	2	3	
epiphytes	epiphytes	veg	2	6	
bacteria and microphytobenthos	micr	veg	2	2	
SSOM	SSOM	veg/unveg	2/2	3/3	
POM	POM	veg/unveg	3	3/3	
meiofauna					
Paraleptastacus spinicauda, (Scott & Scott, 1895)	meiofauna	veg/unveg	3	2/3	200/200
Tachidius discipes, Giesbrecht, 1881	meiofauna	veg/unveg	3	3/3	200/200
macrofauna					
Cerastoderma glaucum, (Bruguière, 1789)	sdf	veg/unveg	3/3	3/3	8/10
Macoma balthica, (Linnaeus, 1758)	sdf	unveg	2	3	15
Amphibalanus improvisus, (Darwin, 1854)	sf	veg	3	3	18
Mya arenaria, Linnaeus, 1758	sf	unveg	3	3	2
Mytilus edulis, Linnaeus, 1758	sf	veg/unveg	2/1	3/1	10/15
Bathyporeia pilosa, Lindström, 1855	g	unveg	3	3	60
Gammarus spp., Fabricius, 1775	g	veg	8	9	5
Hydrobia spp., Hartmann, 1821	g	veg/unveg	2/2	3/3	50/50
Idotea balthica, (Pallas, 1772)	g	veg	2	2	5
Idotea chelipes, (Pallas, 1766)	g	veg	2	2	5
Jaera spp., Leach, 1814	g	veg	-	-	3
Pygospio elegans, Claparède, 1863	g	veg	0	1	3
Radix peregra, (O F. Müller, 1774)	g	veg	2	3	23
Sphaerona hookeri Leach, 1814	g	veg	-	-	2
Theodoxus fluviatilis, (Linnaeus, 1758)	g	veg	3	3	34
Crangon crangon, Balss, 1913	o	veg/unveg	-	-	1
Cyathura carinata, (Krøyer, 1847)	o	veg/unveg	2/2	2/2	8/12
Hediste diversicolor, (O.F. Müller, 1776)	o	veg/unveg	0/5	0/6	2
Marenzelleria spp., Mesnil, 1896	o	veg/unveg	5/2	5/2	1/2
Nerophis ophidion, Rafinesque, 1810	o	veg	3	3	1
Palaemon adspersus, Rathke, 1837	o	veg	4	4	1
Palaemon elegans, Rathke, 1837	o	veg	5	5	1
Planaria torva, (O.F. Müller, 1773)	o	unveg	1	1	4
Pomatoschistus spp., Gill, 1863	o	veg/unveg	2/6	2/6	1
Syngnathus typhle, Linnaeus, 1758	o	veg	3	3	1

abbreviations: macrofauna feeding types (sdf –suspension/detritus feeders, sf – suspension feeders, g – grazers, o – omnivores)

two habitats (veg – vegetated, unveg – unvegetated)

Fatty acid and stable isotope composition

Lipid extraction, fatty acid methylation and analysis of fatty acid methyl esters (FAMEs) were performed in one step method according to Abdulkadir and Tsuchiya (2008) and De Troch et al. (2005) at Marine Biology laboratory of Ghent University. The boron trifluoride-methanol reagent was replaced by a 2.5% H_2SO_4 methanol solution (copepods and microphytobenthos - 700 μl, the other samples - 2 ml) to prevent loss of polyunsaturated fatty acids (PUFAs) (Eder 1995). The fatty acid non-adecanoic acid C19:0 was added (to copepods and microphytobenthos - 20 μl, to the other samples - 40 μl, Fluka 74208) as an internal standard to allow later quantification. FAMEs were isolated through heating in water for 1.5 h (at 80 °C), adding hexane (copepods and microphytobenthos - 350 μl, the other samples - 1 ml) and deionized water (copepods and microphytobenthos - 350 μl , the other samples - 1 ml) and centrifuging (Eppendorf Centrifuge 5810R; 3 min at 1000 rpm). FAMEs were separated using a HP88 column (Agilent J&W; Agilent) in a gas chromatograph (HP 6890N) coupled to a mass spectrometer (HP 5973). According to the fatty acids concentrations, samples were run in splitless, split-5 and split-10 mode, and 1 μl was injected per run at an injection temperature of 250 °C on a HP88 column. The oven temperature was programmed at 50 °C for 2 min, followed by a first ramp to 175 at 25°C min^{-1} and a second ramp to 230 at 2 °C min^{-1} with a 4-min hold. Blank sample measurements were performed every 10 samples. FAMEs were identified based on comparison of relative retention time and on mass spectral libraries by means of the software MSD ChemStation (Agilent Technologies). FAME concentrations (μg FA per g sediment dry weight) were calculated based on the internal standard 19:0, through linear regression of the chromatographic peak areas and the corresponding known concentrations of the standards (ranging from 25 to 200 mg ml^{-1}). The FA shorthand notation A:BωX was used, where A represents the number of carbon atoms, B. gives the number of double bounds and X the position of the double bound closest to the terminal methyl group (Guckert et al. 1985). Results for each fatty acid were expressed as the relative percentage [%] of the total fatty acid content ± standard deviation. Fatty acids are further abbreviated as "FA".

The isotopic composition of carbon and nitrogen isotopes of sediment, POM, macrophytes, epiphytes, microphytobenthos and meio- and a macrofauna, fish samples

were analyzed as described in subchapter 2.3.1. Together with the sediments samples, few macrofauna samples (*Hydrobia sp., A. improvisus*, all fish species) were acidified with direct addition of HCl (Hedges and Stern 1984) and proceed as described in subchapter 2.3.1.

2.4. Data analysis

2.4.1. Seagrass vegetation and sediment characteristics

Seagrass meadows vegetation biometrics

The differences in the macrophyte vegetation characteristics (seagrass shoot density [shoot m^{-2}], above-ground seagrass biomass, total seagrass biomass, and total macrophyte (seagrass + other macrophytes) biomass [g dry mass m^{-2}]) among the sampling locations (L) were tested using a one-way univariate PERMANOVA model (with one fixed factor: L) based on a similarity matrix created from the Euclidean distances among the samples (untransformed data) (Anderson et al. 2008).

Organic matter content in the sediments

The grain size statistics were calculated using the Folk-Word method with the Gradistat software (Blott and Pye 2001). The sediments were classified according to Friedman and Sanders (1978). Mean grain size [φ] and fine sand percentage (fine sand %) were used as sediment indicators in statistical analysis. The concentrations of Chl a and Pheo were summed to a total and referred to as the chloroplast pigment equivalent (CPE, according to Thiel 1979). The Chl a to POC and Chl a to CPE [%] ratios were calculated. Carbon enhancement at the vegetated bottom for the three locations was expressed as ratio of average POC recorded at the vegetated to unvegetated bottom. The differences in the sediment characteristics (Chl a, Pheo, CPE, Chl a/CPE, Chl a/POC, POC, POC/TN, δ^{13}C, δ^{15}N, mean grain size, and fine sand %) between habitats (H - vegetated bottom versus bare sands) and among locations (L) were tested using a two-way univariate PERMANOVA model (with two fixed factors: H and L) based on a similarity matrix of Euclidean distances among the samples (untransformed data). For samples collected with use of 10 cm long cores the differences in sediment characteristics between the habitats and among locations

and sediment layers (La) were tested with use of a three-way univariate PERMANOVA model (with three fixed factors: H, L, La). When significant effects were found by the main tests, post-hoc pairwise tests were conducted (for factor location (L)). Spearman correlation tests were performed to check whether the sediment descriptors (Chl a, Pheo, CPE, Chl a/CPE, Chl a/POC, POC, POC/TN, δ^{13}C, δ^{15}N, mean grain size, and fine sand %) were correlated to the macrophyte vegetation characteristics of the seagrass meadows (seagrass shoot density, above-ground seagrass biomass, total seagrass biomass, and total macrophyte biomass).

Sources contributions to the sediment organic matter (mixing models)

SIAR mixing models (Stable Isotopes Analysis in R package) were used to numerically estimate the contributions of sources to the sediment organic matter pools. Two stable isotope ratios were used: δ^{13}C and δ^{15}N. The SIAR mixing model is based on Bayesian methods, which are capable of dealing with uncertainty and variability in input data, even in underdetermined systems (Parnell et al. 2010). Several potential sources were sampled and analyzed – POM (particulate organic matter), *Z. marina* leaves and roots, *Ruppia maritima* Linnaeus 1753, *Potamogeton* spp. (*P. perfoliatus* Linneus, 1753 and *P. pectinatus*) *Z. marina* detritus (degraded, black parts of seagrass material), macroalgaes with filamentous structure (*Pylaiella littoralis, Cladophora* spp. Kützing 1843, and *Polysiphonia* spp. Greville 1823) and epiphytes (mainly diatoms overgrowing seagrass leaves).

The differences in the isotopic signals (δ^{13}C, δ^{15}N) of the potential sources were tested by a two-way univariate PERMANOVA (with two fixed factors: Location: L and Source type: S) based on a similarity matrix of the Euclidean distances among the samples (untransformed data). The isotope signatures in the *Z. marina* leaves and roots did not differ from those of *R. maritima*. There were significant differences (considering both isotopes) between the POM and epiphytes and between those two sources and the vascular plants (p < 0.05). In addition, the *Potamogeton* spp. and *Z. marina* detritus differed significantly from the other sources (p < 0.05). Based on these results and on the data of the dominant components in the macrophyte biomass in the study area (Jankowska et al. 2014, present study), three sources were selected for the mixing model – plants (*Zostera marina*

living leaves and roots and *Ruppia maritima* grouped together as their δ^{13}C and δ^{15}N values were similar), POM and epiphytes (epiphytes – detached diatoms and filamentous algae - *Pylaiella littoralis, Cladophora,* and *Polysiphonia,* grouped together as their δ^{13}C and δ^{15}N values were similar). Other potential sources were neglected as their biomass and, thus, potential importance are relatively low in the study area. Isotopic fractionation factors were applied to sources following Lehman et al. (2002) recommendations based on measurements of in situ survey and 3 months-long experimental incubations of aquatic sediments and expressed as an organic matter diagenesis values - 1.5‰ for δ^{13}C and 1.2‰ for δ^{15}N. The model solutions were presented using a Bayesian credibility intervals (95%) of probability density function distributions and modes (most likely solution [%]) (Parnell et al. 2010). Additionally, when differences between the two habitats in sources contributions to the sediment organic matter pool were detected, a probabilistic test has been applied to check what is the probability that certain source contribution is higher in sediments from one habitat with Pr, i.e. the probability that a given situation occurs (1 is the highest possible probability).

Sediment accumulation rate assessment

The profiles of the total ^{210}Pb activity concentrations in the function of sediment depth [cm] were prepared. The supported ^{210}Pb was calculated as an arithmetic mean activity of sediment layers where no further decrease in ^{210}Pb activity was noted. The sediment accumulation rates were estimated from the profile of δ ^{210}Pb$_{ex}$ activity concentration versus porosity-corrected sediment depth [cm] and mass sediment depth (calculated using sediment porosity and density). The linear accumulation rate (LAR, cm y^{-1}) and mass accumulation rate (MAR, g m^{-2} y^{-1}) were calculated assuming an exponential decrease in ^{210}Pb$_{ex}$ with sediment depth and using Simple Constant CS:CS model (Robbins and Edgington 1975):

$$A_t = A_0 e^{-\lambda t},$$

where:
A_t - the ^{210}Pb activity at time t

A_0 - the activity at time 0

λ - is the radionuclide decay constant (for ^{210}Pb, $\lambda = 0.031$).

When t is replaced by $t = x/v$ (x – depth of a given sediment layer, v – sediment accumulation rate), the above formula can be rewritten:

$$A_t = A_0 e^{-\lambda\,x/v},$$

$$\ln A^{210}Pb_{ex}(x) = \ln A^{210}Pb_{ex}(0) - (\lambda/v)x,$$

where:

$A^{210}Pb_{ex}(x)$ - the activity at layer x

$A^{210}Pb_{ex}(0)$ - the activity at the surface (layer 0)

λ - is the decay constant

v - is the sediment accumulation rate

Carbon stock and accumulation in the vegetated sediments

The calculations of C_{stock} (organic carbon content in the sediment, g m^{-2}) and C_{accu} (organic carbon accumulation rate, g m^{-2} y^{-1}) within eelgrass meadows were done on 10 cm sediment profiles for the three locations based on POC [%] concentrations and the sediment accumulation rate measured for the Inner location of 0.13 cm y^{-1} (regarded as a representative of accumulation rate for shallow seabed's thus applied for C_{accu} calculations for all three localities).

Additionally, the total carbon stock and total carbon accumulation stored in eelgrass meadows of the Puck Bay (amount of carbon captured within the existing meadows for the whole area) was estimated for the seagrass meadows of Inner location using formula described in Lavery et al. (2013):

$$C_{stock} = \Sigma\,C \times A \times D,$$

$$C_{accu} = \Sigma\,C \times A \times R,$$

where:

C – mean organic carbon amount in the seagrass vegetated sediments [mg m^{-3}]

A – estimated area of seagrass [m^2]

D – depth of sediment layer [m]

R – rate of sediment accumulation [m y^{-1}]

Total carbon stock and total carbon accumulation calculations were performed only for data from the Inner location (average of POC from Inner location) as the most recent data of eelgrass area coverage are only available for the Inner Puck Bay (48 km^2,

Węsławski et al. 2013). The calculation have been done for upper 10 cm of sediment (i.e. as detected by ^{210}Pb measurements - last 50-60 years; the profile slope indicated that the upper 10 cm layer are also mixed) and for 10- 60 cm layer (representing the time before seagrass decline).

Abbreviations used in the text

Chl a –chlorophyll *a* concentration [μg g^{-1}]

Pheo – pheophytin concentration [μg g^{-1}]

CPE – chloroplastic pigment equivalent [μg g^{-1}]

Chl a/CPE – chlorophyll a percentage in the total pigments [%]

Chl a/POC – ratio of chlorophyll a in POC [%]

POC – particulate organic carbon [%]

TN – total nitrogen [%]

δ^{13}C – carbon isotope composition [‰]

δ^{15}N – nitrogen isotope composition [‰]

C_{stock} – organic carbon amount in the sediment, [g m^{-2}]

C_{accu} – organic carbon accumulation rate, [g m^{-2} y^{-1}]

2.4.2. Benthic food web structure

The dataset consisted of data on relative FA composition and SI composition in three main groups of samples: potential food sources (11 sources), meiofauna (2 copepod species), macrofauna (22 species) (Table 1).

Macrofauna species have been assigned to feeding groups (defined as groups of species that share similar feeding functional attributes) based on published literature. Four feeding groups have been distinguished (based on the references mentioned between brackets for each species):

1. suspension feeders (s feeders) – feed on organic matter particles suspended in water
   - *Mytilus edulis* (Gogina and Zettler 2010), *Mya arenaria* (Gogina and Zettler 2010); *Amphibalanus improvisus* (Hayward and Ryland 1995);

2. suspension/detritus feeders (s/d feeders) – facultatively feed on organic matter particles suspended in water or deposited on the sea-bottom - *Cerastoderma glaucum* (Gogina et al. 2016), *Macoma balthica* (Gogina and Zettler 2010);

3. grazers/herbivores (grazers)– feed on many possible sources but mainly on plant originated material – *Bathyporeia pilosa* (Nicolaisen and Kanneworff 1969) (Gogina and Zettler 2010), *Gammarus* spp. (Kotta et al. 2006), *Hydrobia* spp. (Gogina and Zettler 2010), *Idotea* spp. (Kotta et al. 2006), *Jaera* spp. (Gogina and Zettler 2010), *Pygospio elegans*, *Radix peregra, Sphaeroma hookei Theodoxus fluviatilis* (Nielsen 1995);

4. omnivores (omnivores) – with diet based on both plants and animal material - *Cyathura carinata* (Hart and Fuller 1987), *Hediste diversicolor* (Nielsen 1995)*, Marenzellaria* spp. (Zaiko, 2015), *Nerophis ophidion* (Rutkowski, 1982), *Palaemon* spp. (Grabowski 2006), *Planaria torva* (Reynoldson and Sefton, 1976), *Pomatoschistus* spp., *Syngnathus typhle* (Rutkowski 1982).

Fatty acids and stable isotopes composition

To explore the patterns of similarity in FA composition among the sources and consumers and between the two habitats (vegetated vs. unvegetated), Bray-Curtis similarities were calculated for log(x+1) transformed data of relative total FA concentrations. The patterns of FA composition in samples were illustrated with the PCO (Principal Component Analysis, unconstrained ordinations) plot based on single samples and centroids for the sources and consumers groups. Spearman's rank correlation vectors of FA contributions with two canonical axes were overlaid on the PCO. PERMANOVA tests were used to test the differences in a relative FA composition among groups of samples. When significant differences were detected, pairwise tests were applied. One-way tests were performed to test for differences among sources (in groups defined in Table 1). Two-way tests to identify contrasts between the consumers groups and between the two habitats (with fixed factor habitat (H) and consumer group (CG)) were performed for the meiofauna and macrofauna consumers samples. The SIMPER procedure was applied to identify FA that were responsible for differences between groups of samples defined by the consumer group (meiofauna, macrofauna feeding groups) and habitat. The SIMPER procedure is

based on the breakdown of average dissimilarity between groups into separate contributions from each FA. To identify discriminating FA, the average contribution to the overall dissimilarity divided by standard deviation (Diss/st.dev.) and the percentage of this contribution to total dissimilarity (Cont%) were considered.

FA trophic markers (FATM) were identified and assigned to particular food sources (bacteria, diatoms, flagellates, vascular plants, detritus, terrestrial vegetation) based on a published literature (Table 2). One-way PERMANOVA test on Euclidean distances was used (untransformed data) to compare the relative contribution of selected FATM in the FA profile of different sources and consumers (belonging to different feeding groups). Post-hoc pairwise test were performed to investigate statistical differences between specific pairs of sources/ consumers.

Table 2 Fatty acids trophic markers (FATM) used as a tracers of particular food sources within this study; FATM defined based on the published literature

food source	FATM	references
bacteria	14:0	Jaschinski et al. 2008
	18:1ω7	Jaschinski et al. 2008
diatoms	16:0	Dalsgaard et al. 2003, Kelly and Scheibling 2012
	16:1ω7	
	20:5ω3	
flagellates	22:6ω3	Nelson et al. 2002
detritus	18:0	Søreide et al. 2008
	18:1ω9	
vascular plants	18:2ω6	Richoux and Froneman 2008, Kelly and Scheibling 2012
	18:3ω3	
terrestrial vegetation	22:0	Budge and Parrish 1998
	24:0	

The variability in raw δ^{13}C and δ^{15}N values of sources and all consumers was illustrated in the isotopic C/N bi-plot. To test for differences in δ^{13}C and δ^{15}N among the sources and the consumers from two habitats, univariate PERMANOVA tests based on Euclidean distances (non-transformed data) of δ^{13}C and δ^{15}N values in samples were applied (designed in the same way as for FA composition described above).

Mixing models application

The Bayesian mixing models were applied to calculate the relative contribution of potential food sources to the diets of meio- and macrofauna consumers from the two habitats (vegetated and unvegetated) based on SI and FA data. MixSIAR is a general framework that can create Bayesian mixing models to analyze biotracers data (i.e. stable isotopes, fatty acids, most commonly used for diet analysis), taking into account uncertainty in source values, prior information and allowing to apply a model consisting of random and/or fixed factors (Stock and Semmens 2013).

The best performance of mixing models requires that the number of considered sources is higher than the number of tracers (i.e. SI and/or FA), the points representing SI values of consumers fit within the polygon representing source data and the discrimination factors (trophic enrichment factors) are added to the source data (Parnell et al. 2010, Parnell et a. 2013). Moreover, the model will not differentiate the sources contributions to the consumers diet in a case the tracer values for sources overlap (Stock and Semmens 2013). To meet all these methodological requirements, the potential food sources were grouped for the purposes of these analyses. The grouping was made based on similarity of FA composition and SI values of the sources (based on the FA composition as indicated on ordination plot PCO and isotopic bi-plot for SI as well as PERMANOVA tests presented in subchapter 3.2.). The final set of sources used as input for the mixing models included: plants (all macrophytes and *Zostera* tissues), epiphytes (filamentous algae and epiphytes), POM, SSOM, microphytobenthos and bacteria (micr). Two additional sources have been included in omnivores diet modelling: meiofauna prey (mean values of traces of all meiofauna individuals) and macrofauna prey (mean values of tracers of all macrofauna individuals, except from omnivores). Both SI and FA data were used as tracers, because combining those biotracers improves the precision in discriminating sources (Stock and Semmens 2014) and helps to fulfil the model assumptions regarding the relative numbers of sources and tracers. FA used in the models were selected based on assignment of certain FA to particular food sources (FATMs as defined in subchapter 2.4.2., Table 2) and their contributions in sources and consumers documented in the present study (mean value higher than 10%). Moreover, only FATMs belonging to different biosynthetic pathways of animals (so one of them cannot be a product of a transformation of another one), and

preferably representing basic dietary FA sources were applied in models (Kelly and Scheibling 2012).

Due to lack of δ^{15}N values for most of the meiofauna samples, three traces were applied for meiofauna diet modelling: δ^{13}C, bacteria FATMs (summed contributions of 14:0 and 18:1ω7) and detritus FATMs (18:0 and 18:1ω9) (Table 2). Regarding the selection of sources in the model, plants were not included because meiofauna is unlikely to graze directly on a living plant material (Vafeiadou et al. 2014). Microphytobenthos, detritus and epiphytes have been regarded as the main food sources for copepods in the previous studies (De Troch et al. 2008, Lebreton et al. 2012, Vafeiadou et al. 2014, Mascart et al. 2013). Therefore, the final model for meiofauna included: microphytobenthos and bacteria (micr), epiphytes and SSOM (surface sediment organic matter) as sources.

δ^{13}C and δ^{15}N values were available for all macrofaunal consumers and were used as tracers in all macrofauna models. Additionally, FATMs of food sources that are known to be potentially important for a given consumer group were used as tracers in models as described below.

Suspension and suspension/detritus feeders consume particulate organic matter suspended in the water, particles of primary producers and components of the sediment (Baeta et al. 2009). Therefore POM, epiphytes and microphytobenthos and bacteria (micr) have been used in modelling their diet. Only δ^{13}C and δ^{15}N values were used as tracers, because number of used food sources in this model did not exceed 3. As SSOM and POM reflected very similar isotopic composition, those two sources could not be included together in the model as their values overlap and thus make it impossible to differentiate their contribution from each other. Therefore, the mean of POM and SSOM has been included in the model, and the results were interpreted with regard to the fact that POM strongly originated from the sediment organic matter (as indicated by the fatty acids results, see discussion in subchapter 4.2.).

Grazers can feed on the vast number of sources, including detritus, seagrass tissue, microalgae, epiphytes and microphytobenthos (Jaschinski et al. 2008, Lebreton et al. 2011, Ouisse et al. 2012, Vafeiadou et al. 2013, Michel et al. 2014). Therefore four sources - SSOM, microphytobenthos and bacteria (micr), epiphytes and plants were considered in the

model. An additional tracers, detritus FATMs (18:0 and 18:1ω9) and diatoms FATMs (16:1ω6 and 20:5ω3) were included.

Omnivores diet consists of other invertebrates but also primary producers and detritus (Mittermayr et al. 2014), so the model of omnivores included SSOM, plants, meiofauna prey and macrofauna prey as sources, while detritus FATMs (18:0 and 18:1ω9, 18:1ω9 also regarded in some studies as carnivory marker, Kelly and Scheibling, 2012) as an additional tracers.

The design of mixing models

Models with two factors (fixed factor habitat (H) and random factor species (Sp)) were run for meiofauna and four macrofaunal consumer groups taxa (suspension and suspension/detritus feeders, grazers, omnivores) and included only species that were represented by at least two replicate samples in the collected material. The model solutions (95% Bayesian credibility intervals, modes solutions [%]) were presented and probability test were applied on the same manner (Pr) as described in subchapter 2.4.1. Bayesian models for SI data are commonly based on the assumption that SI ratios are normally distributed. For FA, the concentration of individual FAs is standardized to the total FA content of the sample (Neubauer and Jensen 2014) and so the data are expressed as proportions. Therefore, relative FA data were logit transformed following recommendations by Budge et al. (2006). Applied fractionation factors for SI were based on previous studies - carbon isotope 0.8 ± 0.2, nitrogen isotope 3.4 ± 0.4 (Ouisse et al. 2011). For FAs 0 value was used as a fractionation factor, as the FAs used in the models were basic dietary FA sources that were abundant both in sources' and consumers' tissue, and it was assumed that they were not bioconverted by the consumers.

All models were run on 100 000 interactions, with no resource contribution data defined a priori (uninformative prior). Several diagnostics were used to define whether the model was run correctly: Gelman-Rubin Diagnostics smaller than 1.05, Geweke diagnostics similar among 3 chains. The models were run using MixSIAR (R package, Stock and Semmens 2013).

3. Results

3.1. Seagrass vegetation and sediment characteristics

Seagrass meadows vegetation biometrics

Eight macrophytes taxa were identified in the collected material. They represented Ectocarpales (*Pylaiella littoralis*), Ceramiales (*Ceramium* spp., *Polysiphonia* spp.*),* and Angiospermae *(Z. marina, Ruppia maritima, Zanichellia palustris, Chara baltica, Potamogeton perfoliatus, Myriophyllum* spp.). 7 taxa were present at Inner and Outer, while only *Z. marina, P. littoralis* and *Ceramium* spp. were collected at GS. *Z. marina* was dominant in terms of biomass at all three study sites, comprising 99.5 % of the total biomass at GS, 74.9 % at Outer and 72.7 % at Inner. Seagrass shoot density, the total seagrass biomass and total macrophytes biomass were significantly higher at GS than at Inner and Outer locations (p < 0.01, Table 3).

Table 3 Seagrass density [shoot m^{-2}], above ground and below ground biomass, the total macrophytes biomass [g dwt m^{-2}] and total number of macrophyte species at three study locations

seagrass meadows characteristics	**GS**	**Outer**	**Inner**
	mean ± st.dev.	mean ± st.dev.	mean ± st.dev.
shoot density	84.93 ± 29.96	46.87 ± 18.30	53.16 ± 23.95
seagrass above ground biomass	12.75 ± 8.89	8.70 ± 4.83	7.36 ± 4.69
seagrass below ground biomass	11.26 ± 6.78	6.55 ± 4.52	6.04 ± 4.12
total macrophytes biomass	24.01 ± 12.70	18.55 ± 7.41	19.29 ± 11.87
total no of macrophytes species	3	7	7

Seagrass shoot density ranged from the lowest of Outer to the highest of GS locations. The lowest total seagrass biomass was noted for Inner, whereas the highest at GS. The same trend was observed for the total macrophytes biomass – the lowest values were found at Inner and the highest at GS (Table 3).

Organic matter content in the sediments

The sediments in the study area consisted of either medium or fine sand (according to the Fork and Word classification). There was no significant difference in the mean grain size or fine sand % between the two bottom types (pattern consistent across the three studied sites, Table 5).

Significant differences between habitats in POC, δ^{15}N, Chl a, Pheo, Chl a/CPE ($p < 0.05$) and CPE were noted ($p < 0.001$, Table 5). Higher values of POC, δ^{15}N, Chl a, Pheo and CPE were documented in the vegetated sediments compared to the bare sands (Fig. 5, Table 4). Only Chl a/CPE was significantly higher in the unvegetated bottom (Fig. 8, Table 4). The POC content in the sediments varied from 0.03% (average for vegetated stations at Outer) to 0.1% (vegetated GS), while the δ^{13}C varied from -20.1‰ (of the vegetated Inner) to -18.0‰ (of the unvegetated GS) (Table. 4). The Chl a content in the sediments ranged from 4.0 μg g^{-1} (of the unvegetated Outer) to 10.0 µg g^{-1} (the vegetated GS), and the CPE varied from 4.8 μg g^{-1} (unvegetated Outer) to 15.3 μg g^{-1} (vegetated GS). For seven parameters (POC, Chl a, Pheo, CPE, mean grain size, fine sand %), differences among the locations were also identified ($p < 0.001$, Table 5). In most cases, the highest values were observed at GS and the lowest at Outer. The largest differences between the mean values recorded at the two bottom types were found at GS. For example, the difference in the respective mean values for Pheo was 3.8 μg g^{-1} at GS, 2.9 μg g^{-1} at Outer and 2.0 μg g^{-1} at Inner ($p < 0.001$). In the vegetated areas, no significant correlation was detected between the macrophyte vegetation and sediment characteristics (Spearman rank correlation, $p > 0.05$).
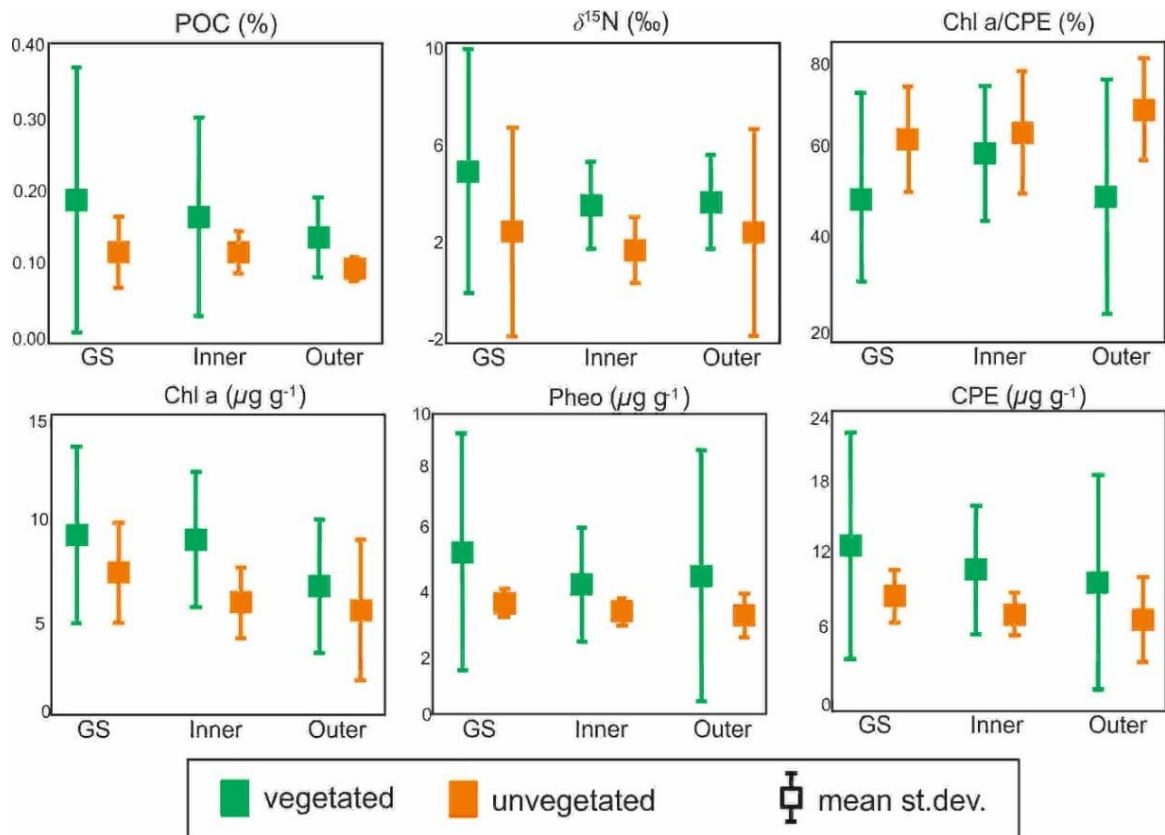
Fig. 8 **S**ediment organic matter characteristics at three locations in the two habitats (presented as mean ± st.dev. of 36 replicates at the Inner and Outer, 24 replicates at GS)

Table 4 Sediment characteristics in the upper 2 cm sediment layer at two bottom types (vegetated - veg, unvegetated - unveg) and three locations

sediment properties	habitat	GS	Outer	Inner
		mean ± st.dev.	mean ± st.dev.	mean ± st.dev.
POC	veg	0.14 ± 0.11	0.08 ± 0.03	0.11 ± 0.08
	unveg	0.06 ± 0.03	0.02 ± 0.01	0.05± 0.02
δ^{13} C	veg	-19.29 ± -8.87	-19.12 ± -1.07	-20.14 ± -1.44
	unveg	-18.05 ± -1.70	-18.21 ± -4.61	-18.27 ± -1.83
δ^{15} N	veg	4.88 ± 2.35	3.69 ± 0.90	3.56 ± 0.84
	unveg	2.55 ± 2.01	2.51 ± 2.00	1.85 ± 0.63
POC/TN	veg	6.78 ± 4.54	3.19 ± 0.71	6.43 ± 1.40
	unveg	4.99 ± 1.65	4.03 ± 2.34	4.38 ± 1.96
Chl a	veg	9.79 ± 3.41	5.85 ± 2.57	9,45 ± 2.61
	unveg	6.88 ± 1.94	4.01 ± 2.72	4.54 ± 1.36
Pheo	veg	5.54 ± 4.39	3.77 ± 4.67	3.14 ± 2.11
	unveg	1.76 ± 0.52	0.82 ± 0 80	1.12 ± 0.52
Chl a/CPE	veg	53.48 ± 12.22	54.10 ± 13.41	64. 08 ± 7.74
	unveg	67.30 ± 5.99	74.07 ± 5.73	68.89 ± 7.04
Chl a/POC	veg	69.76 ± 31.10	74.73 ± 77.78	83.94 ± 31.80
	unveg	110.28 ± 71.87	149. 88 ± 351.15	84.66± 77.86
CPE	veg	15.33 ± 7.80	9.61 ± 7.24	12.59 ± 4.72
	unveg	8.64 ± 2.45	4.82 ± 3.52	5.66 ± 1.87
mean grain size	veg	2.39 ± 0.48	1.68 ± 0.17	2.01 ± 0.42
	unveg	1.88 ± 0.56	1.52 ± 0.10	2.02 ± 0.37
fine sand %	veg	0.29 ± 0.18	0.32 ± 0.11	0.26 ± 0.11
	unveg	0.44 ± 0.30	0.12 ± 0.10	0.57 ± 0.34

Table 5 Results of two way PERMANOVA tests for differences in the sediment characteristics between two habitats (H) and among three locations (L). Main tests (Ps-F) and post hoc tests (only significant effects of pairwise comparisons, p<0.05) are presented. Significant effects are listed (***p < 0.001; ** p <0.01; * p <0.05)

sediments		POC	$\delta^{13}C$	$\delta^{15}N$	POC/TN	Chl a	Pheo	Chl a/ CPE	Chl a/ POC	CPE	mean grain size	fine sand %
factors	df	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F
H	1	33.2***	1.4	23.8***	0.6	42.6***	69.9***	35.7***	0.4	58.5***	3.4	0.6
L	2	6.7***	0.5	0.2	1.2	19.5***	10.6***	2.8	0.8	14.1***	6.7**	3.5*
H x L	2	0.3	0.4	0.1	0.6	2.3	1	5.3**	2.1	0.5	1.4	6.0**
Res	90											
pairwise tests for L		GS> Inner> Outer	-	-	-	GS> Inner> Outer	GS> Inner, Outer	-	-	GS> Inner> Outer	Inner> Outer> GS	Inner> Outer, GS

Significant differences between the layers in 10 cm cores were only noted for sediment characteristics related to photosynthetic pigments – Chl a (p < 0.001, Table 6), Pheo, Chl a/CPE (p < 0.05), Chl a/POC and CPE (p < 0.001). In the first (0-2 cm) or second (2-4 cm) upper layers of the cores, the values of these characteristics were much higher than those in the deeper layers (4-10 cm) (Fig. 9, Table 6, AI). The difference between the upper and lower layers was observed in both habitats; however, the magnitude of these differences was larger in the vegetated habitat. The significant differences in sediment characteristics between the habitats were detected for POC (p < 0.01), $\delta^{15}N$ (p < 0.05), Pheo, Chl a/CPE (p < 0.001), Chl a/POC and CPE (p < 0.01, Table 6, AI). Some differences in the organic matter descriptors in the vegetated sediments among localities were also documented by post-hoc tests e.g. the POC, Chl a/CPE and $\delta^{13}C$ differed among all localities, whereas POC/TN of GS was different than Inner and Outer (p < 0.001, Table 6).

Table 6 Results of three way PERMANOVA tests for differences in the sediment characteristics between two habitats (H), among three locations (L) and five layers (La) for samples collected with use of 10 cm cores. Main tests (Ps-F) are presented. Significant effects are listed (***p < 0.001; ** p <0.01; * p <0.05)

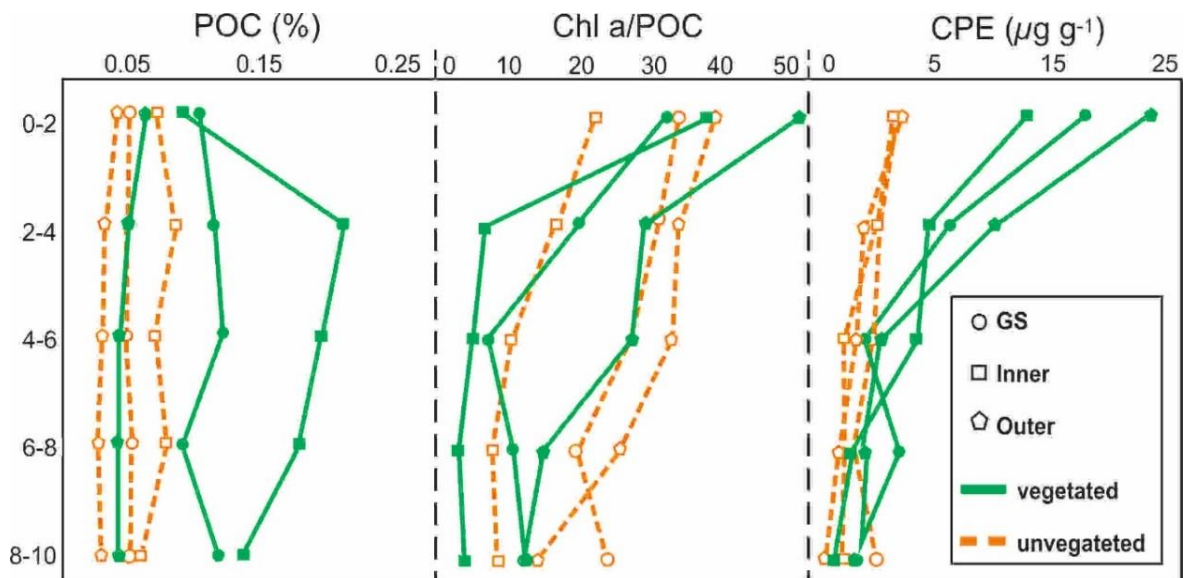| sediments		POC	$\delta^{13}C$	$\delta^{15}N$	POC/ TN	Chl a	Pheo	Chl a /CPE	Chl a /POC	CPE
factors	df	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F
H	1	9.2**	3.5	7.4*	0.0	0.0	19.8***	23.0***	8.5**	8.1**
L	2	4.5*	5.4**	2.7	4.8*	4.8*	0.4	4.6*	9.0***	1.4
La	4	0.1	0.0	1.7	1.0	12.1***	3.3*	2.9*	5.7***	7.1***
H x L	2	1.5	4.2*	0.5	1.8	1.2	1.2	0.4	1.5	1.1
H x La	4	0.1	0.0	1.7	1.0	2.0	1.3	0.5	1.2	1.5
L x La	8	0.1	0.0	0.5	0.7	0.5	0.1	0.7	0.5	0.1
H x L x La	8	0.1	0.0	1.0	0.4	0.4	0.4	0.3	0.3	0.3
Res	30									

Fig. 9 Vertical profiles of sediment organic matter characteristics in the samples collected with a use of 10 cm sediment cores at three locations and two bottom types

Isotopic characteristics of sedimentary organic matter and its potential sources

Mean δ^{13}C values in potential sources ranged from -25.2‰ (*Polyspihonia* spp.), to -9.5‰ (*P. pectinatus*, Fig. 10, Table AII). Carbon and nitrogen isotopic ratios of *Z. marina* leaves, roots and *R. maritima* were similar (named 'plants') with mean values of -10.3‰ and 7.5‰, respectively. The other potential organic matter sources had much lower carbon isotope ratios. Epiphytes, *Cladophora* spp. and filamentous algae had very similar carbon and nitrogen isotopic composition (δ^{13}C from -25.2‰ to -21.8‰ and δ^{15}N from 7.5‰ to 8.3‰). POM had the lowest δ^{15}N values among all sources (6.2 ‰ Fig. 10, Table AII).

Considering the sediment samples from three localities, carbon isotope ratios were lower in the vegetated comparing to the unvegetated bottom, except Outer location. Opposite trend was noted for nitrogen isotope ratios that in three study locations were higher within seagrass meadows. The δ^{13}C values for samples from the vegetated bottom ranged from -19.1‰ to 20.1‰, the δ^{15}N values ranged from 3.6‰ to 5.9‰. Whereas the δ^{13}C values for samples from the unvegetated bottom ranged from -18.1‰ to -19.3‰ and the δ^{15}N values ranged from 1.9‰ to 3.4‰ (Fig. 10, Table AII).
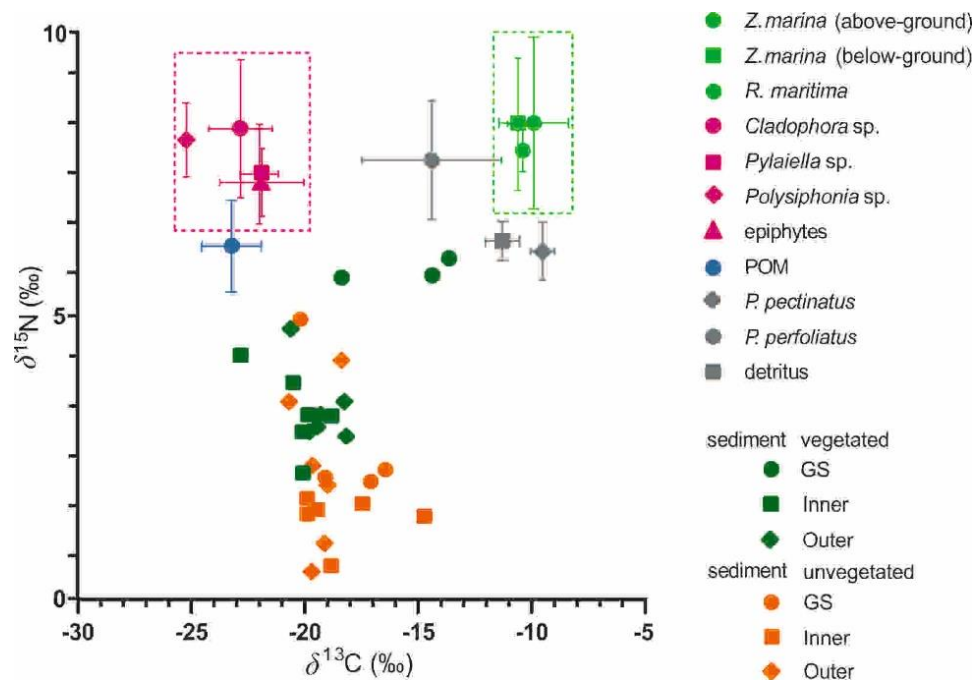

Fig. 10   Bi-plot of carbon and nitrogen isotope composition in the sediments collected at three locations and two habitats together with the potential organic matter sources (mean ± st.dev.). Dashed rectangles indicate a grouped sources (pink – epiphytes, green –plants)

Sources contribution to the sediment organic matter pool (mixing models)

The SIAR mixing model results indicated that the proportions of the three potential organic matter sources to sediment organic matter pool were not consistent between the vegetated and unvegetated bottom with similar patterns of difference in all studied localities (Fig. 11, Table 7).

The strongest contrasts among two habitats was observed in contributions of plants as a potential organic matter source. The contribution of plants in the bulk sediment organic matter pool was much higher in the vegetated bottom (average, i.e. 'mode of solutions', from 39% to 41% depending on the location (95% credibility intervals presented in Table 7)) compared to the bare sands (mode from 9% to 17%) at all studied locations (Fig. 11, Table 7). In addition, contribution of plants material to sediments was higher in sediments from the vegetated bottoms in 90% of performed model runs (probability that contribution of plants is higher in vegetated bottom Pr = 0.9 for all locations). On the other hand, epiphytes contributed much less to the bulk organic matter pool in the vegetated sediments, with modes from 8% to 21% at three locations compared to the unvegetated bottom, where the contribution was much higher (modes from 32% to 39%). Epiphytes contribution to sediment organic matter was actually higher for the unvegetated bottoms in 50 to 90 of model runs, depending on the location (Pr equal -0.5 for Inner, -0.7 for GS and -0.9 for Outer). Additionally, the model showed that POM was an important source of organic matter in the studied area, with little difference between the two bottom types (modes from 38% to 41% for vegetated and from 44% to 50% for unvegetated bottoms at three locations). The proportion of model runs where POM contributed more to sediment organic matter in the vegetated bottoms varied slightly according to the site, with Pr ranging from -0.1 to -0.4.
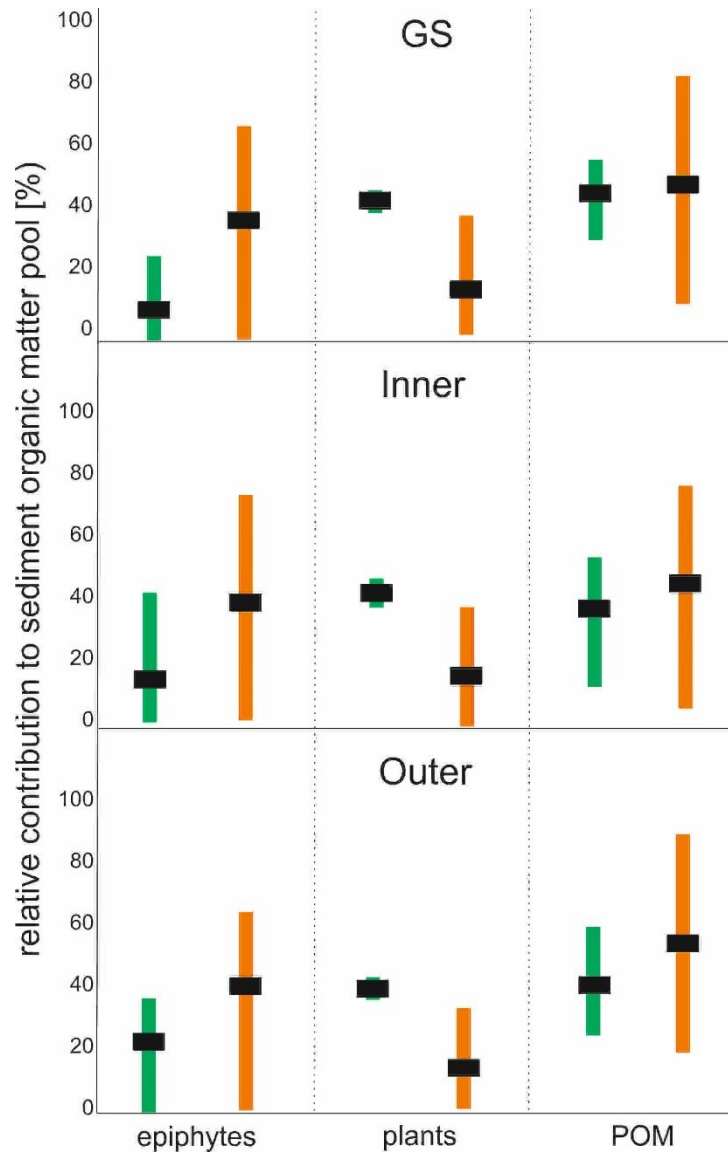
Fig. 11   Relative contributions of sources (epiphytes, plants, POM) to the sediment organic matter pool in the vegetated (green lines) and unvegetated (orange lines) habitats at three locations. The lines indicate 95% Bayesian credibility intervals, points indicate modes

Table 7 Relative contributions of sources (epiphytes, plants, POM) to the sediment organic matter pool in two habitats and three locations based on results obtained from the SIAR mixing models. Mode, Bayesian credibility intervals – BCI 95% and probability test that a contribution of a given source is higher in the vegetated habitat (Pr) are presented

	GS				
sources	**vegetated**		**unvegetated**		**Pr**
	mode	BCI 95%	mode	BCI 95%	
epiphytes	8	0-21	38	0-63	-0.7
plants	41	38-43	17	0-39	0.9
POM	41	24-58	45	9-81	-0.4
	Outer				
epiphytes	21	0-37	32	0-61	-0.9
plants	39	37-41	9	1-32	0.9
POM	40	21-60	50	19-89	-0.1
	Inner				
epiphytes	12	1-40	39	2-73	-0.5
plants	40	38-44	17	0-38	0.9
POM	38	10-52	44	2-78	-0.1

Sediment accumulation rate

The water content in all the sediment samples from the 60 cm-long cores was very low (ranging from 10 % to 19 %) due to the high sand fraction content in the sediments. The pelite sediment fraction (< 0.063 mm) constituted approximately 0.1% of the sediment in these samples. The upper 40 cm of the core contained much more sand than the lower part of the core, probably due to constant re-suspension in the upper sediment layers.

The total ^{210}Pb activity concentrations decreased from 262.6 ± 9.1 Bq kg^{-1} to 33.1 ± 1.0 Bq kg^{-1} in the lower part of the core (Fig. 12). The ^{210}Pb supported activity was estimated to be 39.0 ± 2.8 Bq kg^{-1}. The top 10cm of the core showed similar ^{210}Pb, indicating sediment mixing of the surface sediment layers. Below 10 cm, the ^{210}Pb excess activities exhibited an exponential decrease until 22-24 cm. The best-fit equation determination coefficient is satisfactory (r^2=0.93). The LAR was estimated to be 0.13 ± 0.02 cm y^{-1}, while the MAR was estimated to be 0.24 ± 0.01 g cm^{-2} y^{-1}.
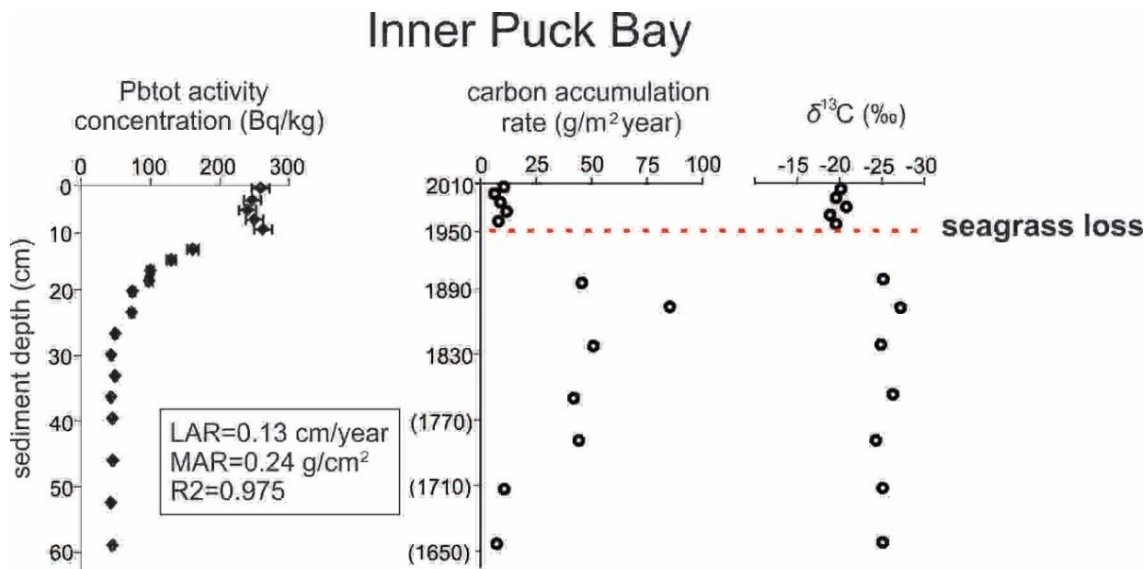
Fig. 12   [210]Pb activity concentration (Bq/kg) and water content versus porosity corrected sediment depth (cm) (left) plus carbon accumulation rate and δ^{13}C (right) in the sediment cores collected at the Inner location. The red dotted line on the right plot indicate the 10 cm depth representing mid XXth century – the starting time of the seagrass decline in the Gulf of Gdańsk

Carbon stock and accumulation in the vegetated sediments

Carbon stock (C_{stock}, g m^{-2}) and carbon accumulation (C_{accu}, g m^{-2} y^{-1}) based on POC concentration in the upper 10 cm varied among three locations – the highest values were documented in Inner location (228.0 g m^{-2}, 3.85 g m^{-2} y^{-1} accordingly), lower in GS (116.5 g m^{-2}, 2.78 g m^{-2} y^{-1}) and the lowest in Outer (50.2 g m^{-2}, 0.8 g m^{-2} y^{-1}) (Table 8).

The total carbon stock and total carbon accumulation for the Inner Puck Bay calculated for the upper 10 cm sediment was 0.10 Mt and 0.02 Mt y^{-1} respectively. Regarding total carbon stock and total carbon accumulation for the lower part of sediment profile (from 10 to 60 cm) the values were 7.46 Mt and 0.28 Mt y^{-1} (calculated for the most recent estimation of the eelgrass area in the Inner Puck Bay, i.e. 48 km^2, Table 8).

Table 8 POC [%], C_{stock} [g m^{-2}], C_{accu} [g m^{-2} y^{-1}] calculated for the upper 10 cm in the vegetated habitat at three studied locations and for 10-60 cm layer based on cores collected at station at Inner location. Ratio of differences for POC concentration between the vegetated and unvegetated sediments is presented. Accumulation rate measured only for the Inner location has been used for carbon accumulation calculations at three locations

location (number of replicate cores)	environmental settings	sediment depth layer [cm]	POC [%]	ratio of differences in POC between veg/unveg	Cstock [g m^{-2}]	Caccu [g m^{-2} y^{-1}]
GS (4)	exposed, high density	0-10	0.11 ± 0.03	3.67 ± 0.00	166.46 ± 4.10	2.78 ± 0.28
Outer (4)	exposed, low density	0-10	0.03 ± 0.02	4.8 ± 0.00	50.17 ± 2.20	0.84 ± 0.16
Inner (4)	sheltered, low density	0-10	0.24 ± 0.10	1.50 ± 0.00	228.00 ± 11.57	3.85 ± 1.15
Inner (4)	sheltered, low density	10-60	1.70 ± 1.10	-	3630.17 ± 222.39	41.00 ± 26.00

3.2. Benthic food web structure

Fatty acids and stable isotopes biomarkers in food sources

In total, nineteen FA have been identified and used for the food source composition analysis. The identified FA included seven saturated FA (SAFA), seven monounsaturated FA (MUFA) and five polyunsaturated FA (PUFA). There were significant differences in the relative FA composition (PERMANOVA, Table 9) among potential food sources and several significant post hoc pair-wise contrasts were also identified (Table 9).

Table 9 Results of one-way PERMANOVA tests of FA composition (multivariate tests) and trophic markers (FATM) contribution (univariate tests) in different potential food sources. Main tests (Ps-F) and post hoc tests (only significant effects of pairwise comparisons, p<0.05) are presented. Significant main tests are indicated by ***p < 0.001, **p < 0.01, *p < 0.5

	main test Ps-F	post hoc test's
FA composition	5.3***	p-epi,fila,POM,SSOMv,uv POM-SSOM
FATM		
bacteria	12.37***	p-epi,POM,SSOMv,uv POM-SSOMv,uv
diatoms	3.50*	p-epi,fila
flagellates	8.43***	p-POM POM-SSOMv,uv
detritus	4.90**	p-epi,fila,POM,SSOMv,uv
vascular plants	56.62***	p-epi,fila,POM,SSOMv,uv SSOMv,uv-POM
terrestrial vegetation	1.16	-

abbreviations: (p – plants, fila – filamentous algae, epi – epiphytes,
SSOM v/ uv – SSOM vegetated/ unvegetated

For relative FA composition in sources, the first two axis of PCO explained 54.1% of the total variability, whereas in the PCO based on centroids, explained 69.1% of the total variability. The vectors plotted on the ordination plots indicated the FA that were best correlated to the axis of variability that best discriminated the groups of sources (Fig. 13).
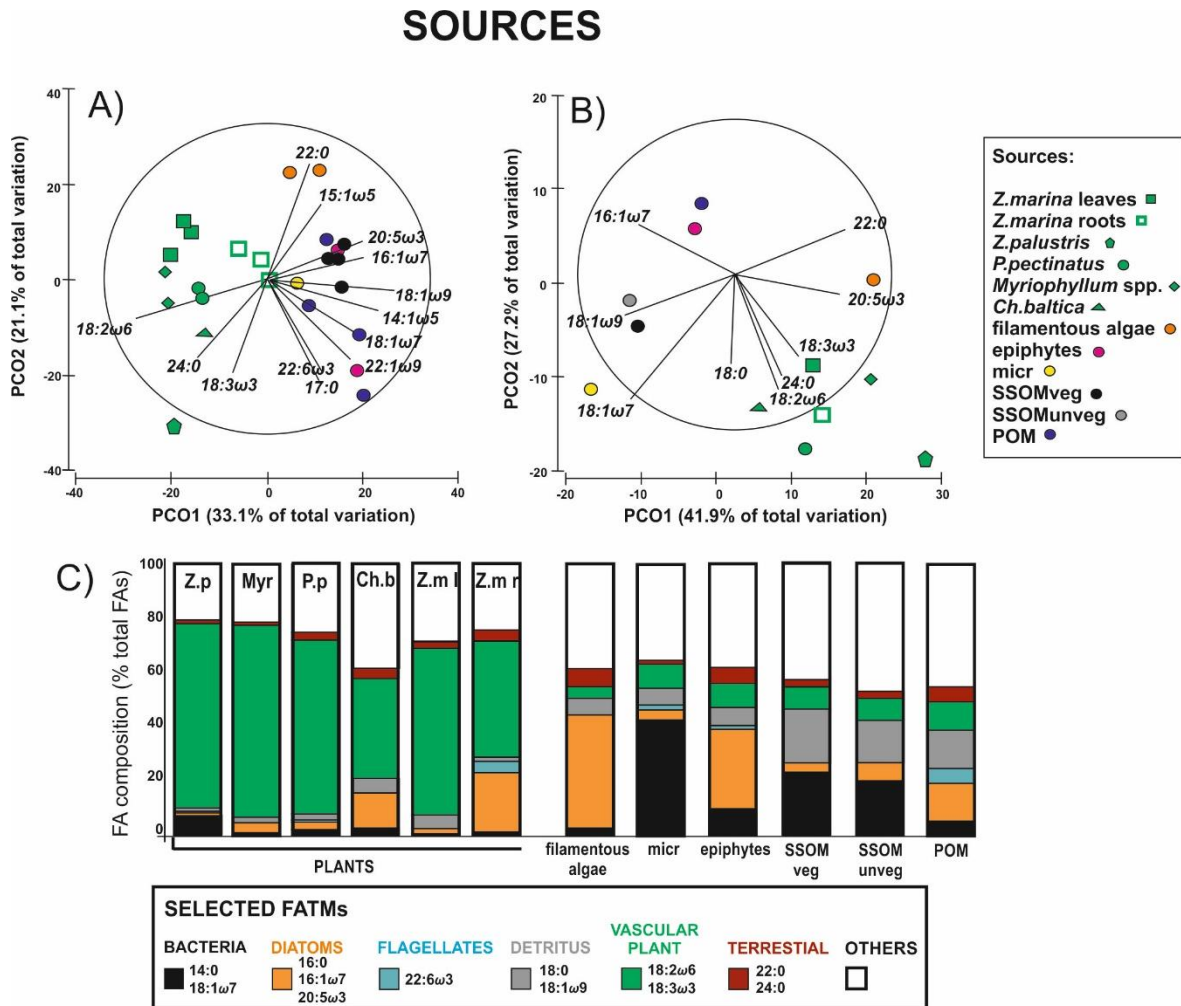
Fig. 13 FA composition of potential food sources: A) PCO ordination of samples, B) PCO ordination of centroids for sources type; vectors indicate FA with Spearman correlation to ordination axis > 0.5; data were log(x+1) transformed, ordination was based on Bray-Curtis similarities; C) relative composition of FATM (see Table 2) in samples of potential food sources

abbreviations: Z.p– *Z. palustris*, Myr– *Myriophyllum* spp., P.p– *P. pectinatus*, Ch.b– *Ch. baltica*, Z.m l– *Z. marina* leaves, Z.m r – *Z. marina* roots, micr – microphytobenthos/ bacteria, SSOMveg/unveg– surface sediment organic matter of the vegetated/ unvegetated bottom

Two PCOs separated vascular plants sources from the other sources (Fig. 13A and B). Samples representing different plant species were grouped on the left side of the PCO (A) and were defined by vector of correlation for 18:2ω6, 18:3ω3 and 24:0, whereas other sources were placed on the right side of the PCO (A). Samples of filamentous algae were grouped on the upper part of the PCO (A) ordination, in the direction defined by vector of

correlation for 22:0 and 20:5ω3 (Fig. 13A, B). Microphytobenthos/bacteria and SSOM (both vegetated and unvegetated) grouped closely on both PCO (A, B) plots. On PCO (A) they were defined by 16:1ω7, 18:1ω9 and 20:5ω3 (Fig. 13A), whereas on PCO (B) based on centroids by 18:1ω7 for microphytobenthos/bacteria and 18:1ω9 for SSOM (both vegetated and unvegetated, Fig. 13B). Epiphytes and POM, were widely dispersed on the right side of the PCO (A) ordination plot (Fig. 13A). However, on the PCO (B) based on centroids, epiphytes and POM were placed close to each other and defined by vector of correlation for 16:1ω7 (Fig. 13B).

There were significant differences in selected FATMs contributions, except for terrestrial plants markers (grouped as indicated in Table 2, PERMANOVA, Table 9) among potential food sources and several significant post hoc pair-wise contrasts were also identified (Table 9).

FA composition of plants species were clearly distinguished from almost all other sources (except of microphytobenthos/bacteria) as indicated by significant results of post hoc pairwise tests (Table 9). Each of the plants species *(Z. marina* leaves and roots, *Z. palustris, P. pectinatus, Myriophyllum spp., Ch. baltica*) contained large amounts of the two vascular plants FA markers (18:2ω6 and 18:3ω3) that represented together 56.3% (on average) of the total FA (Fig. 13C, Table AIII).

Filamentous algae and epiphytes contained the highest proportions of SAFA 16:0 (0.9% and 13.4%, respectively) and PUFA 20:5ω3 (36.2% and 14.5%, respectively) that are both considered as the diatoms markers (Fig. 13C, Table AIII). The FA composition of microphytobenthos/bacteria was dominated by MUFA 18:1ω7 (41.0%) regarded as bacterial marker (Fig. 13C, Table. AIII). Surface sediment organic matter (SSOM) had very similar FA profiles at the two sampling locations (vegetated, unvegetated) and contained high proportions of three MUFA FA (18:1ω7 bacteria marker- 19.1% (vegetated), 16.4% (unvegetated), 18:1ω9 detritus marker- 5.6% (vegetated), 6.8% (unvegetated) and 16:1ω7 diatoms marker – 19.5% (vegetated), 14.8% (unvegetated)) (Fig. 13C, Table 9). POM samples had high proportions of SAFA 18:0 (detritus marker) -10.3% and 16:0 (diatom marker) - 7.6%. In addition, three more PUFA had considerable contributions in POM: 18:2ω6 (vascular plants marker) - 7.3%, 20:5ω3 (diatoms marker) - 5.18% and 22:6ω3 (flagellates marker) - 5.3% (Fig. 13C, Table AIII).

The contributions of all other FAs (14:1ω5, 15:0, 15:1ω5, 17, 17:1ω5, 20:1ω9) ranged from 24.2% in plants to 40.8% in POM (Table AIII).

The composition of both carbon and nitrogen stable isotopes differed significantly among sources (PERMANOVA main tests p < 0.05, Table 10). Post-hoc pairwise comparisons indicated that plants were different from all the other sources in δ^{13}C value, and from microphytobenthos/bacteria, POM, SSOM in δ^{15}N value. Moreover, POM was different from all other sources except for SSOM in both δ^{13}C and δ^{15}N values (Table 10).

Table 10 Results of one way PERMANOVA tests of the differences in stable isotopes among potential food sources (S) and two way PERMANOVA tests of the differences in stable isotopes composition among consumers groups (CG) and between the two habitats (H) (univariate tests for δ^{13}C and δ^{15}N). Main tests (Ps-F) and post hoc tests (only significant effects of pairwise comparisons, p < 0.05) are presented. Significant main tests are indicated by ***p < 0.001, **p < 0.01

	isotopes	**factors**	**main test, Ps-F**	**post hoc test's**
sources	δ^{13}C	S	239.3***	p-micr,epi,fila,POM, SSOMv,unv POM-micr,epi,fila, p
	δ^{15}N	S	13.6***	p-micr,POM,SSOMv,unv POM-micr,epi,fila, p
consumers	δ^{13}C	H	6.7	-
		CG	12.4***	all pairs except for mp-sdf, mt-o, g-sf, g-o
		CGxH	3.5**	none
	δ^{15}N	H	0.0	-
		CG	48.9***	all pairs except for g-sf
		CGxH	0.8	-

sources abbreviations: p– plants, micr – microphytobenthos and bacteria, fila– filamentous algae, epi– epiphytes, SSOMv/unv– SSOM vegetated/ unvegetated; consumers abbreviations: mp- meiofauna *P. spinicauda*, mt-meiofauna *T. discipes,* sf- suspension feeders, sdf– suspension/detritus feeders, g- grazers, o- omnivores

Mean δ^{13}C values of sources ranged from -25.0‰ (POM) to -10.6‰ (plants) (Fig. 14, Table AIV). The second most δ^{13}C-enriched source was microphytobenthos/bacteria (- 5.3‰). Epiphytes and filamentous algae had very similar carbon isotopic composition: -19.3‰ and -18.7‰, respectively. δ^{13}C values of SSOM was comparable at the two habitats, however δ^{15}N was higher for SSOM in the vegetated bottom (by 2,5‰). The mean

δ^{15}N values ranged from 1.0‰ (SSOM unvegetated) to 6.4‰ (filamentous algae) (Fig. 14, Table AIV).
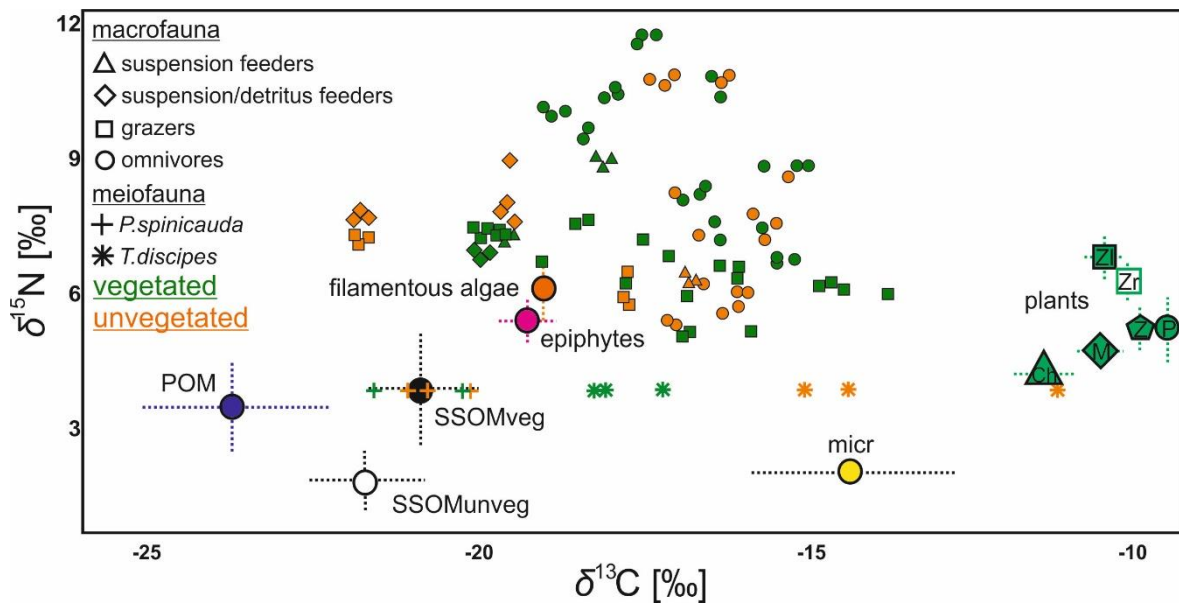

Fig. 14 Bi-plot of carbon and nitrogen isotope composition for two meiofauna species and macrofauna feeding groups from the vegetated and unvegetated habitats with possible food sources presented as mean ± st.dev.

sources abbreviations: micr – microphytobenthos and bacteria, SSOMveg/unveg– SSOM in vegetated and unvegetated habitat

Fatty acids and stable isotopes biomarkers in consumers

The 19 FAs (the same as in sources) have been identified and used for consumers composition analysis. There were significant differences in the relative FA composition among consumers groups but no significant contrasts among habitats was noted ($p < 0.05$, PERMANOVA, Table 11). Additionally, significant differences were noted in interactions between habitats and consumer groups (Table 11). Several significant post-hoc pair-wise contrasts were also identified in relative FA composition (Table 11).

The first two axis of PCO for the relative FA composition in consumers, explained 43.9% of the total variability, whereas the PCO based on centroids for consumers feeding groups accounted for 79.9% of the total variability. The vectors plotted on the ordination plots indicated the FAs that were best correlated to the axis of variability that best discriminated the groups of consumers (Fig. 4A, B).

Table 11 Results of one-way PERMANOVA tests for differences in FA composition (multivariate tests) and trophic markers (FATM) contributions (univariate tests) in consumers (meiofauna, macrofauna CG) from the two habitats (H). Main tests (Ps-F) and post-hoc tests (significant effects of pairwise comparisons, p<0.05) are presented. Significant main tests are indicated by ***p < 0.001, **p < 0.01, *p < 0.5

	main test, Ps-F	post hoc test's
FA composition		
H	0.76	-
CG	8.00***	all except for mp-mt and sf-sdf
H x CG	2.68***	o:veg-unveg
FATM		
bacteria		
H	0.94	-
CG	2.01	-
H x CG	0.32	-
diatoms		
H	0.13	-
CG	7.91***	all except for sf-sdf, sdf-o
H x CG	2.37	-
flagellates		
H	0.49	-
CG	20.09***	all except for sf-sdf
H x CG	2.41	-
detritus		
H	0.26	-
CG	6.81***	all except for sf-sdf, g-o
H x CG	3.57*	g, o:veg-unveg
vascular plants		
H	0.07	-
CG	0.43	-
H x CG	1.92	-
terrestrial vegetation		
H	1.84	-
CG	0.68	-
H x CG	1.41	-

consumers abbreviations: mp-meiofauna P. spinicauda, mt-meiofauna

T. discipes, sf-s feeders, sdf- s/d feeders, g-grazers, o-omnivores

Two PCO separated meiofauna samples (placed on the right side) from macrofauna samples (placed on the left side of the ordination plot, Fig. 4A). Only *T. discipes* meiofauna species of the vegetated bottom was widely dispersed on the ordination. On both PCO plots, meiofauna were defined by vectors of correlation for the FA 18:1ω7. PCO (A) ordination did not clearly separated the feeding groups of macrofauna (Fig. 15A). Whereas on the PCO (B) plot based on centroids, the grazers were placed on the bottom side, in the direction defined by the vector of correlation for 18:3ω3 (Fig. 15B). Omnivores were placed between grazers and suspension feeders and defined by vector of 16:0. Centroids of suspension and suspension/detritus feeders were placed in the most upper side of the plot and those two feeding groups were defined by vector of 16:1ω6 (Fig. 15B).
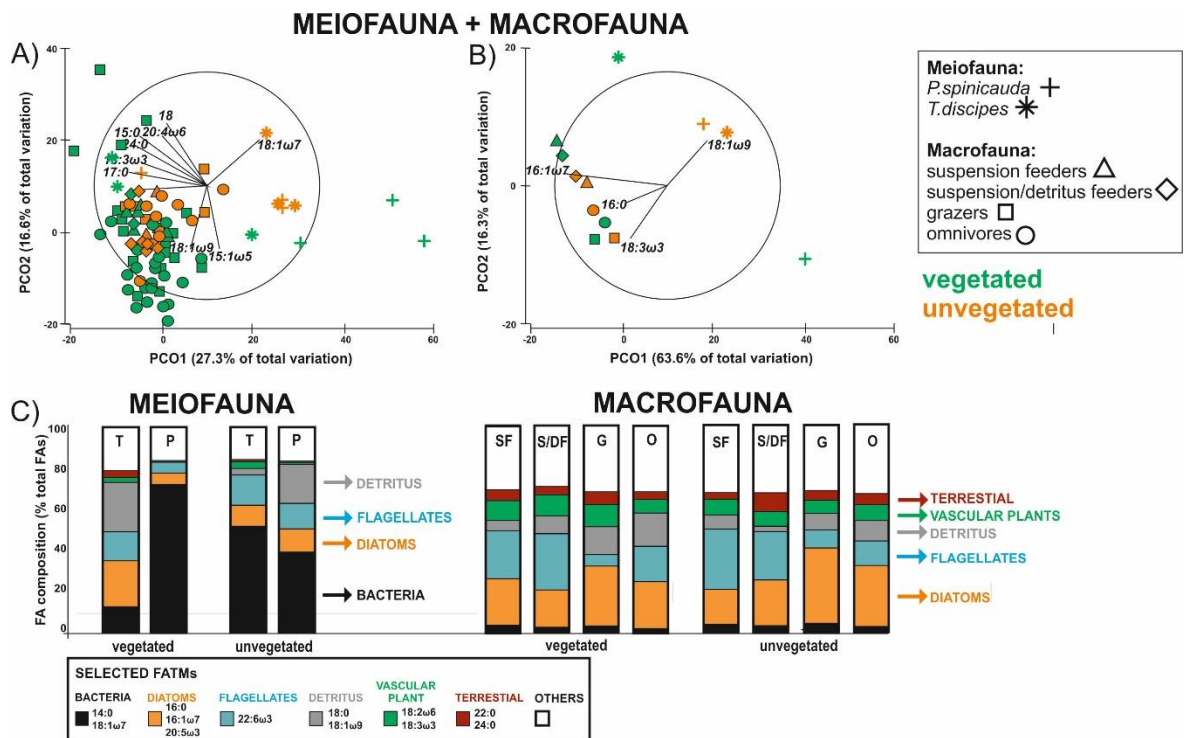
Fig. 15 FA composition of consumers (meiofauna and macrofauna): A) PCO ordination on samples, B) PCO ordination on centroids for species (in meiofauna)/feeding groups (in macrofauna); vectors indicate FA with Spearman correlation to ordination axis > 0.5; data were log(x+1) transformed, ordination made based on Bray-Curtis similarities; C) relative composition of FATM (see Table 2) in samples of consumers

abbreviations: T – *T. discipes*, P – *P. spinicauda*., SF – suspension feeders, SDF –suspension/detritus feeders, G – grazers, O – omnivores

There were significant differences in the four selected FATMs (diatoms, flagellates, detritus, vascular plants) contributions among consumers groups but no significant contrasts among habitats was noted ($p < 0.05$, PERMANOVA, Table 10). Additionally, significant difference in interactions between habitats and the consumer groups was noted for detritus FATMs (Table 10). Several significant post-hoc pair-wise contrasts were also identified (Table 10).

FA composition of two meiofauna species was clearly distinguished from all macrofauna functional groups (Table AV). The meiofauna species, contained large amounts of bacteria marker MUFA 18:1ω7, encompassing on average 70.7% and 37.0% in *P. spinicauda*, 11.3% and 49.6% in *T. discipes* (from the vegetated, unvegetated habitat respectively). Another MUFA 18:1ω9, the marker of detritus, was found in high concentrations in *T. discipes* from seagrass (22.2% on average) and also in *P. spinicauda* from the bare bottom (17.5% on average). Moreover, SAFA 16:0, the marker of diatoms, was quantified in considerable proportions in *T. discipes* at the vegetated habitat (13.2% on average) (Table AV). SIMPER analysis identified 5 FA for *P. spinicauda* and 4 for *T. discipes* with a Cont% ≥7% (Table. 8). For both meiofauna species, SIMPER identified 18:1ω7 and 18:1ω9 as the FA that best discriminate the two habitats; 18:1ω7 occurred with higher contributions in both species from the seagrass beds, whereas 18:1ω9 occurred with higher contributions in species from the bare seabed.

Table 12   SIMPER results for FA contributing most to the dissimilarity between FA profiles of meiofauna species and macrofauna trophic groups from two habitats. Diss/st.dev. – the overall dissimilarity divided by standard deviation, Cont% - the percentage of this contribution to total dissimilarity. Only species of Cont% equal to or higher than 7% are listed

FA	Diss/st.dev.	Cont%	vegetated	unvegetated
	P. spinicauda			
18:1ω9	1.14	12.97	0.43	1.95
18:1ω7	0.81	10.9	4.26	2.84
22:6ω3	1.18	10.07	1.39	2.57
16:0	1.09	8	1.11	1.98
20:4ω6	1.18	7.23	0	0.94
	T. discipes			
18:1ω7	1.61	13.58	1.56	3.91
18:1ω9	1.6	10.13	2.66	1.08
16:1ω7	1.66	8.63	1.68	0.2
15:1ω5	1.39	7.68	1.33	1.73
	suspension feeders			
22:0	1.17	10.35	1.64	1.15
20:4ω6	1.04	9.5	1.75	1.34
18:1ω7	1.56	9.14	0.16	1
	suspension/detritus feeders			
22:0	1.43	10.31	2.03	1.17
16:1ω7	2.33	10.09	1.71	1.16
15:0	1.88	9.61	1.34	0.6
24:0	1.74	9.36	1.12	0.5
18:1ω9	1.12	8.76	1.19	1.91
18:2ω6	1.36	7.35	1.36	1.96
	grazers			
16:0	1.43	9.28	1.61	2.71
18:1ω9	1.12	8.34	2.09	1.23
18:0	1.38	7.8	1.11	1.2
20:4ω6	1.32	7.76	1.01	1.47
22:0	1.29	7.04	1.47	1.34
	omnivores			
20:4ω6	1.38	10.57	0.38	1.38
16:0	1.31	10.55	1.29	1.76
22:0	1.32	7.74	1.26	1.24
16:1ω7	1.18	7.02	1.06	1.11

Suspension and suspension/detritus feeders species, had very similar FA profiles in two habitats (Fig. 15C, 16) with two PUFAs encompassing the highest contribution (20:5ω3, 22:6ω3). The concentrations of diatom marker 20:5ω3 were ranging from 10.9% in suspension/detritus feeders of the vegetated to 15.0% in suspension/detritus feeders of the unvegetated habitat (on average). The concentrations of flagellates marker 22:6ω3 ranged from 22.6% of suspension/detritus feeders in seagrass beds to 29.0% of suspension feeders at bare bottom. Additionally, both suspension and suspension/detritus feeders from the vegetated habitat had twice as high concentration of 22:0 as the representatives of the contrasting habitat (Table AV). SIMPER analysis identified 3 FAs that had Cont% equal or higher than 7% in samples of suspension feeders, whereas 6 for suspension/detritus feeders (Table 12). For suspension feeders, 22:0 and 20:4ω6, were the FA acids that best discriminated the samples from two habitats, with higher contributions in consumers of seagrass beds. Similarly, for suspension/detritus feeders, 22:0 and 16:1ω7 best discriminated the samples from two habitats, and both had higher contributions on the vegetated habitat.
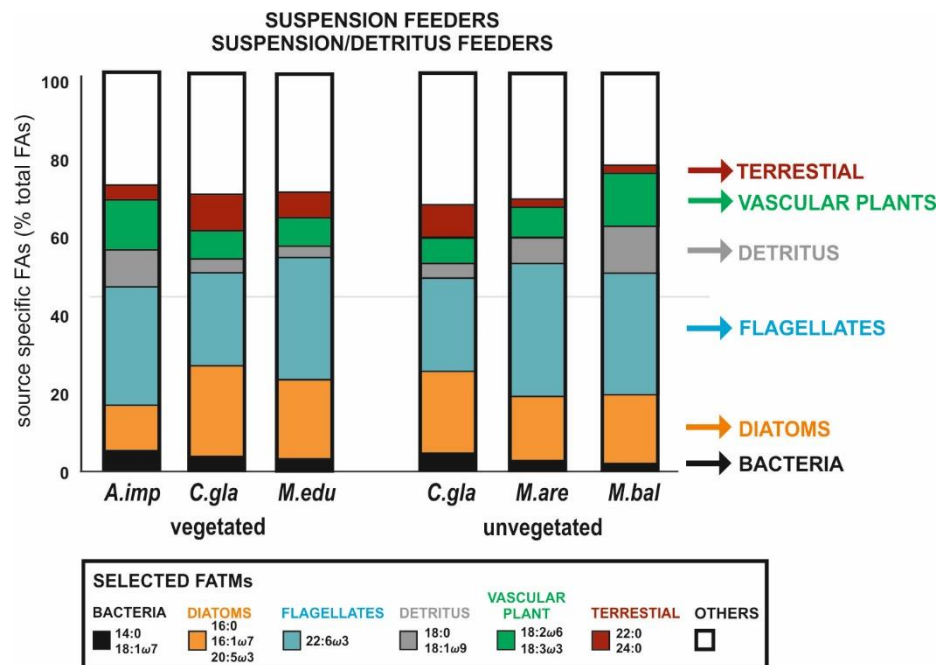
Fig. 16 Relative composition of FATM (see Table 2) in suspension, suspension/detritus feeders species

species abbreviations: *A.imp- A. improvisus, C.gla- C. glaucum, M.edu- M. edulis, M.are- M. arenaria, M.bal- M. balthica*

The FA profiles of grazers were dominated by the diatom marker PUFA 20:5ω3 (on average 19.7% in the vegetated and 15.3% in the unvegetated habitat). The grazers of seagrass meadows had also considerable proportions of MUFA 18:1ω9 (9.0% detritus marker) and two PUFA: 18:2ω6 (8.9% vascular plant marker), 20:5ω3 (19.7% diatom marker). Whereas, the grazers from the unvegetated habitat had considerable contribution of SAFA 16:0 (19.6% diatom marker) and PUFA 22:6ω3 (8.7% flagellates marker, Fig. 15C, Fig. 17, Table AV). SIMPER analysis identified 5 FAs that had Cont% equal or higher than 7% in samples for grazers (Table 12). For grazers, SIMPER identified 16:0 (higher for the unvegetated habitat) and 18:1ω9 (higher for the vegetated habitat) as the FA discriminating best the two habitats.
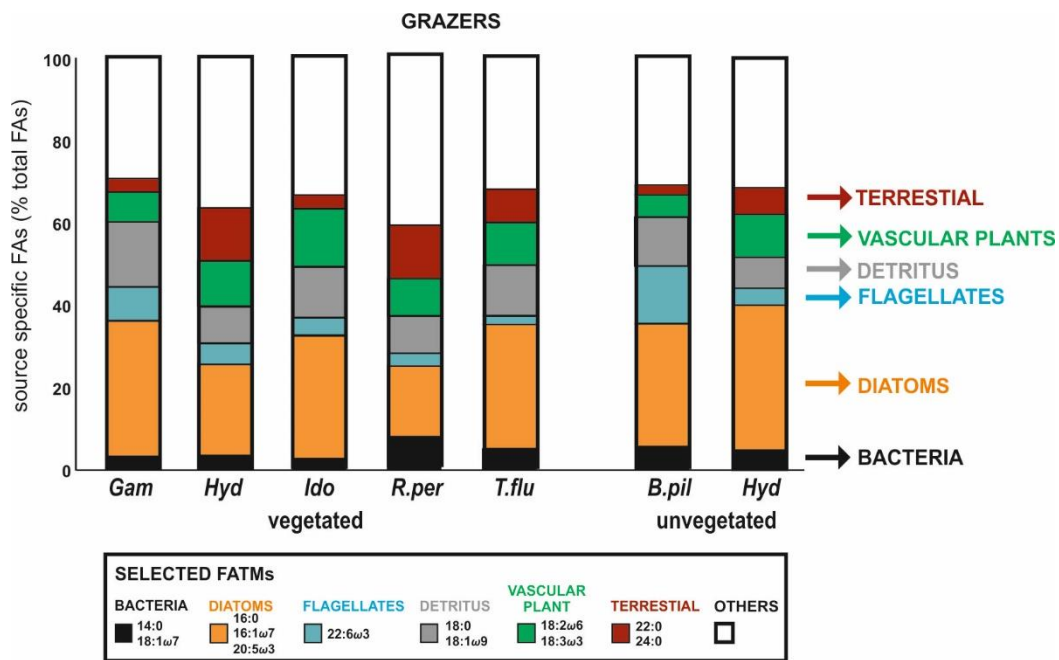
Fig. 17 Relative composition of FATM (see Table 2) in grazer species

species abbreviations: *Gam- Gammarus* spp*., Hyd- Hydrobia* spp*., Ido- Idotea* spp*.,*
R.per- R. peregra, T.flu- T. fluviatilis, B.pil- B. pilosa

Omnivores contained the highest proportion of PUFAs 20:5ω3 (diatom marker, 15.3% in the vegetated and 19.8% in the unvegetated habitat) and the 22:6ω3 (flagellates marker 16.9% in the vegetated and 11.8% in the unvegetated habitat). Omnivores species of seagrass beds had higher contribution of MUFA 18:1ω9 (detritus marker, 14.1%)

compared to species from the bare seabed (Fig. 15C, Fig. 18). Within the vegetated habitat *N. ophidion* and *S. typhe* contained the highest percentage of flagellates marker. Within the unvegetated habitat *Pomatoschistus* spp. had higher percentages of flagellates marker (Fig. 18, Table AV). SIMPER analysis identified 4 FAs that had Cont% equal or higher than 7% in samples of omnivores (Table 12). For omnivores, 20:4ω6 and 16:0 best discriminated the habitats and occurred with higher contributions in samples collected on the unvegetated habitat.

The contribution of other FAs (14:1ω5, 15:0, 15:1ω5, 17:0, 17:1ω5, 20:1ω9) ranged from 15.7% in *P. spinicauda* associated with seagrass meadows to 32.6% in omnivores from the contrasting habitat (Table AV).
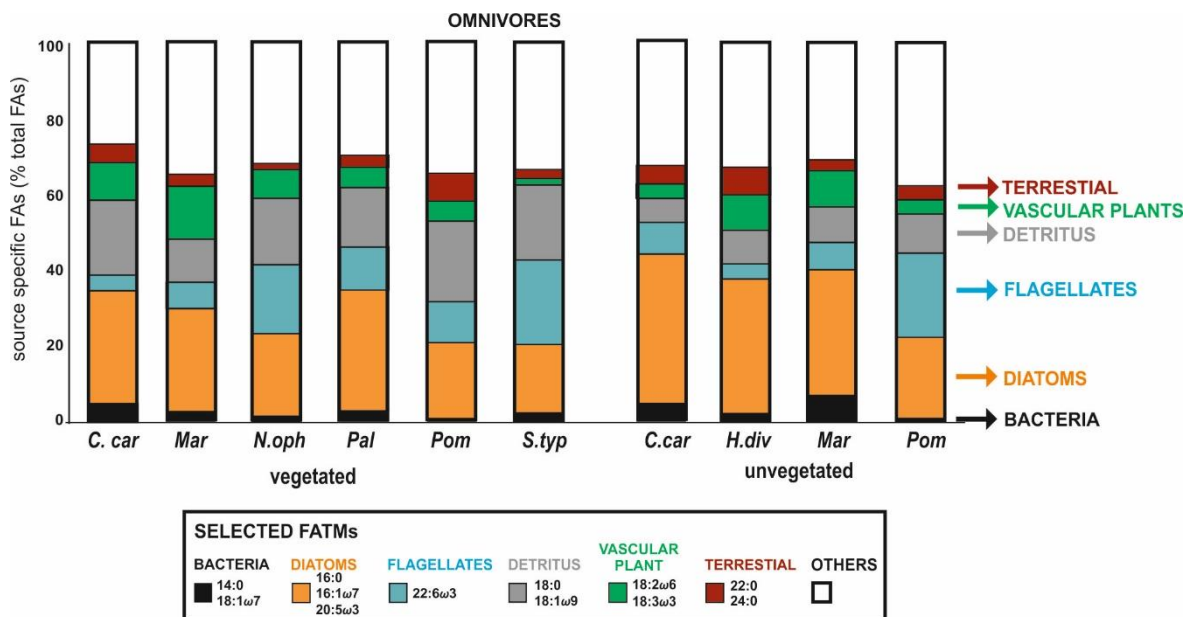
Fig. 18 Relative composition of FATM and other FA (see Table 2) in omnivores species

species abbreviations: *C.car- C. carinata, Mar- Marenzellaria* spp.*, N.oph- N. ophidion, Pal- Palaemon* spp.*,*
Pom- Pomatoschistus spp.*, S.typ- S. typhe, H.div- H. diversicolor*

The values of carbon and nitrogen stable isotopes in consumers differed significantly among consumer groups but not between habitats, with significant interaction between the two factors (PERMANOVA main tests, p < 0.05 Table 10).

As indicated by the post-hoc pairwise comparisons, two species of meiofauna differed in δ^{13}C values. When samples from two habitats were compared for each species –

the tests indicated no significant difference for *P. spinicauda* (average δ^{13}C values around -20.5‰ in both habitats), but significant contrasts for *T. discipes* (-17.7‰ on average in the vegetated, -13.3‰ in the unvegetated seabed, Fig. 19, Table AVI). Only two measurements of the nitrogen isotopes has been obtained during analyses of meiofauna samples, for *T.discipes* from the unvegetated habitat (3.29‰ and 3.26‰, mean 3.3‰).

For macrofaunal consumer groups, δ^{13}C values ranged from -20.4‰ (suspension/detritus feeders) to -16.3‰ (omnivores both form the unvegetated habitat), δ^{15}N values ranged from 5.9 ‰ (suspension/detritus feeders in the unvegetated) to 8.9 ‰ (omnivores in the vegetated habitat, Fig. 19, Table AVI). There were significant differences in carbon and nitrogen isotopic ratio among macrofaunal consumer groups (PERMANOVA main test, $p < 0.05$). Post-hoc comparisons indicated significant contrasts for most pairs of macrofauna consumer groups. No significant differences were only noted for grazers and suspension feeders and grazers and omnivores (Table 10).

For suspension/detritus feeders, δ^{13}C values varied from -21.7‰ (*C. glaucum*) to -16.6‰ (*M. arenaria*) in unvegetated seabed (Fig. 19, Table AVI). At vegetated bottom *C. glaucum* and *M. edulis* had similar average carbon (-19.6‰) and nitrogen (6.7‰) isotopes composition while *A. improvisus* had higher ratios for both isotopes (δ^{13}C -17.9‰, δ^{15}N 8.5‰, Fig. 19, Table AVI),

Grazers species had higher δ^{13}C values in the vegetated compared to unvegetated habitat (Fig. 19, Table AVI). The highest carbon isotope ratio was noted for *Idotea* spp. of seagrass beds (-14.2‰). δ^{13}C values in species sampled in the bare seabed were shifted towards depleted values with the lowest value noted for *Hydrobia* spp. (-21.7‰, Fig. 19, Table AVI).

Among omnivores, the most [13]C- enriched values in the vegetated habitat were noted for *Palaemon* spp. (-15.5‰), similar carbon isotope ratio were documented for *Marenzellaria* spp. and *P. torva* of the other habitat (-15.9‰). Mean δ^{15}N value of omnivores (at both habitats) was around 8 - 9 ‰ and was considerably higher than in the other consumer groups (Fig. 19, Table AVI). The most [15]N- enriched values were noted for *S. typhle* (11.3‰), whereas the most depleted values for *Palaemon* spp. (6.9‰), both from the seagrass beds.
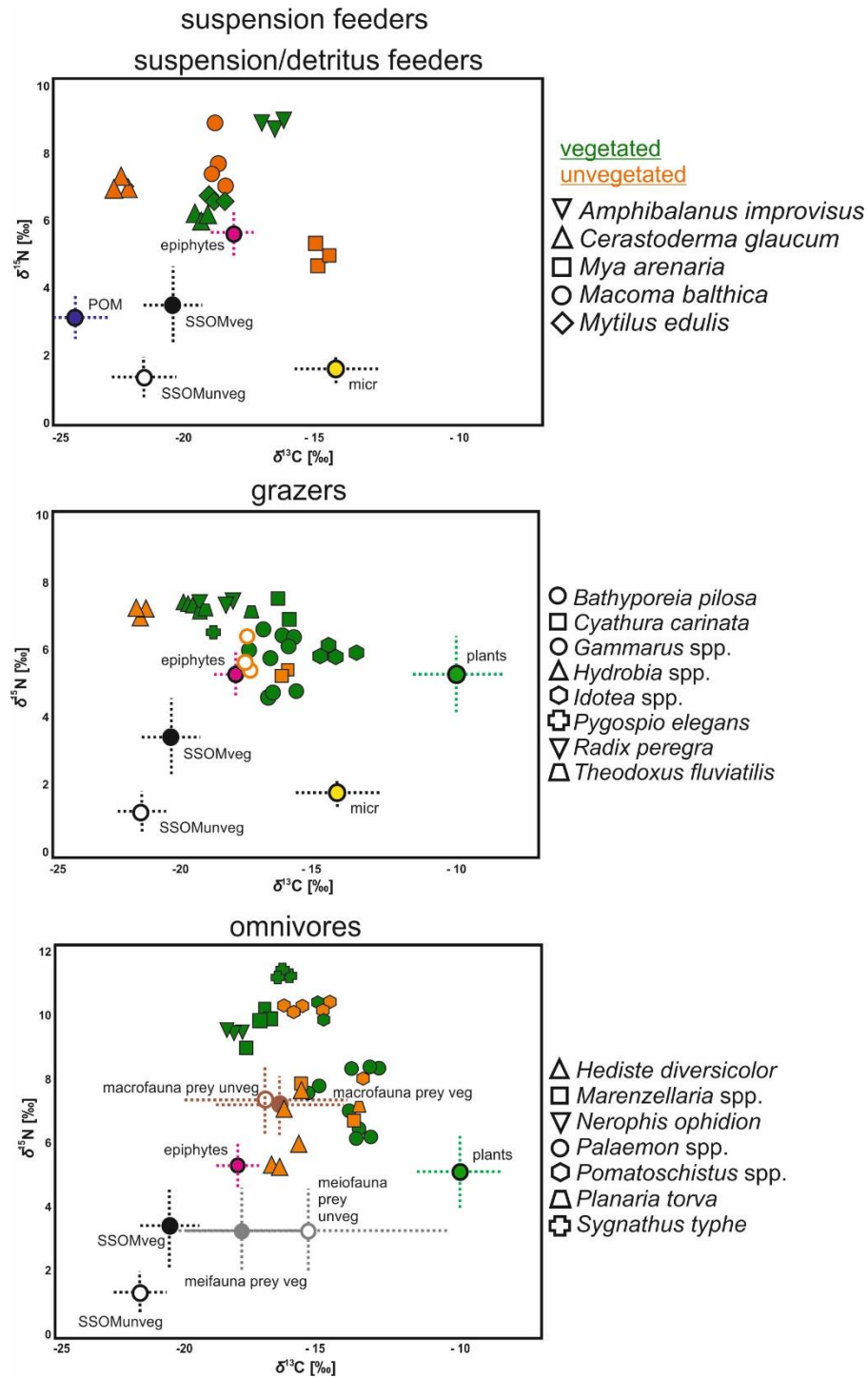
Fig. 19 Bi-plot of carbon and nitrogen isotope composition of sources and macrofauna species from the vegetated and unvegetated habitats plotted separately for consumer groups. Possible food sources are presented as mean ± st.dev.

abbreviations: micr – microphytobenthos/ bacteria, SSOMveg/unveg- SSOM in vegetated and unvegetated habitat

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Sources contribution to consumers diet (MixSIAR models)

The MixSIAR mixing models (Fig. 20, Table 13) documented that *P. spinicauda* diet, was composed of SSOM ('averages' mode of solutions=99%, Fig. 20, Table. 13), regardless of the habitat. Contrastingly, the SSOM contribution to *T. discipes* diet was negligible. The other two sources contributed greatly to *T. discipes* diet with different proportions in the two habitats. Individuals collected in the vegetated bottom had higher epiphytes contribution together with wide credibility intervals (57% mode and 3-90% BCI 95%), compared to the one of unvegetated habitat (16% mode and 4-53% BCI 95%, Pr = 0.66, Pr - probability that contribution was higher in the vegetated habitat). Whereas individuals collected in the unvegetated habitat had higher microphytobenthos/bacteria contribution (55%) in contrast to the one from seagrass meadows (24%, Pr=-0.92, Fig.20, Table 13).
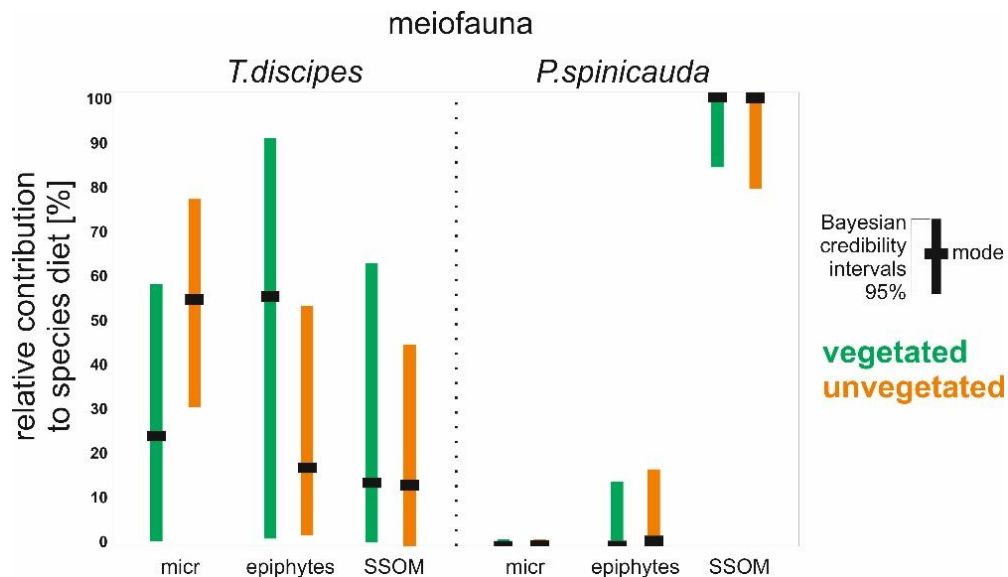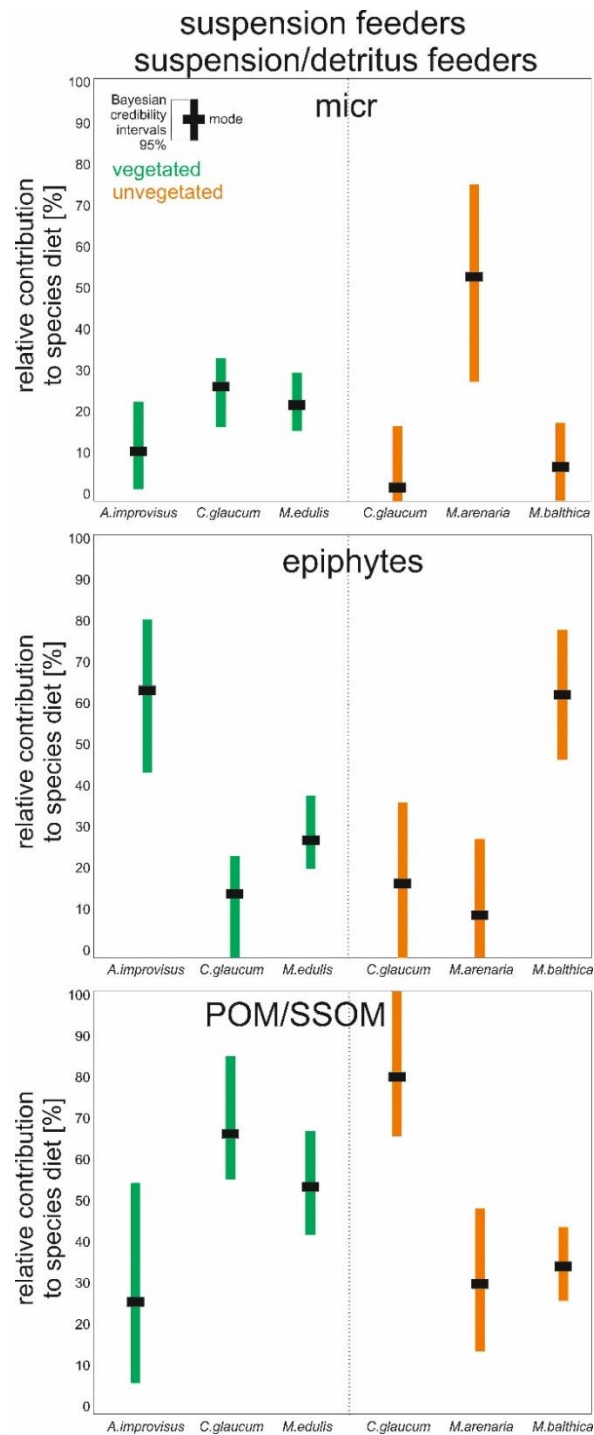

Fig. 20 Relative contribution of the food sources (microphytobenthos/bacteria - micr, epiphytes, SSOM) to diet of two species of meiofauna sampled in the vegetated (green lines) and unvegetated (orange lines) habitat. The lines indicate 95% Bayesian credibility intervals, points indicate modes

Table 13　Relative contribution of the food sources (microphytobenthos/bacteria - micr, epiphytes, SSOM) to meiofauna species diet in two habitats based on results obtained from MixSIAR mixing models. Mode, Bayesian credibility intervals (BCI 95%) and results of probability test that source contribution is higher in the vegetated habitat (Pr) are presented

	vegetated		unvegetated		
T. discipes	mode (%)	BCI 95%	mode (%)	BCI 95%	**Pr**
micr	24	6-59	55	31-78	0.92
epiphytes	57	3-90	16	4-53	0.56
SSOM	14	1-62	15	2-45	0.49
P. spinicauda					
micr	0	0-2	0	0-7	0
epiphytes	0	0-14	0	0-17	0
SSOM	99	85-100	99	80-1	0

Within the macrofaunal group of suspension feeders and suspension/detritus feeders, the main food source differed among species and between habitats. For individuals collected in the vegetated habitat POM/SSOM was the main food source for *M. edulis* and *C. glaucum* (contributions 65 and 80% accordingly) whereas epiphytes made the largest portion of the diet of *A. improvisus* (62%). POM/SSOM was also the main food source for *C. glaucum* collected in the unvegetated habitat (88%). Representatives of two other species collected in the bare seabed had other main food sources: *M. arenaria* - microphytobenthos/bacteria (61%), *M. balthica* - epiphytes (58%, Fig. 21, Table 14). Much larger contribution of microphytobenthos/bacteria in the diet of *C. glaucum* collected in the vegetated habitat was noted, when the individuals from the two habitats were compared (Pr = 0.96).

Fig. 21 Relative contributions of the food sources (microphytobenthos/bacteria - micr, epiphytes, POM/SSOM) to diet of macrofauna suspension and suspension/detritus feeders sampled in the vegetated (green lines) and unvegetated (orange lines) habitat. The lines indicate 95% Bayesian credibility intervals, points indicate modes. POM/SSOM represents a mean of particulate organic matter and surface sediment organic matter

Table 14 Relative contribution of the food sources (microphytobenthos/bacteria - micr, epiphytes, POM/SSOM) to macrofauna suspension (*A. improvisus, M. edulis, M. arenaria*) and suspension/detritus feeders (*C. glaucum, M. balthica*) diet in two habitats based on results obtained from MixSIAR mixing models. Mode, Bayesian credibility intervals – BCI 95% and results of probability test that source contribution is higher for *C. glaucum* in the vegetated habitat (Pr) are presented

vegetated	*A. improvisus*		*M. edulis*		*C. glaucum*		
sources	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	
micr	11	3-23	8	0-21	7	0-23	
epiphytes	62	41-80	27	11-41	10	0-26	
POM/SSOM	25	6-53	65	48-82	80	61-99	
unvegetated	*M. arenaria*		*C. glaucum*		*M. balthica*		
sources	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	**Pr**
micr	11	3-23	8	0-21	7	0-23	0.96
epiphytes	62	41-80	27	11-41	10	0-26	0
POM/SSOM	25	6-53	65	48-82	80	61-99	0

Epiphytes were the main food source in the diet of 3 grazer species (*Hydrobia* spp., *R. peregra, T. fluviatilis)* collected in the vegetated habitat (contributions around 50%). Another important food source for four grazers from seagrass beds was SSOM, exceeded from 36% to 50% of contribution in their diet (all gastropods and *Gammarus* spp.). Moreover, considerable contribution of microphytobenthos/bacteria was noted for *Idotea* spp. (66%) and *Gammarus* spp. (27%) from the vegetated habitat. Also *Gammarus* spp. from the same habitat had the highest contribution of plants in the diet (12%). Whereas, considering grazers from the unvegetated habitat, microphytobenthos/bacteria was the main food source for *B. pilosa* (46%). SSOM was also a considerable food source for *B. pilosa* (41%), and the sole food source for *Hydrobia* spp. for grazers collected in the bare seabed. Epiphytes and plants contributions were negligible for all grazer taxa collected in the unvegetated habitat (Fig. 22, Table 15). There was only one the same taxa presented in the vegetated and unvegetated habitat and the contribution of food sources in its diet differed between habitats - *Hydrobia* spp. from the vegetated habitat had higher contribution of epiphytes (Pr=0.93) whereas from the unvegetated had higher contribution of SSOM (Pr=-1).
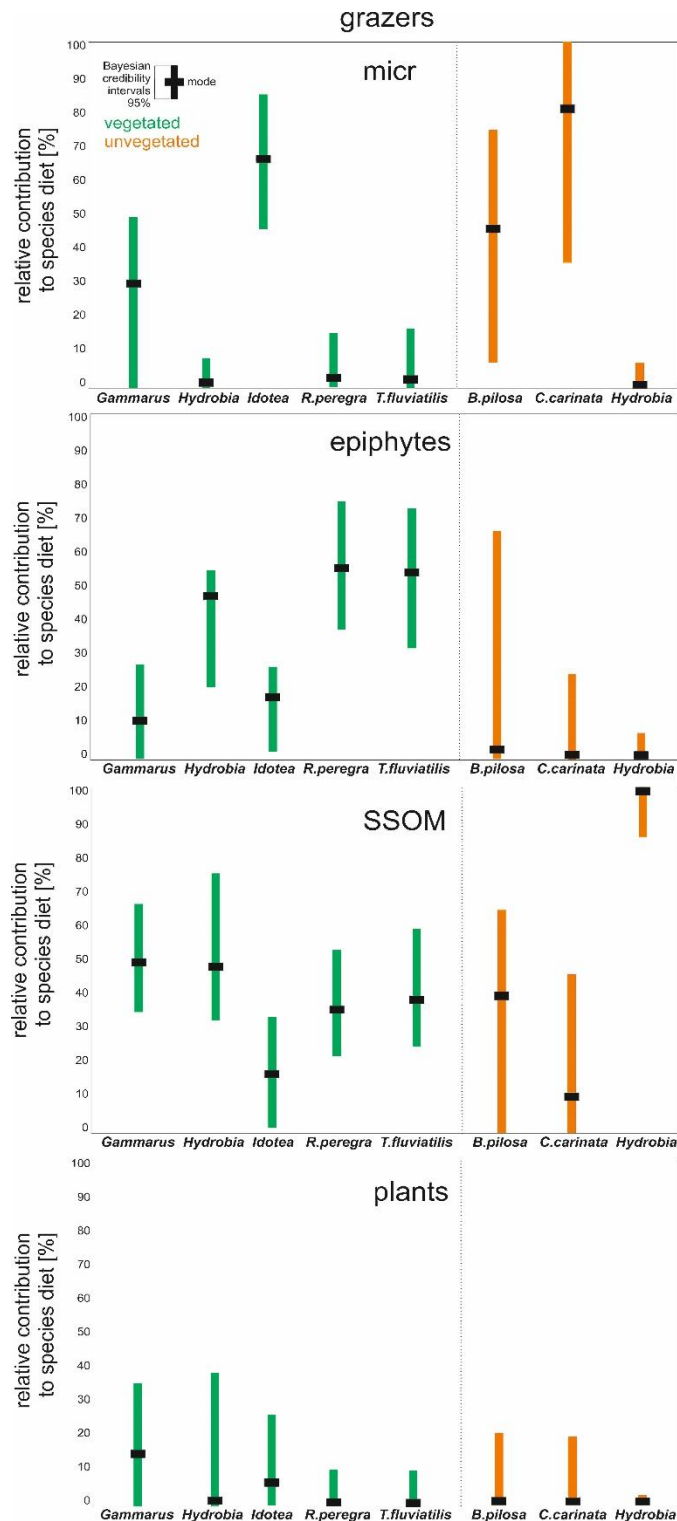
Fig. 22 Relative contributions of the food sources (microphytobenthos/bacteria - micr, epiphytes, SSOM, plants) to diet of macrofauna grazers sampled in the vegetated (green lines) and unvegetated (orange lines) habitats. The lines indicate 95% Bayesian credibility intervals, points indicate modes

Table 15 Relative contribution of the food sources (microphytobenthos/bacteria - micr, epiphytes, SSOM, plants) to macrofauna grazers diet in two based on results obtained from MixSIAR mixing models. Mode, Bayesian credibility intervals – BCI 95% and results of probability test that source contribution is higher in *Hydrobia* spp from the vegetated habitat (Pr) are presented

vegetated	*Gammarus* spp.		*Idotea* spp.		*Hydrobia* spp.		*R. peregra*		*T. fluviatilis*	
sources	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%
micr	29	1-48	66	43-82	1	0-7	3	0-13	3	0-15
epiphytes	9	0-24	15	2-25	49	19-54	58	39-75	53	30-71
SSOM	50	33-65	13	1-31	48	31-76	36	19-52	40	22-59
plants	12	0-33	4	0-23	1	0-33	1	0-8	1	0-10

unvegetated	*B. pilosa*		*Hydrobia* spp.		
sources	mode	BCI 95%	mode	BCI 95%	**Pr**
micr	46	5-77	0	0-5	0
epiphytes	2	0-65	0	0-6	1
SSOM	41	0-66	99	89-100	-1
plants	0	0-20	0	0-2	0

Meiofauna prey food source made considerable contributions to the diet of the four omnivores species collected in the vegetated habitat: *C. carinata* (46%), *Marenzelleria* spp. (55%), *Palaemon* spp. (28%), *N. ophidion* (80%) (Fig. 23, Table 16). Macrofauna prey was the main food source for *S. typhe* (75%) and *Pomatoschistus* spp. (69%) and also a considerable food source for *Marenzellaria* spp. (38%), all collected in the vegetated seabed. In the same habitat, SSOM made almost 50% of the diet of *Palaemon* spp.. For specimens collected in the unvegetated habitat, macrofauna prey was an important food source only for *Pomatoschistus* spp. (67%), meiofaunal prey contributions varied from 16% to 29%, while SSOM had highest contributions to diets of *C. carinata*, *H. diversicolor* and *Marenzelleria* spp. (81%, 64% and 37% respectively) (Fig. 23 Table 16). There were three the same species presented in the vegetated and unvegetated habitat and the contribution of sources differed between habitats for two of them – *C. carinata* and *Marenzelleria* spp. from seagrass meadows had higher contribution of meiofauna prey (Pr=0.89 and Pr=0.65 accordingly) whereas from the bare seabed had higher contribution of SSOM (-0.97).
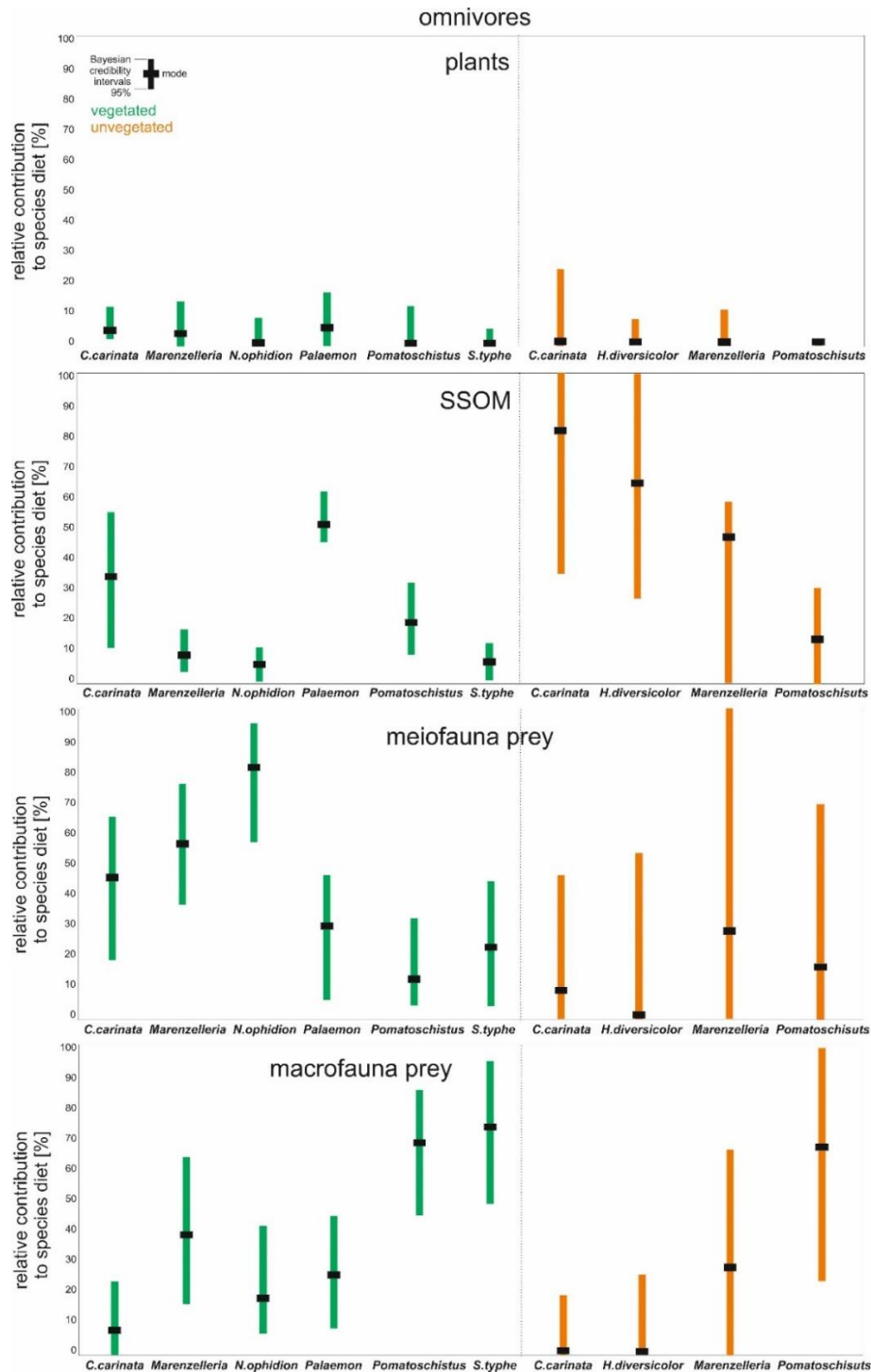
Fig. 23 Relative contributions of the food sources (plants, SSOM, meiofauna prey, macrofauna prey) to diet of macrofauna omnivores sampled in the vegetated (green lines) and unvegetated (orange lines) habitats. The lines indicate 95% Bayesian credibility intervals, points indicate modes

Table 16 Relative contribution of the food sources (plants, SSOM, meiofauna prey, macrofauna prey) to macrofauna omnivores diet in two habitats based on results obtained from MixSIAR mixing models. Mode, Bayesian credibility intervals – BCI 95% and results of probability test that source contribution is higher in *C. carinata* (C), *Marenzelleria* spp. (M), *Pomatoschistus* spp. (P) from vegetated habitat (Pr) are presented

vegetated	*C. carinata*		*Marenzelleria* spp.		*N. ophidion*		*Palaemon* spp		*Pomatoschistus* spp		*S. typhe*	
sources	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%
SSOM	34	10-56	7	4-16	4	0-9	50	42-59	19	5-32	5	1-12
plants	4	2-10	4	0-13	0	0-10	5	0-16	0	0-12	0	0-5
meiofauna prey	46	17-65	55	35-76	80	57-99	28	5-48	11	3-31	24	4-44
macrofauna prey	6	1-21	38	13-61	16	5-23	22	5-43	69	43-88	75	49-93

unvegetated	*C. carinata*		*H. diversicolor*		*Marenzellaria* spp.		*Pomatoschistus* spp.		Pr C	Pr M	Pr P
sources	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%	mode	BCI 95%			
SSOM	81	34-100	64	25-100	37	0-62	13	0-32	0-62	13	0-32
plants	1	0-24	3	0-8	0	0-10	0	0-5	-0.97	0.46	0.21
meiofauna prey	8	0-46	2	0-53	29	0-100	16	0-73	0	0	0
macrofauna prey	0	0-18	0	0-24	29	0-66	67	22-98	0.89	0.65	0.14

4. Discussion

4.1. Seagrass vegetation and sediment characteristics

Effects of vegetation on organic matter content in the sediments

The eelgrass vegetation in the Gulf of Gdańsk caused significant changes in the sediment organic matter pool. The sediments of *Z. marina* meadows had higher organic matter content than the neighboring bare sands. The increased concentrations of POC and TN in the vegetated bottom were clearly noticeable at all three studied locations. These effects were observed both at the very surface of the seabed (upper 2 cm) and when deeper sediment layers were explored. The pattern of increased POC and TN in the vegetated habitats was consistent across the upper 10 cm of sediments at the three sites. Various scenarios of seagrass influence on sediment organic enrichment were documented in other coastal locations worldwide (Gacia et al. 1999, Peralta et al. 2008, Bos et al. 2007). No significant enhancement of organic carbon was observed in the 10 cm sediment profile in the experimental field study of sediment accretion within artificially planted seagrass units in the Wadden Sea (Bos et al. 2007). On the other hand, a two-fold increase in organic matter in the sediments covered by the dwarf eelgrass *Zostera noltii* from the Mauritanian coast was observed within the whole 10 cm profile compared to that in the bare bottoms (Honkoop et al. 2008). The increased amounts of organic matter in seagrass vegetated sediments were explained by favorable conditions for particle trapping by meadows and were reported also by several other studies performed in a range of geographical locations and meadows formed by various seagrass species (Fry et al. 1977, Bowden et al. 2001, Gacia et al. 2002). Ecosystem engineering effects in seagrass meadows can depend on shoot density and biomass (Fonseca and Fisher 1986). Other factors controlling engineering effects included the hydrodynamic regime of the locality, neighborhood of rivers and other sources of organic material (van Katwijk et al. 2010, Lavery et al. 2013). Indeed, in the present study, the organic enrichment (POC in vegetated to POC in bare sediments ratio) were much higher at the sheltered location (Inner) than at the other two, exposed ones (GS, Outer). The organic matter content in sediments within the vegetated habitats in the Gulf of Gdańsk does not seem to be macrophyte density dependent (within the range of densities observed in the present study, i.e. from 46.9 ± 18.3 to 84.9 ± 29.9 shoots m^{-2}) as no

significant correlation between any of the vegetation descriptors to any of the geochemical sediment properties was documented within the seagrass meadows. The environmental engineering effects of seagrass vegetation seem to operate efficiently even in the relatively sparse and recently developed vegetation in the recovering meadows in the Gulf of Gdańsk, and no threshold in the seagrass density (i.e., the density of seagrass too low to produce organic enrichment effects) could be observed. In Jankowska's et al. (2014) seasonal study, these effects persisted throughout the year, regardless of the dramatic seasonal variability in seagrass cover (significant effects occurred even at very low biomass and density in winter). However, when the two exposed sites (GS, Outer) were compared the higher carbon enhancement was noted at the one with higher *Z. marina* density, indicating the significance of vegetation development in a meadow for its engineering properties.

The quantity of the organic matter (as indicated by POC concentration) and the differences in this parameter between the vegetated and unvegetated sediments at the three sites remained constant within the vertical profile of the upper 10 cm of the sediments. It is consistent with sediment dating results – the upper 10 cm layer was indicated as mixed. A different pattern was observed for photosynthetic pigments, especially the chlorophyll *a* concentration, which is an indicator of fresh, recently produced organic and unstable material (Gacia et al. 2002). The increased concentrations of chlorophyll *a* and CPE were documented only down to 4 cm; at deeper parts of sediment profile, the contrasts between vegetated and unvegetated sediments were much less visible or not detected. The differences in the vertical distribution patterns of the POC and photosynthetic pigments result from the different natures of these two descriptors of an organic matter. Photosynthetic pigments reflect recent organic matter production and accumulation in the sediments, while the more stable particles of organic carbon and nitrogen compounds in the sediment reflect accumulation over a longer period (Fry et al. 1977). In addition, their vertical distribution can be influenced by deep sediment mixing events that occur mostly during heavy storms, which are common in winter and autumn. In the surface layers (as indicated by the analyses of 2 cm surface samples and analyses of the upper layers down to 4 cm in the 10 cm core samples), the concentrations of chlorophyll *a* and CPE are much higher in the vegetated bottoms. It is consistent with the difference pattern observed for POC. On the other hand, chlorophyll *a* comprised a much larger portion of the total

organic matter pool in bare sands (as shown by higher values of Chl a/CPE and Chl a/POC). That indicates a higher proportional input from recent production and likely the better development and higher productivity of microphytobenthos in the unvegetated sea bottoms. Reports on the influence of seagrass vegetation on microphytobenthos are scarce, and documented effects are not consistent. It has been suggested that the high biomass of microphytobenthos in seagrass beds could also be a consequence of lower levels of sediment disturbance (Widdows et al. 2008, Friend et al. 2003). A study of pigment concentrations and microphytobenthos biomass in sediments was performed in several habitats (mud, sand, silty sand, *Sarcocornia*, *Zostera*, pioneering *Spartina*, established *Spartina*) along the southern coast of Portugal and reported lower values in the bare sandy sediments than in the vegetated seabed sites (Friend et al. 2003). On the other hand, the results of an experimental study of factors driving primary production in the sediments of seagrass beds in Florida indicated no difference in microphytobenthos production within and outside seagrass beds (Bucolo et al. 2008). However, in the Gulf of Gdańsk in summer, seagrass is accompanied by dense vegetation of filamentous brown algae (*Pylaiella littoralis*, Jankowska et al. 2014) which can limit light transmission to the seabed surface and influence microphytobenthic production. Additionally, the lower portion of chlorophyll *a* in the organic matter in the vegetated sediments may be, due to grazing by macrofauna associated with seagrass meadows. Lebreton et al. (2011) showed that benthic diatoms are an important food source for the macrobenthic invertebrates dwelling in *Z. marina* beds. It was shown that deposit feeders could reduce the abundance of microphytobenthos (Miller et al. 1996). Indeed, this pressure from macroinvertebrate consumers might be higher in the Gulf of Gdańsk's vegetated habitats, as they contain much higher densities and biomass of macrofauna compared to unvegetated areas (Włodarska - Kowalczuk et al. 2014). Additionally, grazing on microphytobenthos by both meio- and macrofauna consumers has been noted within this study (chapter 4. subchapter 4.2.).

The POC enhancement in the seagrass beds was not accompanied by a change in the mean $\delta^{13}C$ signatures (as indicated by no significant effects detected by the PERMANOVA tests). This discrepancy between the clear effect on POC and the absence of response in the mean $\delta^{13}C$ values in the vegetated sediments was observed in other studies (Simenstad and Wissmar 1985, Boschker 2000, Hemminga et al. 1994, Kennedy

et al. 2010). The clear difference between different habitats was only noted for δ^{15}N (as for TN), with higher values recorded in the vegetated bottom. The variation in δ^{15}N values among the vegetated and unvegetated habitats remains poorly understood but is usually explained by inorganic nitrogen incorporation by seagrass and sediments (Lepoint et al. 2004). The fixation of nitrogen by sulfate reducers in seagrass bed rhizospheres has been previously documented (Welsh 2000). This microbial fixation is an additional source of organic nitrogen for seagrass bed sediments, pore waters and living plants (Sacks and Repeta 1999). Papadimitriou et al. (2005) stated that δ^{15}N changes within the sediments of western Mediterranean *Posidonia* meadows may be a result of the mixing of ^{15}N-enriched nitrogen from primary sources with ^{15}N-depleted nitrogen fixed in the sediments. Indeed, significantly higher bacteria abundance and biomass were detected in the Puck Bay sediments within the seagrass meadows compared to the bare bottoms in the studied area (Jankowska et al. 2015) and other coastal locations (Pollard and Moriarty 1989, Danovaro et al. 1996). The increased numbers of bacteria in the vegetated bottoms may also more efficiently decay organic matter, resulting in higher δ^{15}N signatures. Despite the nearby location of the Gdańsk - Sopot agglomeration, no effects of sewage disposal (i.e. sewage-derived NH_4^+ which can be the source of ^{15}N-enriched particulate matter, Cifuentes et al. 1988) could be detected at the GS site, which did not differ in its δ^{15}N signatures from the other sites.

The sources of organic matter in the vegetated and unvegetated habitats

The SIAR modelling of the stable isotope signatures of the organic matter deposited in the sediments showed that an important fraction of an organic matter in the Gulf of Gdańsk is derived from seagrass tissues. This fraction was much higher in vegetated bottoms, where seagrass-derived organic matter comprised 39 - 41% of the organic carbon in the surface sedimentary organic matter pool. This is similar to values reported from the other seagrass meadows systems – previous studies in the Mediterranean Sea and in Australian seagrass meadows documented that approximately 50% of the organic matter in the sediments originated from seagrass tissues (Papadimitriou et al. 2005, Lavery et al. 2013). On the other hand, macroalgae-derived organic matter in the intertidal sediment of southern France was as low as 17% (Dubois et al. 2010). At a global scale, it is estimated

that 30 to 50% of the net community production of seagrass meadows is buried in situ within the meadows (Kennedy et al. 2010). The rest of the seagrass material (not buried) is probably consumed or exported to surrounding areas (Kennedy et al. 2010). In the present study, much less organic matter that originated from seagrass was detected on bare bottoms than in vegetated sediments. It suggests that seagrass-produced organic matter is decomposed and stored mostly within the meadows. The seagrass tissues decompose relatively slowly (because of the high C:N:P ratio) and are not commonly consumed by invertebrates (Jaschinski et al. 2008) or intensively decomposed by bacteria (Boeschker et al. 2000), so their remnants can be detected in the sediment even after several months (Mateo et al. 1997, Duarte et al. 2010). It is important to note that the SIAR modelling has identified differences in the organic matter sources' compositions between the vegetated and unvegetated bottoms, while simple comparisons (statistical testing for differences in mean values) of δ^{13}C suggested very similar situation in both habitats. That result points to the need of applying analysis methods that explore the full spectrum of data and take uncertainty into consideration (such as SIAR mixing models, Parnell et al. 2010).

Other sources of sediment organic matter usually considered in seagrass meadow system studies are plankton and terrestrial sources along with bacterial carbon sources, but the last one usually does not exceed 10% (Bouillon et al. 2006). The isotopic POM signatures (δ^{13}C -23.3, δ^{15}N 6.23) in the present study were similar to the values reported in the other studies in the southern Baltic Sea (Maksymowska et al. 2000, Sokołowski 2009). The POM had similar, relatively high contributions in the vegetated and unvegetated sediments (38 - 50‰), reflecting the importance of pelagic production for the organic matter pools in both habitats.

The lower input of seagrass-derived carbon in bare sands was compensated by a higher portion of material defined in the model as derived from filamentous algae and epiphytes (32-39%). The significant epiphyte contribution in the bare sands may seem intriguing because the isotopic signal of the epiphytes in this study was measured in samples of epiphytes growing on seagrass leaves and filamentous algae occurring within the meadows. In the study area in summer months, filamentous algae occur with high biomass within seagrass shoots but are also floating near the bottom all around shallows of the bay (Jankowska et al. 2014). Thus, the high proportion of 'epiphyte' derived organic

carbon in the bare sand samples may reflect both the strong export of organic matter produced within seagrass meadows to adjacent bare seabed and/or input from floating filamentous algae. Reports from other coastal systems indicated the importance of seagrass meadows in supporting neighboring areas with organic matter (Vafeiadou et al. 2013, 2014).

Carbon stock and accumulation in the vegetated sediments

The present thesis provides the first report of the carbon sink capacities of the underwater *Z. marina* meadows in the southern Baltic Sea. Our results indicate that eelgrass meadows in the southern Baltic Sea can act as "sediment blue carbon sinks" by accumulating larger amounts of organic carbon than the unvegetated sediments. The estimated C_{stock} for the top 10 cm of sediment of present study ranged from 50.2 to 228.0 g m^{-2}, whereas C_{accu} ranged from 0.84 to 3.85 g m^{-2} y^{-1}. The estimation of total stored carbon within eelgrass meadows in the Inner Puck Bay area (based on total eelgrass area for the Inner Puck Bay of 48 km^2) amounted 0.1 Mt with an annual rate of carbon accumulation of 0.02 Mt y^{-1}. Despite the relatively low development of seagrass vegetation (low density and biomass values compared to other seagrass meadows (Jankowska et al. 2014, Clausen et al. 2014)) the C_{stock} and C_{accu} values documented for the southern Baltic Sea are in the same order of magnitude as other *Zostera*-dominated system (Table 17). They are similar to disturbed eelgrass meadow from east Atlantic coast and represent lower end values of a worldwide variability (Table 17). Our results were smaller than those reported for other, well developed *Zostera* meadows and dramatically smaller than those reported for *Posidonia*-dominated systems in warmer regions. The Mediterranean Sea species *Posidonia oceanic*a is considered to comprise the largest pool of stored carbon in both leaf structures and soils, and the stored organic carbon in its meadows is estimated to be between 100 and 410 kg C m^{-2} (Mateo et al. 2006, Fourqurean et al. 2012, Serrano et al. 2012), i.e. three orders of magnitude higher than those recorded in the present study. A recent study of Australian seagrass meadows dominated by various species (total area of 92569 km^2) reported total organic carbon stock as high as 155.5 Mt for the top 25 cm of sediment and annual carbon accumulation from 0.09 to 6.16 Mt y^{-1} (considering different sediment accumulation rates applied for different regions, Lavery et al. 2013). This study proved that the carbon sink

capacity of seagrass strongly depended on a particular habitat and seagrass species characteristics. The largest species (*Posidonia australis*) was found to be the most efficient in carbon storage. However, the nearby terrigenous material inflows, hydrodynamic regime and depth were indicated as even more important factors that influence the stock capacity (Lavery et al. 2013). The present study also shows that sediment enhancement in organic carbon varies depends on the local environmental settings and the macrophyte species composition of a meadow (see the above discussion on the differences in organic carbon enhancement in vegetated habitat among the studied localities). The existing current day global estimates of seagrass sediment carbon stock that are based mostly on data from *Posidonia* dominated meadows should be revisited to take into account this worldwide variability. Carbon stock and accumulation values estimated for the Gulf of Gdańsk meadows may serve as an useful, low-density case for global seagrass carbon stock estimations.

Based on the information provided by the ^{210}Pb analysis, the upper 10 cm of sediment represented approximately last 60 years so the period after eelgrass decline in the second half of the last century and the last years after recent natural recovery. The sediment layers from 10 cm down to 60 cm depth represent the time before 1950. The higher concentrations of POC in sediments in deeper layers (10 – 60 cm) indicate a much higher carbon stocks in the past and very high potential in carbon sequestration of the studied habitats (C_{stock} 3630.17 g m^{-2}, C_{accu} 41.00 g m^{-2} y^{-1}, Table 9). Sediments deeper than 10 cm represent time before 1950, i.e. period before eelgrass decline, when eelgrass meadows covered larger area (almost whole Inner Puck Bay, Ciszewski et al. 1992) with presumably better developed vegetation (higher plant density and biomass) at present. The higher POC content in these sediment layers also corroborates the notion, that present meadows are still in the recovery phase and have not attained the levels of vegetation development and carbon storage capacity from before 1950.

Table 17 Organic carbon stock (C_{stock}, g m^{-2}) and accumulation rate (C_{accu}, g m^{-2} y^{-1}) for different seagrass species and geographic regions as reported by the literature and the present study. Mean ± st.dev. are reported if available

seagrass species	region	sediment layer [cm]	C_{stock} [g m^{-2}]	C_{accu} [g m^{-2} y]	reference
multispecies	global	-	-	83	Duarte et al. 2005
multispecies	global	-	-	138 ±38	McLeod et al. 2011
multispecies	global	0-100	252	-	Fourqurean et al. 2012
Z. marina	Virginia, Atlantic coast	0-5	208 ± 99	-	McGlathery et al.2012
multispecies	Australia coast	0-25	1262 ±1483	-	Lavery et al. 2013
Z. marina	Virginia, Atlantic coast	0-10	-	37 ±3	Greiner et al.2013
multispecies	Dongsha Island, South China Sea	0-5	443 ± 6	33	Huang et al. 2015
Z. muelleri	Port Curtis, central Australia	0-10	600	-	Ricart et al. 2015
P. australis	Jervis Bay, NSW Australia	0-100	750 ±212	-	Macreadie et al. 2015
P. australis	Oyster Harbour, Western Australia	0-15	2770 ±117	26 ±1	Marba et al.. 2015
P. australis	Oyster Harbour, western Australia	0-150	10790 ±120	3	Rozaimi et al.. 2016
Z. marina	Denmark coast, Baltic Sea	0-25	4324 ±1188	-	Röhr et al. 2016
Z. marina	Finland coast, Baltic Sea	0-25	627 ±25	-	Röhr et al. 2016
Z. marina	Inner Puck Bay, southern Baltic Sea	0-10	228 ±12	3.9 ±1	
Z. marina	Inner Puck Bay, southern Baltic Sea	10-60	3630 ±222	41 ±27	present study
Z. marina	Outer Puck Bay, southern Baltic Sea	0-10	50 ±2	0.8 ± 0	
Z. marina	GS, southern Baltic Sea	0-10	166 ±4	2.78 ± 0	

Summarizing remarks

The presented results show that even relatively sparse vegetation of the small temperate eelgrass species *Z. marina* may play a considerable role in carbon sequestration at the local scale in

the southern Baltic Sea. The C_{stock} (from 228.0 to 50.17 g m^{-2}) were in the order of magnitude of those recorded for other degraded *Zostera*-based meadows from east Atlantic, however annual C_{accu} values (from 3.85 to 0.84 g m^{-2} y^{-1}) were the lowest ever reported (Table 17). Moreover, the organic matter content (POC concentration), including its fresh components (as indicated by the Chl a concentration), was enhanced at vegetated compared to unvegetated bottoms. Additionally, SIAR model showed that the percentage of seagrass-derived organic matter was higher in a vegetated sediment, indicating that seagrass produced matter is mostly buried within the vegetated patches. Our results showing the differences between the present results and those reported for other *Zostera* and *Posidonia* beds, indicate that a number of regional assessments (reflecting the species, local hydrodynamic regimes, geographical variability), such as the presented one (representing the lower end of variability range), needs to be considered to update the global seagrass carbon sink estimations. The recently published study (Fourqurean et al. 2009) based mostly on estimates from warmer regions and *Posidonia* beds, may be overestimated.

4.2. Benthic food web structure

Description of food sources

High number of collected potential food sources (12) indicates the complexity of shallow water habitats in the Outer Puck Bay. On the bi-plot graph presenting carbon and nitrogen SI composition (Fig. 14) the isospace created by the signals of collected sources encompasses the isospace of the consumers. That indicates that the wide and representative spectrum of the food sources supporting the benthic food web in the studied system was collected. All sources were lower or similar in nitrogen isotope ratio compared to macrofauna consumers, suggesting that they were at the base of the studied food web.

All plant sources (including four vascular plants *Z. marina, Myriophyllum* spp.*, Z. palustris, P. pectinatus* and charophyte C*h. baltica*) had very similar FA and SI composition. FA composition was highly dominated (around 56%) by the markers previously described as specific for vascular plants –18:2ω6, 18:3ω3 (Kharlamenko et al. 2001, Jaschinski et al. 2008, Lebreton et al. 2011, Kelly and Scheibling et al. 2012, Michel et al. 2014). The carbon and nitrogen isotopes composition of the vascular plants varied from -11.4‰ to -9.4‰ and from 3.4‰ to 6.6‰, respectively. These values match with the isotope ratios of the plant sources documented in other seagrass dominated systems (Kharlamenko et al. 2001, Lebreton et al. 2011, 2012, Ouisse et al. 2011, Vafeiadou et al.

2013) and particularly with those reported from seagrass dominated habitats in the western Baltic Sea and the Puck Bay (Jaschinski et al. 2008, Sokołowski 2009). Similar composition of fatty acids and stable isotopes among five species of plants make it impossible to distinguish them as separate food sources in the diet of the consumers by means of biochemical tracer analyses. Therefore, in the present study they could have only been grouped and treated as one food source. However, the total biomass of macrophytes in the study area is strongly dominated by the eelgrass. In summer *Z. marina* makes up 80% of the total macrophyte (i.e. both plant and macroalgae) biomass and in winter it is the only macrophyte species occurring in the study sites (Jankowska et al. 2014). Therefore we can expect that the contribution of plant food source to the consumers' diet represents mostly the organic matter derived from *Z. marina* tissues.

Next two sources with overlapping tracer signals were filamentous algae (*P. littoralis*) and epiphytes (mostly diatoms) detached from the seagrass leaves. These two sources had very similar FA composition with dominance of the diatom markers (16:0, 16:1ω7 and 20:5ω3) both in filamentous algae (around 41%) and in epiphytes (around 29 %). High concentrations of 16:0, 16:1ω7 and 20:5ω3 FA in epiphyte diatoms have been previously noted in seagrass systems from Marennes-Oléron Bay (east Atlantic coast, Lebreton et al. 2011). Similarity of filamentous algae and epiphytes was also remarkable in terms of SI composition (carbon isotope ratio -18.7‰ for filamentous algae and -19.3‰ for epiphytes, nitrogen isotope ratio 6.4‰ for filamentous algae and 4.7‰ for epiphytes). Other studies reported higher δ^{13}C values in epiphytes compared to the present study and often similar isotopic composition of epiphytes and seagrass (Ouisse et al. 2011, Kharlamenko et al. 2001 and Jaschinski et al. 2008). This was not observed in the present study, epiphytes were lower in δ^{13}C value by around 8‰ compared to vascular plants. The epiphytic communities may be very variable depending on the region and seagrass species (leaf size) and biofilm overgrowing the seagrass leaves may be composed of various species of algae ranging from unicellular algae to macrophytes (Mazzella et al. 1995, Borowitzka et al. 2006, Lebreton et al. 2009). In the Puck Bay, *Z. marina* leaves are overgrown by diatoms and rarely by *Ceramium* spp. (personal observations). The differences in both taxonomic composition and isotopic ratios of epiphytes reported by different studies may also stem from the inconsistent methods of epiphytes collection. In

most of the previous studies, epiphytes were scratched from the seagrass leaves with use of hand, cover glass or scalpel (Hoschika et al. 2006, Jaschinski et al. 2008, Ouisse et al. 2011, Vafeiadou et a. 2013), whereas in the present study epiphytes were detached by shacking and sonificating the seagrass placed in a container with filtered seawater. Scraping may cause a bias in isotopic signal as parts of seagrass leaves may be accidently scratched together with epiphytes (and so the final epiphyte signal is biased by the unexpected seagrass contamination). On the other hand, nitrogen isotopes ratio of epiphytes measured in the current study is within a range of values previously noted for epiphytes by other studies (Lebreton et al. 2011, 2012, Ouisse et al. 2012, Vafeiadou et al. 2013). The isotopic ratios of filamentous algae measured within this study are similar to the values reported by Sokołowski (2009) for *Ectocarpus* spp. and *Cladophora* spp. in the Puck Bay. Again, similarly to vascular plants, the almost identical biomarkers values of tracers in epiphytes and filamentous algae measured within current study made it impossible to distinguish them as separate food sources. Such similarity may result from the fact that both epiphytic diatoms and the filamentous algae have similar high concentration of xanthophyll fucoxanthin pigment (Ringer 1972). Moreover, *P. littoralis* which forms dense mats on the seabed, may be overgrown by diatoms. Despite the fact that the *P. littoralis* samples were shaken and sonificated prior to analyses to remove contaminants (as diatoms), it is possible that they still contained some amounts of diatoms as complete removal of them from the dense filamentous structures is very difficult. On the other hand *P. littoralis* is commonly overgrowing the eelgrass aboveground structures (personal observation), so it can also constitute some part of the epiphytes. Therefore, these two sources were grouped and treated as one source called epiphytes.

There are few published data available on microphytobenthos FA and SI composition, probably due to technical problems with obtaining samples large enough to perform the biochemical analyses (Ouisse et al. 2011). In microphytobenthos samples collected during this study, the contribution of FA typical for diatoms was relatively low (4.5%) taking into account the dominance of diatoms in microphytobenthic assemblages of the Puck Bay (Urban-Malinga and Wiktor 2003). On the other hand, the samples contained high percentage (41%) of $18:1\omega7$, a marker of bacteria, suggesting that they consisted largely of bacteria. Therefore this source was treated as a mixture of bacteria and

microphytobenthos, not sole microphytobenthos. In terms of the SI composition, the values obtained for microphytobenthos samples in this study were within the wide range (-15 to -20‰) of carbon isotopes ratios previously reported from east Atlantic coast by Lebreton et al. (2011, 2012) and Vafeiadou et al. (2013) and west Baltic Sea by Jaschinski et al. (2008). However, nitrogen isotopes ratios (from 5 to 10‰) reported in the same studies for microphytobenthos were much higher than those recorded in the present study (1.6‰). In other studies microphytobenthos materials were mainly characterized by diatom FA markers and their FA composition was similar to that of epiphytes (Jaschinski et al. 2008, Lebreton et al. 2011). This discrepancy between previous and present study may be caused by the differences in composition of microphytobenthos in the relevant regions. In the intertidal *Z. noltii* habitat studied by Lebreton et al. (2011), microphytobenthos was mainly composed of few diatom species, whereas in the Puck Bay the dominant diatoms are accompanied by numerous dinoflagellates and cyanobacteria (Urban-Malinga & Wiktor 2003).

POM, usually treated in food web studies as a proxy of phytoplankton, is a composite food source. It consists of several alive and dead microalgae cells together with other particles of organic matter of both marine and terrestrial origin (Volkman et al. 1989, Sokołowski 2009). Therefore, the tracers composition of POM in coastal waters may be very variable, both temporarily and spatially (depending e.g. on the distance from the coast and river mouths or depth). The FA composition of POM measured in this study indeed indicated a mixture of different FA markers: high concentration of diatoms (16:0, 20:5ω3), followed by detritus (18:0), flagellates (22:6ω3) and vascular plants markers (18:2ω6). Similarly high contribution of fresh and decaying diatoms and flagellates to POM was observed in shallow coastal waters of Marennes-Oléron Bay (eastern Atlantic coast) studied by Lebreton et al. (2011). Carbon isotopes ratios of POM (on average -23.5‰) recorded in the present study were in the range of values previously noted in the Puck Bay (Sokołowski 2009, Maksymowska et al. 2000), their relatively low values indicate estuarine rather than marine origin. The low isotope carbon ratio as well as considerable contribution of 22:0 terrestrial FA marker in POM suggests that terrestrial discharge has some influence on its composition. Indeed there are a few river mouths in the Puck Bay. Considerable vascular plants FA markers contribution (around 10 %) in the POM composition may be explained

by a common mixing of the water column and resuspension of organic matter particles from the seabed, what is highly likely considering the depth (only 1.5 m) and dynamic character of the coastal zone in this area (due to both waves and along-shore upwelling, Nowacki 1993).

The other composite food source, is surface sediment organic matter (SSOM). It contains organic matter of different origins (microbes, remnants of producers and animal organisms tissues, advected organic matter of terrestrial and marine origin, Fry and Sherr 1984) and is to different degree subjected to decomposition and remineralization processes (Lehman et al. 2002). The FA composition of SSOM collected in the present study is quite similar to that of the POM and constitute a mixture of markers indicating different origins. High contribution of bacteria (14:0, 18:1ω7), detritus (18:1ω9), diatoms (16:1ω7) and vascular plants (18:2ω6) markers was noted. The FA composition of SSOM did not significantly differ between seagrass meadows and the bare seabed habitats, however slightly higher bacteria and diatom FA markers were noted in vegetated sediment organic matter. The carbon isotope ratios of SSOM were similar in two habitats (-20.95‰ in the vegetated and -21.34‰ in the unvegetated habitat) and were within the range of previously noted in the study area (Sokołowski 2009). SSOM composition in the vegetated bottom was however ^{15}N- enriched compared to the unvegetated one. It suggests that more active decomposition processes may occur at seagrass beds bottom that is characterized by significantly higher density and biomass of bacteria within the study area (Jankowska et al. 2015). The sources contribution to the sediment organic matter pool has been estimated and compared among several stations located in the vegetated and unvegetated habitats of the Puck Bay (present study, subchapter 4.1.). When only three sources (plants, epiphytes and POM) were considered in the model, plants were estimated to constitute around 40% of the organic matter in sediments under seagrass and twice as low in bare sediments.

Food sources used by meiofauna consumers in the vegetated and unvegetated habitats

The collected meiofaunal copepods represented the primary consumers as their nitrogen isotope ratios were lower than those of macrofaunal species. FA profiles and carbon isotopes composition of *P. spinicauda* were very similar in two habitats and SSOM was estimated to be the sole food source (mixing models using carbon isotope ratio and FA

markers). Contrastingly, the diet of the other copepod species, *T. discipes* differed between habitats. *T. discipes* from the vegetated habitat had more diversified FA profile with considerable proportions of four markers (bacteria, diatoms, flagellates, detritus), whereas the profile of *T. discipes* from the unvegetated habitat was dominated by bacterial markers. The carbon isotope ratios of *T. discipes* from seagrass beds were placed between signals of microphytobenthos/bacteria and SSOM or epiphytes, whereas the carbon isotope ratios of the same species collected in bare seabed were very close to signals of microphytobenthos/bacteria. This observation agrees with the mixing models results. According to modelling, epiphytes were the main food source in the *T discipes* diet from the vegetated habitat whereas in the other habitat copepod consumed mostly microphytobenthos/bacteria. Benthic copepods dwell in the upper part of the sediment layer or the sediment surface (Lebreton et al. 2012). The difference in diets of the two studied species are most likely related to the differences in occupied microhabitats. *P. spinicauda* has elongated, cylindrical body shape (average length 430 μm and width 0.06 mm measured within this study on 100 individuals) and lives in the interstitial spaces within the sediment grains, whereas *T. discipes* has cyclopoid body shape (average length 0.57 mm and width 0.20 mm measured within this study on 100 individuals) and stay on the surface of the sediment and/or among seagrass leaves (Giere et al. 2006, Fig. 24).

Paraleptastacus spp.
length 430 μm
width 60 μm

Tachidius spp.
length 570 μm
width 200 μm
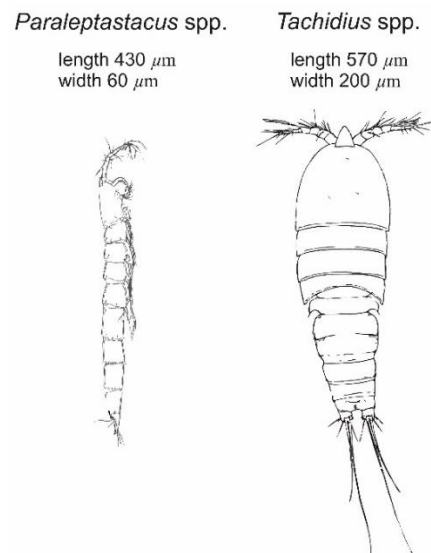
Fig. 24 Schematic drawings of two studied harpacticoid species with the average body length and width measured within the current study on 100 individuals (modified after Lang 1994)

P. spinicauda remains within the sediment, thus it has access mostly to the SSOM regardless of the habitat. *T. discipes* can feed on more variable food resources accessible on the sediment surface and among the vegetation. Therefore, *T. discipes* from the vegetated habitat that probably stays on seagrass leaves feeds on epiphytes (growing on the leaves), whereas *T. discipes* from the unvegetated habitat use mostly microphytobenthos that occurs with higher biomass at the bare sandy bottom (as indicated by higher proportion of chlorophyll a to organic matter, present study, subchapter 4.1.).

A large contribution of bacterial FA marker ($18:1\omega7$) was a common feature of *P. spinicauda* FA profile from both habitats and *T. discipes* from unvegetated habitat. The contribution of bacteria FA marker in the consumers was higher than in SSOM (the sole food source of *P. spinicauda* according to the modelling) and similar to microphytobenthos/bacteria (main food source of *T. discipes* according to the modelling). Higher amount of bacteria FA marker in copepod consumers than in their food sources may derive from the selective grazing and the strong preference towards the bacteria among the available pool of microphytobenthos/bacteria/detritus components. Experimental studies showed that copepods can selectively graze on unicellar organisms (diatoms) of different cell size or growth phase (De Troch et al. 2006, De Troch et al. 2012) as well as consume diatoms cells overgrown by bacteria but digest only bacteria and excrete living diatom as fecal pellets (De Troch et al. 2005). The strong interactions between meiofauna and bacteria in the studied area is supported by a positive correlation between bacterial and meiofaunal abundance and biomass documented by Jankowska et al. (2015). Bacteria isotopic composition usually reflects the composition of their substrate (Danovaro et al. 1998), therefore the selective feeding of copepod consumers in the present study could be detected only by application of FA analyses. This result shows that the usage of both SI and FA markers in food web studies is crucial to get a comprehensive understanding of the consumers' diet composition, particularly when the composite food sources are considered.

Up to date there are no studies performed in seagrass system that addressed the meiofauna copepods food sources composition in consumers identified to the species level. Previous studies indicated that benthic copepods at the genus level are opportunistic feeders feeding on various food sources including bacteria, microphytobenthos, macroalgae or seagrass detritus matter (Vizzini et al. 2002, Leduc et al. 2009, Lebreton et al. 2012,

Vafeiadou et al. 2014). Leduc et al. (2009) studied diets of copepod in New Zealand coastal waters, and based on C, N and S stable isotopes analysis reported that in bare seabed copepods mostly fed on microphytobenthos whereas in vegetated sediments mostly on bacteria. Only one study of seagrass systems in the Portuguese coastal waters studied SI in copepods identified to the family or genus level (Cletodidae, Ectinosomatidae, *Sunaristes*) (Vafeiadou et al. 2014). They found no differences in food source composition in copepod consumers from vegetated sediments and bare sands - in both habitats they fed on SOM that is a mixture of different origins. The similarity in diets was explained by the export of seagrass detritus to the adjacent bare areas.

The present study, is the first one on copepods identified to the species level, proving different diet composition of the two studied copepod species as well as variability in feeding preferences between the habitats. These results indicate that the meiofaunal consumers should not be grouped into higher taxa in the food web studies. The importance of performing the diet analyses on materials identified to the species level, was also underlined by Lebreton et al. (2012).

Food sources used by macrofaunal consumers in the vegetated and unvegetated habitats
Suspension, suspension/detritus feeders

In macrofaunal suspension and suspension/detritus feeders the dominant food sources differed among species and no consistent trend of difference between two habitats could be noted, based on the modelling results. Only one species was collected in both habitats (*C. glaucum*) and its diet was similar and dominated by POM/SSOM. When all taxa were considered – the diet within seagrass meadows was composed of epiphytes (in *A. improvisus*) or POM/SSOM (in *C. glaucum, M. edulis*), while in the bare seabed of epiphytes (in *M. balthica*), microphytobenthos/bacteria (in *M. arenaria*) and POM/SSOM (*C. glaucum)*. The common feature of the diet composition of all species in this group according to mixing modelling results, was a considerable contribution of POM/SSOM. The importance of POM/SSOM as a food source, is supported by the FA profiles as high contribution of flagellates' marker (marker of pelagic production, Kelly and Scheibling 2012) characterized all taxa. The major POM/SSOM contribution to the diet of *M. edulis* and *C. glaucum* was also detected in the Kiel Bight (west Baltic Sea), where seston was the

sole food of *M. edulis* (based on SI composition analyses, Mittermayr et al. 2014) and specifically in the Puck Bay where *C. glaucum* and *M. edulis* were shown to feed on POM or SSOM depending on the season with higher POM uptake during spring and summer when the intense primary production occurred (based on SI analyses, Sokołowski 2009).

In the present study FA and SI composition of POM and SSOM were very similar, perhaps due to the intensive water mixing and the resuspension of organic matter from the sediment to the water column. Therefore, it was impossible to differentiate between these two sources in the mixing models. Also, resuspension may be responsible for dominance of microphytobenthos/bacteria in the diet of *M. arenaria* from unvegetated habitat. Similar effects of resuspension were documented in seagrass dominated system from the Atlantic coast where suspension feeders (*Tapes phillipinarium, Cerastoderma edule*) fed on mixture of POM, SSOM and microphytobenthos (Lebreton et al. 2012). The high contribution of epiphytes in the diet of *A. improvises* and *M. balthica* reflected the similarly high δ^{15}N values of these two species and epiphytes. In summer *P. littoralis* form dense mats in the Puck Bay and it is possible that small parts of filamentous algae detached from the mats were suspended into the water and caught by suspension/detritus feeders. The composition of diets of *A. improvisus, M. arenaria* and *M. balthica* documented by mixing modelling of SI and FA data in this study, does not correspond to the results presented for the same fauna from the Puck Bay by Sokołowski (2009) who reported POM and SSOM as sole food sources for suspended feeding species. However, Sokołowski (2009) did not consider bacteria/microphytobenthos and epiphytes as potential food sources for those consumer groups. Overall, the diets of suspension and suspension/detritus feeders documented in the present study (mixed diets, consisting not only of POM/SSOM but also of bacteria/microphytobenthos and epiphytes) are similar to those documented by Lebreton et al. (2011) that reported feeding on a mixture of POM, SSOM and microphytobenthos (French Atlantic Coast).

The *Z. marina* vegetation seems to have no influence on suspension and suspension/detritus feeders' diets in the Puck Bay. The lack of clear differences in the diet composition of suspension and detritus feeders between the vegetated and unvegetated habitat was also noted for the *Z. noltii* system of the Portugal coast (Vafeiadou et al. 2013) and explained by export of organic matter from meadows to the adjacent bare seabed. In the

Kiel Bight (west Baltic Sea) eelgrass was assumed to serve as a habitat and to have no influence on the diet of suspension feeders (Mittermayr et al. 2014). In the present study one interesting difference between habitats was noted - the high microphytobenthos/bacteria contribution was detected only for species from the unvegetated bottom (*M. arenaria*) that may be linked to the higher microphytobenthos biomass in the bare sands as suggested by high chlorophyll *a* to POC ratio (present study, subchapter 4.1.).

Grazers

The high δ^{13}C values in several grazers indicated the possible contribution of a seagrass to their diet (as plants had the highest δ^{13}C among the potential sources). Slightly higher vascular plants FA markers were detected for grazers from the vegetated habitat (10.5% on average) than from bare sands (6.3%). Based on mixing models only two grazer taxa (*Gammarus* spp. and *Idotea* spp.) from vegetated habitat consumed some plants material and its contribution never exceed 15%, therefore it should be treated rather as a minor food source. Still, the plant contribution to the diet of grazers from the vegetated habitat was higher than in the unvegetated habitat (where it was close to 0%).

Most of the previous studies in seagrass systems claimed the lack of seagrass consumption by macrofauna (the west Baltic Sea - Jaschinski et al. 2008, Mittermayr et al. 2014, coast of France - Lebreton et al. 2011, Ouisse et al. 2012) or its uptake only in form of detritus (Sea of Japan - Kharlamenko et al. 2001, Portugal coast - Vafeiadou et al. 2013). Only few studies reported direct consumption of seagrass fresh tissue by specialized consumers - a crab (Woods and Schiel 1997), a herbivorous fish (Marguillier et al. 1997) and a sea urchin (Valentine et al. 2006) in subtropical regions; a sea cucumber in the Mediterranean Sea (Corsica- Lepoint et al. 2000); and certain macroinvertebrates (bivalves, polychaete, snail, crab, shrimp) from the south-east New Zealand (Leduc et al. 2006) or west Baltic Sea (gastropods, Jephson et al. 2008). The seagrass importance for food webs was rather linked to its ecosystem services in providing a habitat and increasing a number of food sources (by enhanced organic matter deposition, supporting epiphytes growth). Seagrass and particularly eelgrass have a low nutritional value for consumers as it contains a lot of lignin and has high POC/TN ratio (Bucholc et al. 2014). Therefore, in a presence of

variety of other food sources, consumers favor to feed on more easily digestible matter (Hemminga and Duarte 2000) rather than on a fresh seagrass tissues. However, seagrass tissues can enter the food web in a form of a degraded organic matter (Vafeiadou et al. 2013). In this form it can be an important source supporting the benthic food webs as often the biomass of seagrass is remarkably high compared to other primary producers (Kharlamenko et al. 2001, Leduc et al. 2006, Vafeiadou et al. 2013). In the Puck Bay around 40% of organic matter within the seagrass meadows may be of a seagrass origin as well as organic matter of seagrass origin can be also exported to the adjacent bare sands (present study, chapter 4.1). SSOM was indicated by the model as a considerable food source for almost all grazer species (13- 50%, regardless of the habitat) or even as a sole food source for *Hydrobia* spp. from the unvegetated habitat. Considering the remarkable contributions of seagrass to sedimentary pool of organic matter in the studied system (present study, subchapter 4.1.), we can expect that plants support benthic consumers in a detrital form (that is expressed in the plant FA markers presence in both SSOM food source and grazer consumers tissues).

Two species of *Idotea* sampled within seagrass meadows had relatively low contributions of SSOM in the diet (compared to the grazers). These species fed mostly on microphytobenthos/bacteria. Apparently, confronted with high accessibility of microphytobenthos and epiphytes, they preferred to feed selectively on fresh components of the organic matter rather than degraded organic matter of SSOM. Indeed, it was previously reported that *Idotea balthica* from the west Baltic Sea favors to feed on fresh diatoms (Jaschinski et al. 2008).

There was a clear difference in the consumption of epiphytes and microphytobenthos/bacteria between habitats; grazers from the seagrass meadows consumed mostly epiphytes (together with filamentous algae), whereas in the other habitat they rather fed on microphytobenthos/bacteria (according to the model). Epiphytes were the main food sources in the seagrass dominated systems from the west Baltic Sea (SI and FA analysis, Jaschinski et al. 2008) and French Atlantic coastal waters near Roscoff (SI mixing models, Ouisse et al. 2012). Lebreton et al. (2011) indicated microphytobenthos as the main food source (based on SI and FA analysis) in seagrass systems in French Atlantic coastal waters near the Marennes-Oléron Bay. The importance of epiphytes in benthic consumers'

diets differ among the regions and dominant seagrass species. *Posidonia* spp. that dominate in Mediterranean Sea meadows, have large and wide leaves with a lot of surface for epiphytes to grow. Therefore, in these systems epiphytes are the main food sources for several benthic consumers, for example for amphipods (Michel et al. 2014, based on SI and FA analysis). Different situation is observed in the intertidal temperate meadows dominated by *Z. noltii*, characterized by significantly smaller leaves and lower biomass of epiphytes (Lebreton et al. 2009) where microphytobenthos serve as a dominant food source as reported from the Portugese Atlantic coast (Baeta et al. 2009 indicated by SI analysis) and the French Atlantic coast (Lebreton et al. 2011, SI and FA analyses). The biomass of filamentous algae in the Puck Bay seagrass meadows increases dramatically in summer (Jankowska et al. 2014) and several grazer species from the vegetated habitat (*Hydrobia* spp., *R. pergra, T. fluviatilis*) take advantage of the high availability of this food source. Microphytobenthos is rarely considered as a separate potential food source in the benthic food web studies, mostly due to the difficulties to obtain the samples for tracers analyses (Ouisse et al. 2011). However, it has been regarded as a 'hidden garden' of the unvegetated habitats, highly supporting the local zoobenthic communities (Miller et al. 1996). In the shallow sediments of the Puck Bay the high ratio of chlorophyll *a* to POC indicate the high microphytobenthos biomass (present study, chapter 4.2.1) that can provide food for a grazers from the bare (*B. pilosa*) and seagrass seabed (*Gammarus* spp.*, Idotea* spp.).

The *Z. marina* vegetation increased the number of food sources available for grazers in the Puck Bay. The main difference between the two habitats studied was an important contribution of epiphytes in the diet of grazers collected in vegetated habitat. Moreover, while plants were generally food source of a low importance, they had higher contributions to the diets of grazers in seagrass seabed. The present study results correspond to the data obtained in previous studies that compared the grazer diets in the vegetated and unvegetated areas. Hoshika et al. (2006) reported that in the Sea of Japan a diet of grazers inside the meadows were based on epiphytes, while outside the meadows on epilithon. Leduc et al. (2006) documented important contribution of seagrass derived organic matter in grazers' diet in the New Zealand seagrass meadows when compared to sandflats where grazers fed mostly on microphytobenthos. It must be noted, however, that some studies report no effect of seagrass vegetation on benthic food webs, e.g. Vafeiadou et al. (2013)

documented no difference in SI composition of grazers collected in the seagrass meadows and bare sands along the Portuguese Atlantic coast. They concluded that in both habitats grazers fed mostly on sediment organic matter that had similar tracers composition due to the export of seagrass derived organic matter to the adjacent bare sandy bottom areas. Similarly, macrofauna from the *P. oceanica* meadows in the Mediterranean Sea had similar isotopic composition as adjacent epilithic macrofauna communities, thus POM and algal material were the main food source in both communities (Lepoint et al. 2000).

Omnivores

The omnivores had the widest δ^{15}N range (from 5.2‰ in *C. carinata* from the unvegetated to 11.3‰ in *S. typhe* from the vegetated habitat) among all macrobenthic consumer groups. Moreover, the range δ^{13}C values (from -18.9 to -15.5‰) of omnivores in the vegetated habitat varied considerably. Similarly wide ranges of isotopic composition of omnivorous macroinvertebrates were noted in the *Z. noltii* meadows from the French and Portuguese Atlantic coasts (Roscoff, Ouisse et al. 2012, Mondego estuary, Baeta et al. 2009). This phenomena can be linked to a large variety of food sources utilized by omnivores and a wide range of isotopic compositions of primary consumers and primary producers that serve as food for omnivores. Several omnivores had a very high nitrogen isotope ratio compared to species representing the other consumer groups, suggesting they represented the highest trophic level. Moreover, omnivores that fed on organic matter of animal origin contained the highest contribution of 18:1ω9, considered as a marker of both detritus feeding and carnivory (Kelly and Scheibling 2012).

Both meiofauna and macrofauna prey were in different proportions consumed by omnivores from the vegetated bottom (all fish species, *C. carinata* and *Marenzelleria* spp.). Meiofauna was the main food source for *C. carinata* (46%), *Marenzelleria* spp. (55%) and *N. ophidion* (80%), while macroorganisms were main food source for *Pomatoschistus* spp. (69%) and *S. typhe* (75%). In the unvegetated habitat macrofauna prey was the main food source for only one fish species (*Pomatoschistus* spp., 67%). The diet of the same fish taxa in the west Baltic eelgrass meadows was based on sand microflora, epiphytes and red algae according to IsoSource model based on SI composition. However this model did not consider food sources of animal origin (Jaschinski et al. 2008). The fish species collected

within the present study are however, commonly classified as carnivores (Rutkowski 1982). It is supported by the present results of the mixing modelling based on FA and SI composition in their tissues (as model indicated that fish consumed both meio- and macrofaunal organisms). *C. carinata* from seagrass meadows of the Portugal Atlantic coast has been assigned as an active predator (Baeta et al. 2009) and this also agrees with the results of the present study. *Marenzelleria* spp. from the vegetated habitat had high nitrogen isotope ratio (as high as some fish species) indicating a high trophic position, indeed its diet was dominated by meiofauna prey (55%) and macrofauna prey (38%). Contrastingly, *Marenzelleria* spp. from the unvegetated habitat had lower δ^{15}N value and based on modelling its diet was dominated by SSOM (37%) with lower importance of both meio- and macrofauna prey (29% per each source). *Marenzelleria* spp. are effective deposit feeders known to bury deep in the sediment, however feeding on meiobenthic and planktonic organisms has also been noted (Zaiko 2015). The high nitrogen isotope ratio of individuals from seagrass meadows may result from indirect feeding on meiofauna (together with sediment organic matter) but also from the isotope enrichment originating from recycling of N in the benthic food web and greater organismal fractionation by those polychaetes (Karlson et al. 2015). In that study, isotope enrichment of N in polychaetes was most probably caused by high contribution of microbially processed organic matter (Karlson et al. 2015). Higher δ^{15}N value of SSOM in the vegetated habitat was noted in the present study and resulted probably from higher bacteria abundance and biomass compared to the bare bottom (Jankowska et al 2015). That could have induced high δ^{15}N value of *Marenzelleria* spp. from seagrass habitat. Moreover, some polychaetes host symbiotic bacteria in their digestive tract, these bacteria decompose organic matter particles and can be responsible for high δ^{15}N values obtained in the SI analyses of the polychaetes (Djikstra et al. 2008). SSOM served as a main food source for *Palaemon* spp. (50%) from the vegetated habitat as well as it was a main food source for three species (so most of the species) from the unvegetated habitat (*C. carinata* 81%, *H. diversicolor* 64%, *Marenzelleria* spp. 37%). The contribution of plants in the diet was negligible for all species regardless of the habitat. It disagrees with the results of previous reports for *Palaemon* spp. that classified them as a herbivore (Sokołowski 2009).

There was a clear difference in sources utilization by *C. carinata* and *Marenzelleria* spp. between habitats - the species collected in the vegetated habitat were carnivorous whereas those from the unvegetated habitat fed mostly on SSOM. Lower abundance, biomass and diversity of macrofauna was noted for the unvegetated bottom compared to seagrass meadows seabed in the Puck Bay (Włodarska-Kowalczuk et al. 2015), therefore it is possible that the same omnivorous species confronted with high prey accessibility in the vegetated habitat feed as carnivores but shift to deposit feeding in the unvegetated habitat.

Overall, the diet of omnivores from the vegetated habitat was based on carnivory, while omnivores collected in the unvegetated habitat only partly consumed organic matter of animal origin. Low number of predators feeding on mesograzers inhabiting eelgrass meadows was found in the field experiment in the Baltic Sea (Baden et al. 2010). Baeta et al. (2009) stated that the *Zostera* meadows offer protection from the predators, therefore the carnivory and feeding on higher trophic levels are more commonly employed in the unvegetated areas. These results contrast with the more common employment of carnivory by omnivores dwelling in the vegetated habitats of the Puck Bay documented by the present study. Possibly the protective function (protection of prey organisms against predators) of relatively weekly developed seagrass vegetation in the Puck Bay is not effective enough to constrain the omnivores' utilization of abundant prey resources in the vegetated habitat. The high diversity of predators in the vegetated habitat found within this study suggests that this trophic group is likely to exert an important top-down control in the local food web. Similarly intensive feeding of fish on large amphipods was documented in mixed *Zostera* spp. meadows of the Swedish west coast (Moksnes et al. 2008).

Remarks on fatty acids bioconvertion

High amounts of polyunsaturated fatty acids (PUFAs: 20:5ω3, 22:6ω3) was a common feature of FA compositions in macrofaunal consumers that differed in this respect from meiofauna and the potential food sources. It has been suggested that biosynthesis or selective retention of certain FA may be a reason for higher concentration of certain FA in consumers tissues than in food sources (Kelly and Scheibling 2012). Macrofauna was reported to select the longest chain FA (PUFAs) that are used to build their tissues (Kelly and Scheibling 2012). Moreover, some species are known to bioconvert

FA that come from the same trophic pathways into the PUFAs (FA elongation, Kelly and Scheibling 2012). Selective retention and bioconvertion may be also the reason of high level of PUFAs in consumers tissue in the studied habitats. As revealed by mixing models, there is a limited feeding on plants, however the plant derived organic matter can be consumed in SSOM (that is partly of seagrass origin as documented in present study, chapter 4.1). Thus the high contributions of $20:5\omega3$, $22:6\omega3$ in macrofauna consumers may result from the transformation of $18:2\omega6$ and $18:3\omega3$ - FAs that are both common in plant tissues and known to be a precursors of the FA chain elongation (Kelly and Scheibling 2012, Fig. 25).
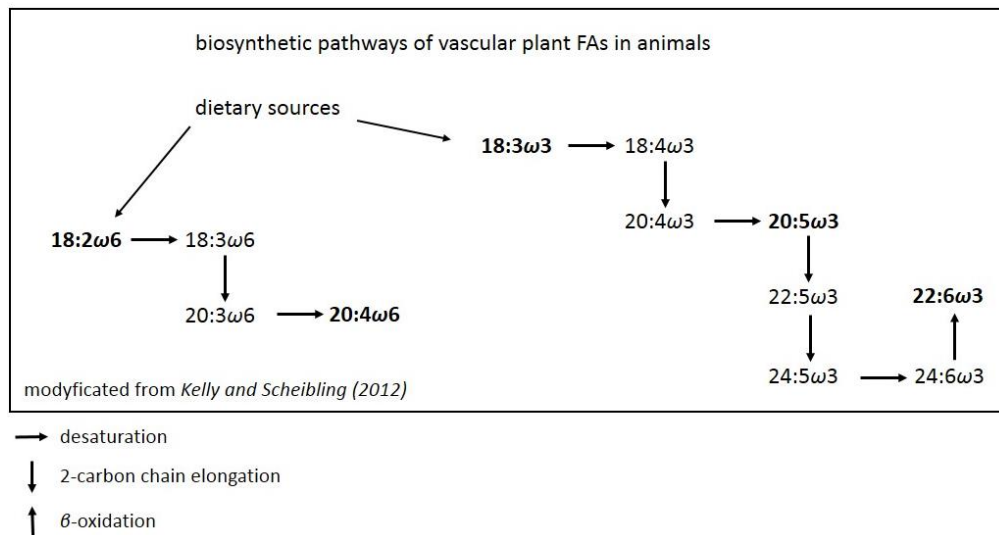
Fig. 25 Biosynthetic pathways of essential FA in animals (modified after Kelly and Scheibling 2012)

Seagrass vegetation effects on the food web structure

In the present study the diet compositions of meiofaunal an macrofaunal consumers were compared in the vegetated and unvegetated benthic habitats in the Puck Bay. Little evidence of direct consumption of seagrass tissues was documented, still the seagrass vegetation could impact the benthic food web functioning in several indirect ways: by increasing number of food sources utilized by meiofauna copepods and macrofaunal grazers (i.e. epiphytes consumed mostly by copepod *T. discipes* in the vegetated habitat, plants and epiphytes consumed by grazers only from the vegetated habitat) and supporting

larger standing stocks of prey organism and thus increasing the feeding at higher trophic levels in omnivores (indicated by higher number of carnivorous species as well as higher meiofauna and macrofauna prey consumption in the vegetated habitat).

Presently, few studies compared benthic food web structure in communities inhabiting seagrass meadows and the adjacent bare seabed. The patterns of differences between the vegetated and unvegetated habitats varied among studied localities. The study of SI composition in macrofauna consumers in the Sea of Japan showed that diet of crustaceans and fish inside the *Z. marina* meadows was based on epiphytes growing on seagrass leaves, whereas the same macrofaunal species dwelling outside the meadows fed on epilithon (Hoshika et al. 2006). Another study using three isotopes (δ^{13}C, δ^{15}N, δ^{34}S) and IsoSource modelling in the *Z. capricorni* meadows off New Zealand, showed that all invertebrates (deposit feeders, grazers, omnivores) except of suspension feeders from seagrass meadows had important contribution of seagrass derived organic matter (coming both from direct or indirect consumption) in their diet, while the same trophic groups from sandflats fed mostly on microphytobenthos (Leduc et al. 2006). On the other hand, several studies reported no difference in the food webs structure between the vegetated and unvegetated habitats. The macrofaunal suspension feeders, grazers and omnivores in the Mediterranean *P. oceanica* meadows and adjacent epilithic seabed had the same main food sources (POM for suspension feeders, algal material for the other groups) and the only invertebrates that consumed *P. oceanica* tissue were sea cucumbers (SI analysis, Lepoint et al. 2000). Similar trophic preferences of macrobenthic suspension feeders and omnivores inhabiting the bare sands and *Z. noltii* vegetated sediments have been documented along the Portugese Atlantic coast (SI analysis, Baeta et al. 2009). Another study using SI analysis and mixing models, showed no differences in resource uptake by macrofaunal bivalves, polychaetes and crabs in seagrass and the adjacent bare sites in the *Z. noltii* meadows from the Portugese Atlantic coast (Vafeiadou et al. 2013). In the same system no differences in resource uptake was noted for meiofauna nematodes and copepods (Vafeiadou et al. 2014). The study of meiofauna nematodes and copepods diet in the *Z. muelleri* from southeast New Zealand (using both FA and SI) showed that microphytobenthos was the most important food source for meiofauna communities regardless of the habitat under study (Leduc et al. 2009).
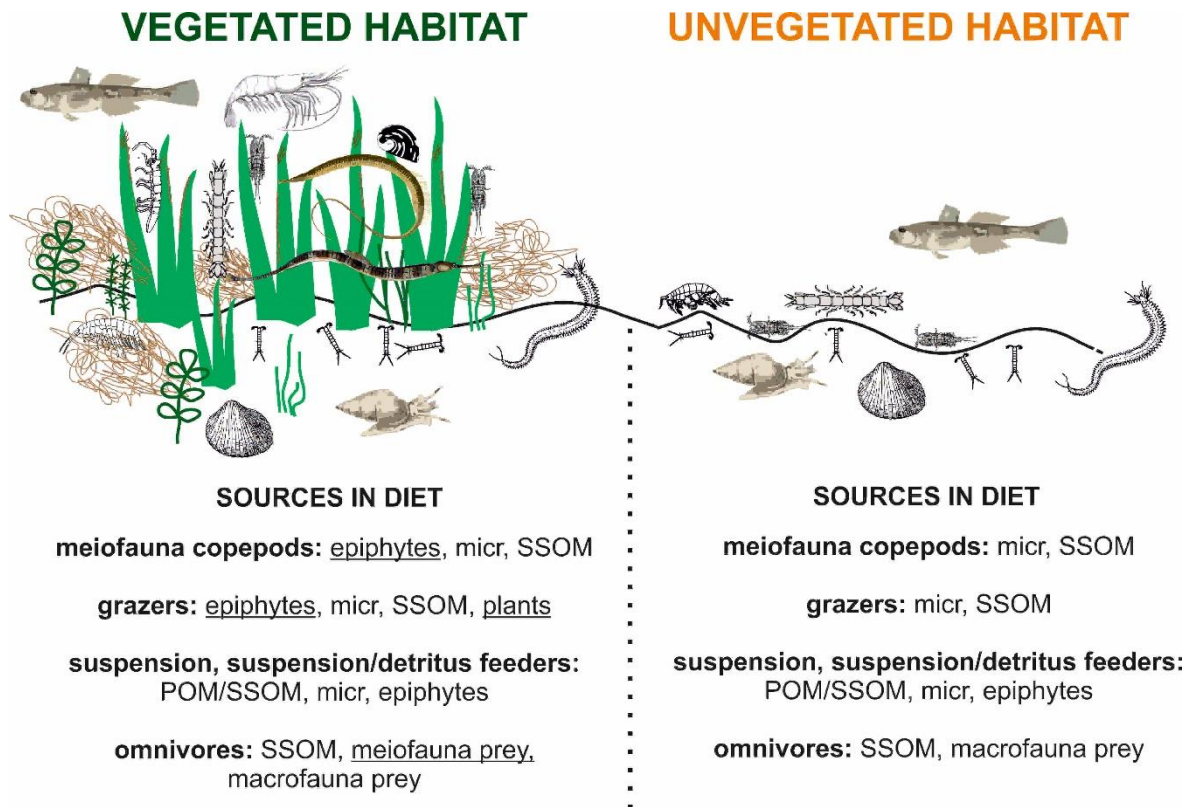
Fig. 26 Illustration of benthic food webs in vegetated and unvegetated habitat in the Puck Bay. Underlined source represents the one utilized only in vegetated habitat (as revealed by MixSIAR)

Bacteria, meiofauna and macrofauna trophic interactions

There are three major carbon transfer pathways considered in a marine benthic food web theory - herbivorous, detrital and microbial (Oevelen et al. 2006). The microbial loop was formalized as the transfer of a dissolved organic matter assimilated by bacteria which are grazed by higher trophic levels both directly (bacterial uptake by selective grazing) and/or indirectly (deposit feeding meiofauna and macrofauna) (Pusceddu et al. 2009). The study from the Adriatic Sea proved that transfer of an organic carbon to higher trophic levels depends on benthic bacteria ability to convert the carbon into bacterial biomass (Manini et al. 2003). However, only very low grazing on benthic bacteria in the North Sea estuarine systems (Van Oevelen et al. 2006) and in the Arabian Sea (Pozzato et al. 2012) has been documented, therefore, bacterial production was regarded to be a carbon sink

rather than an effective link to higher trophic levels in the coastal food webs. So far there are few experimental studies proving direct consumption of bacteria by meiofauna (De Troch et al. 2005, Cnudde et al. 2013).

The assessment of diet composition in meiofauna and macrofaunal consumers presented in this study gives some clues to the understanding of carbon flow pathways through the Puck Bay trophic webs, in particular the pathways of bacterial carbon transfer (Fig. 27).

BACTERIAL CARBON FLOW
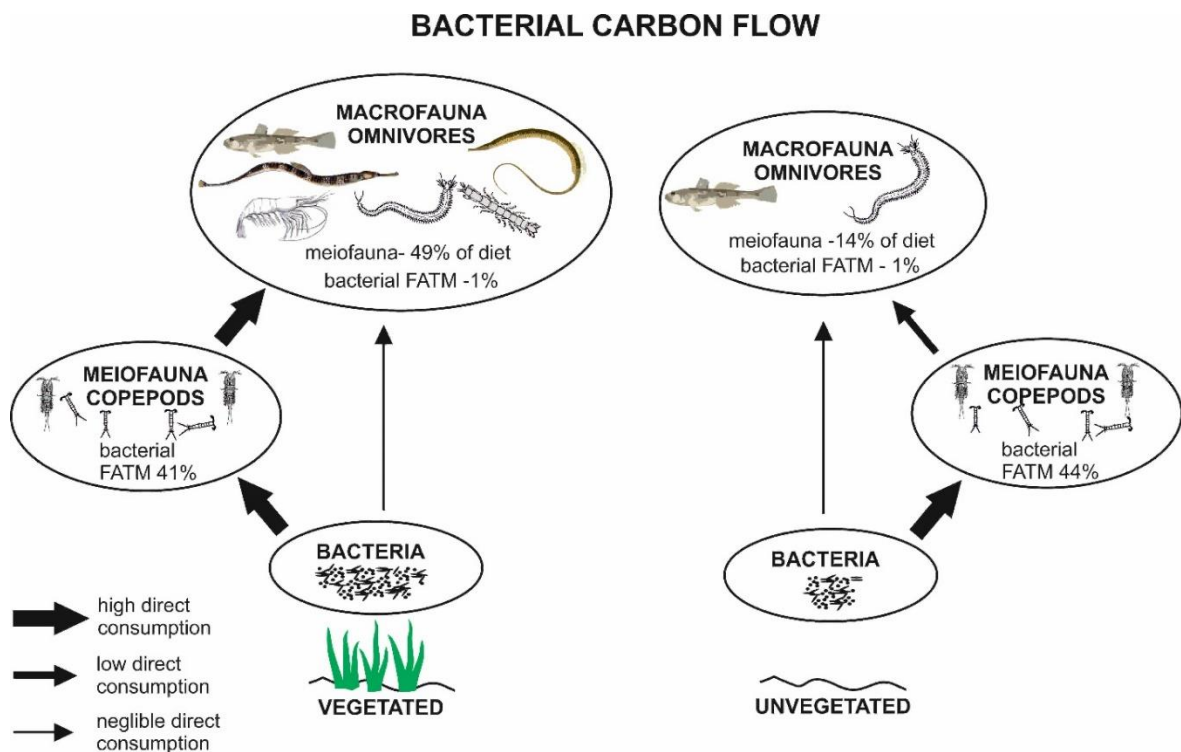
Fig. 27   Scheme of bacterial carbon flow in benthic food webs in vegetated and unvegetated habitats. The bacterial FA trophic marker contribution in consumers tissues indicates the level of direct consumption of bacteria, contribution of meiofauna to omnivores indicates the level of carbon flow between these two benthic groups diet (estimated by MixSIAR model)

High amount of bacterial FATM ($18:1\omega7$) in harpacticoid copepods indicated intensive grazing on bacteria. In contrast to meiofauna, the bacterial FATM contribution in macrofauna consumers never exceeded 3% indicating no or very low direct consumption of

bacteria cells by macroinvertebrates. These results were consistent for two studied habitats and suggested that different food sources were utilized by meiofauna and macrofauna. Food sources uptake may depend on the size of the organisms. Meiofauna feeds on small particles and can be very selective in feeding (Leduc et al. 2009, De Troch et al. 2012), whereas macrofauna feeds on bigger particles (detritus, microphytobenthos, plants, Leduc et al. 2006). The trophic relationships between bacteria and meiofauna in the Puck Bay are also supported by the correlation between abundance and biomass of these two groups documented both in the Puck Bay (Jankowska et al. 2015) and in other coastal localities (Albertelli et al. 1999, Papageorgiou et al. 2007).

Even thought, the direct bacteria consumption by macrofauna was low or lacking, the transfer of bacterial carbon to higher trophic levels occurred through meiofauna copepods. Meiofauna is a high-quality food source (Giere 2006) and is likely to represent an important link between primary and microbial production and higher trophic levels. Harpacticoid copepods are also the second dominant taxa of meiofauna in the study area (Jankowska et al. 2014). Harpacticoid copepods in shallow sandy sediments of the New Zealand have been recognized as an important food item for juvenile flatfish (Hicks 1984). In the present study, meiofauna copepods was an important food source for omnivores, thus it provided a link between microbes and the upper trophic levels. Higher predation on meiofauna (both more omnivore species feeding on copepods and higher contributions of copepods food source in omnivore diets) and more effective transfer of bacterial carbon to higher trophic levels were noted rather in the vegetated than in the unvegetated habitat. Overall, our results suggest that in the Puck Bay, bacterial carbon enters the food web through meiofauna to macrofauna and fish and does not support the notion of bacterial production being a carbon sink as suggested by Van Oevelen et al. (2006) and Pozzato et al. (2012).

5. Conclusions

The main conclusion of the thesis is that despite of the relatively low densities of the macrophyte vegetation, the *Z. marina* meadows considerably change the functioning of the benthic system in the Gulf of Gdańsk.

The effects of vegetation on the sediment characteristics in the studied region were similar to those reported from the other, better developed seagrass systems. However, the values of carbon storage estimated in this study represented the lower end of the worldwide observations range and carbon accumulation rates were the lowest ever reported.

The eelgrass vegetation modifies the food web structure and increases its complexity by providing more food sources and supporting higher standing stocks of consumers and predators. Assessing the contribution of each potential food source to diets of meiofauna and macrofauna taxa in a quantitative way was possible due to use of Bayesian models based on biochemical markers (stable isotopes of carbon and nitrogen, fatty acids).

The most important effects of eelgrass vegetation observed within this study included:

1. enhancement of organic carbon and photosynthetic pigments content in the vegetated sediments (compared to the unvegetated areas)

2. significant contributions of seagrass originating organic matter to sediment organic carbon pool (40% in the vegetated sediments, 14% in the neighboring unvegetated sediments)

3. **modification of food web structure by increasing a number of available and consumed food sources (epiphytes consumed by meiofauna and macrofauna grazers in the vegetated habitat), higher significance of carnivory in diets of omnivorous macrofauna (probably due to higher availability of prey organisms) and higher flow of bacteria-derived organic matter through the metazoan trophic chains in vegetated systems.**

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APPENDIX

Table AI Sediment characteristics of 10 cm sediment profiles collected at two bottom types and three locations

POC	$\delta^{13}C$	$\delta^{15}N$	POC/TN	Chl a	Pheo	Chl a/POC	Chl a/CPE	CPE	layers	habitat	location
0.09 ± 0.07	-21.48 ± -2.36	4.41 ± 0.60	2.11 ± 0.42	11.69 ±4.92	5.01 ±2.76	134.37 ± 68.02	69.90 ± 64.07	16.65 ±7.67	0-2	**veg**	**Inner**
0.21 ± 0.26	-22.24 ± -2.94	3.04 ±2.17	4.51 ± 2.37	2.92 ± 2.62	4.69 ± 5.14	14.05 ± 10.23	38.22 ± 6.85	7.60 ± 7.75	2-4		
0.19 ± 0.23	-19.80 ± -0.79	2.92 ±1.50	5.03 ± 2.10	2.71 ± 2.71	4.26 ± 4.64	14.04 ± 11.98	38.74 ± 36.85	6.96 ± 7.35	4-6		
0.18 ± 0.20	-20.82 ± -0.08	1.28 ± 1.15	6.94 ± 0.39	0.57 ± 0.21	2.14 ± 1.74	3.21 ± 1.05	21.01 ± 10.68	2.72 ± 1.94	6-8		
0.14 ± 0.16	-22.10 ± -2.27	2.58 ± 2.95	4.80 ± 0.82	0.34 ± 0.07	1.07 ± 0.62	2.42 ± 0.44	24.10 ± 10.26	1.42 ± 0.69	8-10		
0.05 ± 0.02	-16.60 ± -3.30	1.81 ± 0.60	3.35 ± 1.26	5.10 ± 1.99	1.81 ± 0.13	95.53 ± 83.14	73.70 ± 13.71	6.89 ± 2.12	0-2	**unveg**	
0.06 ± 0.03	-17.09 ± -4.46	0.67 ± 0.48	4.54 ± 0.84	3.54 ± 1.36	1.77 ± 0.01	54.73 ± 39.09	66.50 ± 19.38	5.30 ± 1.37	2-4		
0.05 ± 0.02	-17.82 ± -3.71	0.29 ± 0.21	4.62 ± 1.57	1.89 ± 0.51	1.22 ± 0.25	36.12 ± 22.20	60.68 ± 67.06	3.10 ± 0.76	4-6		
0.06 ± 0.02	-17.28 ± -4.29	2.53 ± 2.27	5.63 ± 0.95	1.57 ± 0.36	1.14 ± 0.11	26.71 ± 14.67	57.77 ± 76.51	2.71 ± 0.47	6-8		
0.04 ± 0.00	-17.15 ± -5.19	4.88 ± 2.41	6.08 ± 1.19	1.43 ± 0.09	1.11 ± 0.19	33.80 ± 25.84	56.21 ± 32.83	2.54 ± 0.29	8-10		
0.05 ± 0.00	-19.90 ± -0.54	4.52 ± 0.22	2.60 ± 0.08	10.31 ± 1.44	11.82 ± 11.53	224.24 ± 93.21	46.59 ± 11.13	22.13 ± 12.97	0-2	**veg**	**Outer**
0.04 ± 0.00	-20.11 ± -0.69	2.53 ± 0.09	3.32 ± 0.09	4.60 ± 2.23	7.12 ± 8.29	125.14 ± 56.86	39.16 ± 21.20	11.71 ± 10.52	2-4		
0.03 ± 0.00	-20.10 ± -0.92	2.09 ± 1.18	2.70 ± 0.12	3.76 ± 1.45	1.84 ± 0.80	120.75 ± 21.73	67.12 ± 64.38	5.61 ± 2.25	4-6		
0.03 ± 0.00	-20.30 ± 0.89	1.44 ± 0.97	4.05 ± 2.43	1.76 ± 1.14	1.89 ± 0.93	61.04 ± 39.01	48.27 ± 55.19	3.65 ± 2.07	6-8		
0.03 ± 0.00	-20.58 ± -0.09	4.74 ± 4.61	5.23 ± 1.86	1.51 ± 1.19	1.81 ± 0.93	48.23 ± 39.38	45.52 ± 56.25	3.33 ± 2.12	8-10		
0.03 ± 0.02	-19.67 ± -2.17	2.76 ± 1.72	7.41 ± 6.02	6.19 ± 6.70	1.48 ± 1.60	207.87± 40.93	80.6 ± 0.46	7.69 ± 8.30	0-2	**unveg**	
0.02 ± 0.01	-20.95 ± -0.63	1.76 ± 1.03	3.95 ± 1.62	3.65 ± 3.44	1.14 ± 0.93	164.55 ± 61.24	76.26 ± 4.78	4.80 ± 4.37	2-4		
0.02 ± 0.01	-20.88 ± -1.63	2.00 ± 0.43	3.94 ± 2.14	3.12 ± 2.44	0.95 ± 0.60	157.62 ± 36.86	76.68 ± 4.89	4.09 ± 3.04	4-6		
0.02 ± 0.00	-20.94 ± -1.00	1.38 ± 0.58	4.37 ± 0.66	2.04 ± 0.83	0.70 ± 0.23	112.16 ± 28.95	74.45 ± 1.92	2.75 ± 1.07	6-8		
0.02 ± 0.00	-21.45 ± -0.54	1.41 ± 1.41	4.16 ± 1.37	0.99 ± 0.67	0.67 ± 0.14	50.80 ± 10.89	59.72 ± 22.36	1.66 ± 0.81	8-10		
0.11 ± 0.08	-17.36 ± -2.80	5.74 ± 0.07	6.39 ± 2.90	13.30 ± 4.25	6.93 ± 5.20	120.52 ± 54.07	65.75 ± 44.97	20.22 ± 9.46	0-2	**veg**	**GS**
0.12 ± 0.07	-17.05 ± -1.09	3.64 ± 3.64	6.59 ± 2.09	6.56 ± 4.36	3.72 ± 1.28	55.02 ± 58.27	63.83 ± 77.36	10.26 ± 5.63	2-4		
0.12 ± 0.07	-19.64 ± -0.29	1.89 ± 2.67	9.37 ± 13.35	2.47 ± 1.69	1.88 ± 0.55	19.82 ± 23.88	56.82 ± 75.46	4.34 ± 2.24	4-6		
0.10 ± 0.05	-21.33 ± -5.50	1.90 ± 2.68	9.71 ± 12.14	3.36 ± 1.42	2.97 ± 1.37	34.21 ± 28.55	53.08 ± 50.92	6.32 ± 2.80	6-8		
0.13 ± 0.12	-20.28 ± -7.37	0.49 ± 0.69	4.85 ± 0.29	2.39 ± 2.71	1.28 ± 0.23	18.73 ± 22.46	65.03 ± 92.20	3.66 ± 2.93	8-10		
0.04 ± 0.04	-17.64 ± 0.09	0.44 ± 0.05	5.67 ± 0.95	5.51 ± 1.68	1.58 ± 0.38	150.01 ± 28.82	77.74 ± 2.64	7.08 ± 2.06	0-2	**unveg**	
0.04 ± 0.02	-18.12 ± 1.76	1.07 ± 1.52	4.97 ± 2.07	4.80 ± 0.00	1.32 ± 0.05	133.03 ± 0.56	78.44 ± 0.88	6.12 ± 0.05	2-4		
0.03 ± 0.03	-16.04 ± 1.75	0.42 ± 0.59	4.83 ± 0.31	3.88 ± 0.44	1.30 ± 0.34	116.91 ± 14.54	74.84 ± 7.10	5.19 ± 0.68	4-6		
0.04 ± 0.03	-16.74 ± 2.34	0.56 ± 0.80	4.89 ± 0.17	3.04 ± 2.29	0.97 ± 0.40	78.27 ± 18.44	75.71 ± 10.01	4.01 ± 2.69	6-8		
0.04 ± 0.04	-16.20 ± 1.37	1.55 ± 2.20	6.39 ± 1.02	3.97 ± 2.10	1.51 ± 0.10	107.14 ± 27.60	72.44 ± 15.07	5.48 ± 2.20	8-10		

Table AII Carbon and nitrogen stable isotopes ratios (‰) in the potential sources (mean ± st.dev.) and sediments at two bottom types and three localities. Sources abbreviations: POM-particulate organic matter, plants – mean of *Z. marina* leaves and roots and *R matirima* (see chapter 2, subchapter 2.4.1.)

sources		δ^{13}C	δ^{15}N
Z .marinaa **detritus**		-11.29 ± 0.76	6.32 ± 0.35
P. perfoliatus		-14.40 ± 3.08	7.74 ± 1.04
P. pectinatus		-9.52 ± 0.52	6.13 ± 0.52
R. maritima		-10.40 ± 0.10	7.91 ± 0.37
Z. marinaa **leaves**		-9.91 ± 1.52	8.40 ± 1.51
Z. marinaa **roots**		-10.60 ± 0.46	8.38 ± 1.61
plants		-10.32 ± 0.77	7.52 ± 1.08
P. litoralis		-22.00 ± 0.83	7.50 ± 0.88
Polysiphonia **spp.**		-25.22 ± 0.23	8.10 ± 0.65
Cladophora **spp.**		-22.83 ± 1.39	8.30 ± 1.22
epiphytes		-21.83 ± 2.62	7.47 ± 0.42
POM		-23.23 ± 1.31	6.23 ± 0.81
sediments			
vegetated	**GS**	-19.29 ± 8.18	5.88 ± 0.34
	Inner	-20.14 ± 1.21	3.56 ± 0.65
	Outer	-19.12 ± 0.90	3.69 ± 0.63
unvegetated	**GS**	-18.05 ± 1.64	3.39 ± 1.46
	Inner	-18.27 ± 1.86	1.85 ± 0.39
	Outer	-19.27 ± 0.71	2.59 ± 1.34

Table AIII Mean (± st.dev.) FA composition (mass%) in the food sources. FA are grouped into SAFA (saturated fatty acids), MUFA (monounsaturated fatty acids) and PUFA (polyunsaturated fatty acids). Contributions of FATM (Table 2) are also presented

	FA	*Z. palustris*	*Myriophyllum* sp.	*P. pectinatus*	*Ch. baltica*	*Z. marina* leaves	*Z. marina* roots	plants together	filamentous algae	micr	epiphytes	SSOM veg	SSOM unveg	POM
SAFA	14:00	0.22 ± 0.00	0.24 ± 0.03	1.21 ± 0.04	2.09 ± 1.42	0.19 ± 0.01	0.61 ± 0.13	0.81 ± 0.95	2.43 ± 3.11	0.49 ± 0.00	6.66 ± 9.07	8.58 ± 1.84	5.66 ± 0.20	3.54 ± 2.91
	16:00	0.56 ± 0.00	2.70 ± 1.32	1.45 ± 0.11	0.86 ± 0.18	1.05 ± 0.27	4.94 ± 1.94	1.94 ± 1.65	0.94 ± 0.05	1.41 ± 0.00	13.36±18.39	1.92 ± 0.47	1.75 ± 0.01	7.6 ± 7.86
	18:00	0.56 ± 0.00	1.08 ± 0.02	0.87 ± 0.03	3.52 ± 1.06	4.28 ± 0.13	0.16 ± 0.23	2.09 ± 1.72	7.89 ± 0.14	0.33 ± 0.00	1.95 ± 2.21	0.76 ± 0.42	0.48 ± 0.16	10.34 ± 14.72
	22:00	0.04 ± 0.00	0.27 ± 0.09	1.19 ± 0.09	3.36 ± 4.05	2.31 ± 1.62	1.49 ± 2.06	1.66 ± 2.17	6.73 ± 0.25	1.21 ± 0.00	5.32 ± 6.80	2.32 ± 4.43	1.71± 1.27	5.42 ± 9.55
	24:00:00	1.36 ± 0.00	0.77 ± 0.65	1.74 ± 0.12	0.22 ± 0.19	0.20 ± 0.35	2.43 ± 3.44	0.95 ± 1.31	0.00 ± 0.00	0.15 ± 0.00	0.52 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.09
	∑SAFA	2.79	5.05	6.47	10.05	8.03	9.63	7.46	17.99	3.6	27.8	13.58	9.6	26.98
MUFA	16:1ω7	0.07 ± 0.00	0.33 ± 0.03	0.68 ± 0.02	1.63 ± 1.70	0.27 ± 0.21	0.18 ± 0.25	0.60 ± 0.89	4.04 ± 0.24	0.49 ± 0.00	1.17 ± 0.95	19.47 ± 0.09	14.85 ± 1.85	1.03 ± 1.05
	18:1ω7	7.22 ± 0.00	0.35 ± 0.21	0.88 ± 0.04	0.58 ± 0.10	0.49 ± 0.01	0.60 ± 0.30	1.03 ± 1.79	0.33 ± 0.01	41.02 ± 0.00	3.18 ± 1.39	19.11 ± 4.17	16.41 ± 2.67	1.87 ± 0.90
	18:1ω9	0.56 ± 0.00	0.79 ± 0.17	1.37 ± 0.05	1.55 ± 0.69	0.72 ± 0.06	1.64 ± 0.30	1.13 ± 0.52	8.34 ± 0.46	6.35 ± 0.00	4.89 ± 1.68	5.61 ± 0.00	6.77 ± 2.56	3.71 ± 1.45
	∑MUFA	7.85	1.47	2.92	3.76	1.48	2.41	2.76	12.71	47.86	9.25	44.19	38.02	6.61
PUFA	18:2ω6	66.33 ± 0.00	53.09 ± 25.94	61.56 ± 0.09	25.65 ± 13.01	59.85±0.38	30.57 ± 5.96	47.60 ± 19.40	3.34 ± 0.22	8.14 ± 0.00	7.05 ± 1.25	6.19 ± 3.33	7.41 ± 2.06	7.28 ± 2.75
	18:3ω3	0.98 ± 0.00	16.75 ± 27.40	1.29 ± 0.13	10.31 ± 10.11	0.56 ± 0.19	10.75 ± 1.21	7.71 ± 13.03	0.67 ± 0.09	0.72 ± 0.00	1.73 ± 1.65	3.25 ± 4.43	0.47 ± 0.47	2.96 ± 2.12
	20:5ω3	0.26 ± 0.00	1.06 ± 0.76	0.76 ± 0.11	10.24 ± 0.32	0.51 ± 0.22	16.04 ± 21.38	4.95 ± 8.55	36.17 ± 1.90	2.04 ± 0.00	14.48 ± 0.94	2.54 ± 2.60	4.01 ± 1.81	5.18 ± 1.67
	20:4ω6	0.43 ± 0.00	0.25 ± 0.23	0.39 ± 0.08	6.81 ± 4.96	0.27 ± 0.17	0.89 ± 0.67	1.78 ± 3.36	0.27 ± 0.04	2.29 ± 0.00	0.48 ± 0.24	1.66 ± 2.34	1.73 ± 0.31	3.79 ± 6.67
	22:6ω3	0.74 ± 0.00	0.46 ± 0.00	0.62 ± 0.06	0.08 ± 0.00	0.00 ± 0.00	3.75 ± 3.88	0.94 ± 1.40	0.00 ± 0.00	1.35 ± 0.00	1.20 ± 0.43	0.00 ± 0.00	0.07 ± 0.10	5.27 ± 2.22
	∑PUFA	68.74	71.6	64.63	53.09	61.18	61.99	62.75	40.44	14.55	24.94	13.64	13.7	24.48
	Others	20.06 ± 0.00	21.22 ± 0.82	24.38 ± 0.05	30.57 ± 1.02	27.65 ± 1.15	22.66 ± 4.83	24.15 ± 2.85	37.91 ± 0.35	32.31 ± 0.00	37.14 ± 3.08	37.66 ± 12.90	41.99 ±13.19	39.83 ± 6.25
FATM	bacteria	7.44 ± 000	0.58 ± 0.24	2.09 ± 0.08	2.67 ± 1.43	0.68 ± 0.21	1.20 ± 0.43	2.44 ± 2.58	2.77 ± 3.10	41.51 ± 0.00	9.84 ± 10.46	27.69 ± 7.44	22.07 ± 7.60	5.41 ± 3.21
	diatoms	0.90 ± 0.00	4.10 ± 2.08	2.88 ± 0.20	12.73 ± 2.07	1.82 ± 0.50	21.15 ± 19.19	7.26 ± 8.03	41.15 ± 2.19	3.95 ± 0.00	29.01 ± 20.29	23.93 ± 0.38	20.60 ± 7.00	13.82 ± 7.13
	flagellates	0.74 ± 0.00	0.46 ± 0.00	0.62 ± 0.06	0.08 ± 0.00	0.00 ± 0.00	3.75 ± 3.88	0.94 ± 1.40	0.00 ± 0.00	1.35 ± 0.00	1.20 ± 0.43	0.00 ± 0.00	0.07 ± 0.10	5.27 ± 2.22
	detritus	1.12 ± 0.00	1.87 ± 0.19	2.24 ± 0.02	5.08 ± 0.80	5.00 ± 0.19	1.80 ± 0.53	2.85 ± 1.73	13.80 ± 0.32	6.68 ± 0.00	6.84 ± 0.53	6.37 ± 3.43	7.25 ± 4.45	14.05 ± 14.95
	vascular plants	67.31 ± 0	69.83 ± 1.48	62.87 ± 0.05	35.96 ± 2.90	60.41± 0.38	41.32 ± 7.17	56.28 ± 14.16	4.00 ± 0.31	8.86 ± 0.00	8.79 ± 0.40	9.45 ± 2.08	7.89 ± 4.91	10.24 ± 4.62
	terrestrial	1.40 ± 0	1.04 ± 0.74	2.93 ± 0.21	3.58 ± 3.87	2.51 ± 1.27	3.92 ± 1.38	2.56 ± 1.16	6.73 ± 0.25	1.36 ± 0.00	5.84 ± 6.92	2.32 ± 1.64	1.71 ± 1.21	5.50 ± 9.62

Table AIV Carbon and nitrogen stable isotopes ratios (‰) of sources (mean ± st.dev). Sources abbreviations: micr- bacteria and microphytobenthos, SSOMveg- surface sediment organic matter at the vegetated habitat, SSOMunveg- surface sediment organic matter at the unvegetated habitat, POM- particulate organic matter

sources	δ^{13}C	δ^{15}N
Ch. baltica	-11.43 ± 0.17	3.43 ± 0.02
Myriophyllum spp.	-11.04 ± 0.04	4.48 ± 0.18
P. pectinatus	-9.39 ± 0.04	5.01 ± 0.31
Z. palustris	-10.32 ± 0.01	4.99 ± 0.22
Z. marina leaves	-10.66 ± 0.07	6.62 ± 0.19
Z. marina roots	-10.52 ± 0.03	6.15 ± 0.11
plants	-10.56 ± 0.66	5.11 ± 1.09
filamentous algae	-18.69 ± 0.09	6.43 ± 0.20
micr	-15.25 ± 0.1	1.63 ± 0.0
epiphytes	-19.32 ± 0.45	4.69 ± 0.26
SSOMveg	-20.95 ± 0.29	3.49 ± 1.23
SSOMunveg	-21.34 ± 0.65	1.01 ± 0.63
POM	-23.47 ± 1.71	3.25 ± 0.46

Table AV Mean ± st.dev. of fatty acids composition (mass%) in the consumers (meiofauna, macrofauna) collected in two habitats (veg –vegetated, unveg - unvegetated). FA are grouped into SAFA (saturated fatty acids), MUFA (monounsaturated fatty acids) and PUFA (polyunsaturated fatty acids). Contributions of FATM (FA classified as makers of different food sources (according to literature, Table 2) are also presented

	FA	*P. spinicauda*		*T. discipes*		suspension feeders		suspension/detritus feeders		grazers		omnivores	
		veg	unveg	veg	unveg	veg	unveg	veg	unveg	veg	unveg	veg	unveg
SAFA	14:00	1.44 ± 1.51	0.89 ± 0.54	0.88 ± 0.74	0.71 ± 0.66	2.99 ± 1.46	2.22 ± 1.35	3.05 ± 1.17	2.28 ± 1.62	2.41 ± 1.80	2.36 ± 1.35	1.23 ± 1.11	1.89 ± 2.50
	16:00	3.01 ± 2.99	6.90 ± 4.19	13.15 ± 5.90	7.85 ± 6.29	4.57 ± 4.18	2.05 ± 0.41	2.57 ± 0.62	0.87 ± 0.67	7.07 ± 5.57	19.59 ± 10.57	3.58 ± 4.92	6.47 ± 3.79
	18:00	0.0 ± 0.0	1.01 ± 0.00	1.50 ± 1.30	1.10 ± 0.51	0.97 ± 0.46	2.51 ± 1.97	1.05 ± 0.08	1.14 ± 1.44	4.54 ± 6.42	1.74 ± 2.84	1.70 ± 3.19	3.40 ± 2.62
	22:00	0.38 ± 0.66	0.47 ± 0.41	2.65 ± 0.12	0.71 ± 0.64	4.65 ± 2.47	2.90 ± 2.40	6.64 ± 0.66	2.83 ± 2.37	544 ± 4.17	4.12 ± 3.95	2.92 ± 2.66	3.81 ± 3.25
	24:00:00	0.00 ± 0.00	0.31 ± 0.27	0.49 ± 0.42	0.48 ± 0.27	0.65 ± 0.69	0.35 ± 0.48	2.26 ± 1.61	1.02 ± 1.53	0.76 ± 1.75	0.49 ± 0.62	0.75 ± 1.95	1.14 ± 1.89
	∑SAFA	4.83	9.58	18.67	10.37	13.84	10.03	15.57	8.14	20.22	28.3	10.17	16.7
MUFA	16:1ω7	0.60 ± 1.05	2.10 ± 0.71	6.12 ± 5.58	0.25 ± 0.27	4.32 ± 3.46	3.10 ± 0.71	4.56 ± 1.14	3.59 ± 5.24	1.91 ± 3.16	0.86 ± 0.36	3.59 ± 3.91	3.07 ± 2.82
	18:1ω7	70.68 ± 14.92	36.98 ± 31.58	11.25 ± 18.09	49.57 ± 9.94	0.76 ± 0.84	2.13 ± 2.00	0.37 ± 0.26	0.38 ± 0.14	1.24 ± 1.11	2.62 ± 3.01	1.16 ± 2.30	1.23 ± 1.08
	18:1ω9	0.86 ± 1.49	17.50 ± 27.40	22.16 ± 18.11	2.25 ± 1.67	3.94 ± 3.16	4.00 ± 1.67	2.30 ± 0.08	7.32 ± 5.21	8.97 ± 5.27	6.10 ± 4.79	14.10 ± 6.32	6.21 ± 2.45
	∑MUFA	72.14	56.58	39.53	52.07	9.01	9.23	7.23	11.29	12.12	9.58	18.85	10.51
PUFA	18:2ω6	0.00 ± 0.00	0.24 ± 0.21	1.02 ± 0.51	0.64 ± 0.55	6.19 ± 4.30	4.27 ± 3.79	2.93 ± 0.62	6.85 ± 3.73	8.86 ± 3.90	6.10 ± 4.79	5.24 ± 3.76	5.31 ± 4.18
	18:3ω3	0.00 ± 0.00	0.57 ± 0.35	1.59 ± 0.59	2.18 ± 0.86	3.05 ± 1.85	3.13 ± 1.38	3.78 ± 0.87	3.40 ± 0.57	1.64 ±1.51	1.29 ±1.07	1.55 ± 2.00	2.23 ± 2.55
	20:4ω6	0.00 ± 0.00	2.37 ± 2.81	0.49 ± 0.46	3.40 ± 5.24	3.49 ± 3.33	4.40 ± 4.00	3.05 ± 2.83	2.83 ± 2.24	2.84 ± 4.38	5.41 ± 6.40	1.03 ± 1.73	4.60 ± 4.41
	20:5ω3	2.10 ± 2.86	2.26 ± 1.64	3.12 ± 4.55	2.18 ± 1.35	13.50± 5.39	11.60 ± 2.68	15.00 ± 0.94	10.89 ± 2.85	19.70 ± 5.16	15.31 ± 7.47	15.27 ± 6.79	19.80 ± 8.72
	22:6ω3	5.28 ± 6.02	12.35 ± 3.40	13.89 ±11.45	14.40 ± 6.20	23.10 ± 9.41	28.99 ± 6.33	22.62 ± 5.96	26.67 ± 5.18	5.13 ± 3.20	8.74 ± 5.95	16.85 ± 8.79	11.82 ± 8.53
	∑PUFA	7.38	17.79	20.11	22.8	49.33	52.39	47.38	50.64	38.17	35.75	39.94	43.75
	Others	15.65 ± 3.09	16.54 ± 0.32	20.93 ± 4.19	15.66 ± 1.62	31.92± 4.01	32.59 ± 3.88	30.67 ± 4.12	28.53 ± 6.77	31.70 ± 4.79	31.29 ± 5.83	30.84 ± 3.22	32.66 ± 5.76
FATM	bacteria	72.18 ± 14.64	37.86 ± 31.85	12.13 ± 18.78	50.28 ± 10.41	3.75 ± 1.72	4.35 ± 3.28	3.41 ± 1.43	2.66 ± 1.70	3.65 ± 2.11	4.98 ± 2.78	2.39 ± 2.66	3.11 ± 2.79
	diatoms	8.57 ± 6.75	11.26 ± 2.50	22.37 ± 10.41	10.27 ± 6.53	22.39± 7.13	16.75 ± 2.42	22.14 ± 0.82	18.36 ± 6.35	28.68 ± 8.30	35.76 ± 6.15	22.44 ± 8.01	29.35 ± 8.11
	flagellates	5.28 ± 6.02	12.35 ± 3.40	13.89 ± 11.45	14.40 ± 6.20	23.10 ± 9.41	28.99 ± 6.33	22.62 ± 5.96	26.67 ± 5.18	5.13 ± 3.20	8.74 ± 5.95	16.85 ± 8.79	11.82 ± 8.53
	detritus	2.59 ± 0.02	18.51 ± 27.65	23.67 ± 19.39	3.35 ± 1.71	4.90 ± 3.20	6.51 ± 0.87	3.34 ± 0.17	8.50 ± 5.24	13.51 ± 5.27	7.84 ± 3.95	15.80 ± 5.95	9.61 ± 2.36
	vascular plants	0.00 ± 0.00	0.81 ± 0.55	2.61 ± 1.10	2.82 ± 1.13	9.24 ± 3.12	7.40 ± 5.08	6.71 ± 0.25	10.25 ± 4.12	10.50 ± 4.09	6.30 ± 3.24	6.79 ± 5.43	7.54 ± 3.96
	terrestrial	1.15 ± 0	0.78 ± 0.30	3.13 ± 0.43	1.19 ± 0.83	5.31 ± 2.62	3.25 ± 2.56	8.91 ± 2.27	3.85 ± 3.68	6.20 ± 5.66	4.60 ± 4.04	3.67 ± 3.22	4.95 ± 3.42

Table AVI Carbon and nitrogen stable isotopes ratios (‰) in the consumers groups and the species in the two habitats (veg – vegetated, unveg- unvegetated) (mean ± st.dev)

consumers	habitat	species/ feeding group	δ^{13}C	δ^{15}N
meiofauna	veg	P. spinicauda	-20.79 ± 0.97	3.29 ± 0.00
	unveg	P. spinicauda	-20.53 ± 0.48	3.29 ± 0.00
	veg	T. discipes	-17.66 ± 0.55	3.29 ± 0.00
	unveg	T. discipes	-13.33 ± 2.08	3.29 ± 0.00
macrofauna	veg	suspension feeders	-18.68 ± 0.81	7.72 ± 0.90
	unveg	suspension feeders	-16.61 ± 0.06	5.88 ± 0.14
	veg	suspension/detritus feeders	-19.82 ± 0.10	6.49 ± 0.03
	unveg	suspension/detritus feeders	-20.37 ± 1.22	7.51 ± 0.50
	veg	grazers	-17.12 ± 2.91	6.26 ± 0.79
	unveg	grazers	-18.74 ± 2.51	6.26 ± 0.79
	veg	omnivores	-16.75 ± 1.30	8.88 ± 1.61
	unveg	omnivores	-16.27 ± 0.66	7.48 ± 2.19
suspension feeders	veg	A. improvisus	-17.95 ± 0.09	8.54 ± 0.10
	veg	M. edulis	-19.42 ± 0.09	6.90 ± 0.02
	unveg	M. arenaria	-16.61 ± 0.06	5.88 ± 0.14
suspension/detritus feeders	veg	C. glaucum	-19.82 ± 0.10	6.49 ± 0.03
	unveg	C. glaucum	-21.68 ± 0.07	7.24 ± 0.02
	unveg	M. balthica	-19.40 ± 0.07	7.71 ± 0.61
grazers	veg	Gammarus spp.	-16.45 ± 0.61	5.60 ± 0.69
	veg	Hydrobia spp.	19.82 ± 0.10	6.95 ± 0.09
	veg	Idotea spp.	-14.23 ± 0.46	5.74 ± 0.10
	veg	R. peregra	18.69 ± 0.75	7.13 ± 0.11
	veg	T. fluviatilis	18.77 ± 1.26	6.89 ± 0.09
	unveg	B. pilosa	-17.58 ± 0.01	5.74 ± 0.10
	unveg	Hydrobia spp.	21.68 ± 0.07	6.89 ± 0.09
omnivores	veg	C. carinata	-16.18 ± 0.07	6.99 ± 0.27
	veg	Marenzelleria spp.	-17.96 ± 0.23	9.72 ± 0.50
	veg	N. ophidion	-18.70 ± 0.16	9.67 ± 0.06
	veg	Palaemon spp.	-15.49 ± 0.67	7.47 ± 0.92
	veg	Pomatoschistus spp.	-16.21 ± 0.09	10.20 ± 0.28
	veg	P. elegans	-18.87 ± 0.00	6.27 ± 0.00
	veg	S. typhe	-17.29 ± 0.13	11.32 ± 0.08
	unveg	C. carinata	-16.08 ± 0.04	5.24 ± 0.03
	unveg	H. diversicolor	-16.42 ± 0.56	5.80 ± 1.08
	unveg	Marenzelleria spp.	-16.13 ± 0.98	7.32 ± 0.70
	unveg	P. torva	-15.29 ± 0.00	7.15 ± 0.00
	unveg	Pomatoschistus spp.	-16.21 ± 0.09	10.20 ± 0.28