



Contribution of deltaic wetland food sources to coastal macrobenthic consumers (Po River Delta, north Adriatic Sea)☆



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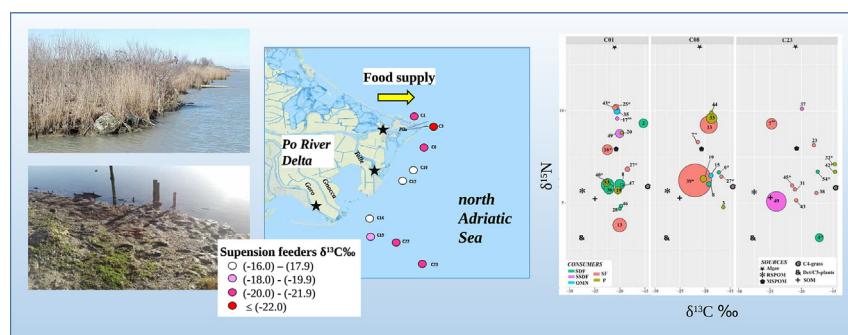
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HIGHLIGHTS

- The study was carried out in the Po River Delta and the nearby coastal area.
- Food sources' contributions to coastal macrobenthos' diets were assessed by stable isotopes.
- Terrigenous isotopic signals decreased at increasing distance from the main river mouth.
- Deltaic wetland detritus mainly contributed to primary consumers' diets.
- Food sources quality shaped macrobenthos community structure along the river plume.

GRAPHICAL ABSTRACT



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ABSTRACT

Estuaries are known to export huge quantities of terrigenous/riverine organic matter and nutrients to coastal areas, subsidizing food sources to their communities; however, this process is seldom investigated in complex multichannel delta-prodelta systems. Stable isotope analysis was used to investigate the contribution of organic sources originated from the Po River Delta, one of the widest deltaic wetlands in the northern Mediterranean Sea, to the diet of the nearby coastal macrobenthic consumers, and their influence on invertebrates' trophic structure and biomass. Following intense river flood events, macrofauna samples were collected in the prodelta area at increasing distance from the main river distributary mouth. Potential primary resources were collected within the delta and the prodelta areas. A terrestrial signal in the primary consumers' diet was evident as a shift in their $\delta^{13}\text{C}$, being this more ^{13}C depleted near the main river distributary. The Bayesian mixing models indicated an important contribution of deltaic sources, in particular C4-grass detritus (25–57%), to primary consumers' diet, confirming a strong energetic link between delta and prodelta areas. Overall, most of the consumers' biomass were concentrated at sites close to the main distributary mouth, mainly as suspension and surface deposit feeders. A simplification of the macrobenthic community structure, accompanied by narrower transfer pathways was also evident at sites more distant from the main river distributary, in relation to changes in the quality of resources. Our data, although limited to winter season, suggest that during periods of low in situ productivity but

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high river flow energy, invertebrates are able to efficiently exploit terrigenous food sources, restraining the detrimental effect of increased turbidity and sedimentation. We conclude that riparian/wetland vegetation associated with river deltas can provide important food sources to marine primary consumers. These results furthermore highlight the need for integrated management and protection strategies of connected land-sea ecosystems.

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1. Introduction

Estuaries and deltas are considered among the most productive habitats on earth, due to high abundance and diversity of primary producers as well as inputs of organic matter (OM) transported from rivers (Heip et al., 1995; Nixon et al., 1986). A considerable fraction of this huge production is exported to coastal ecosystems through tidal water movements and floods, generating among the largest land-sea cross-boundary fluxes globally (Schlünz and Schneider, 1999). The exchange of energy between adjacent ecosystems, initially conceptualized for salt marshes as the “outwelling” hypothesis (sensu Odum et al., 1979), is now recognized to be a widespread process potentially impacting biogeochemical cycles and enhancing biological production and fisheries yields in coastal seas (Connolly et al., 2009; Dagg et al., 2004; Gaston et al., 2006; Gillanders and Kingsford, 2002; McKee et al., 2004). This hypothesis implies that part of the production and nutrients exported from terrestrial/estuarine environments is made available to be consumed by organisms in receiving marine systems (trophic subsidy). This process has been shown to significantly influence coastal communities' dynamics and feeding strategies, thus exerting a relevant positive impact on ecosystems services (Darnaude et al., 2004a; Deegan et al., 2000; Polis et al., 1997; Savage et al., 2012). In virtue of the trophic links existing among coastal ecosystems, and the increasing anthropogenic pressures affecting them, it has recently emphasized that effective management and protection measures can be achieved only through a cross-seascapes approach and a deep understanding of the synergic processes driving biodiversity and functioning in neighbouring environments (Hyndes et al., 2014 and literature therein). Understanding the level of dependence of marine coastal food webs on terrestrial/estuarine trophic resources could be extremely relevant in those areas around the world that are predicted to be impacted by alteration in rivers' discharge due to climate change.

Despite some studies having documented the importance of allochthonous, terrestrial/riverine resource supply for marine communities (e.g. Antonio et al., 2010, 2012; Darnaude et al., 2004b; Savage et al., 2012), their influence on invertebrate biomass, diversity, feeding typology and trophic interactions remains poorly studied, limited to few sites or seldom investigated in complex multichannel delta systems surrounded by wetlands.

Deltas and the connected prodelta systems are highly hydrodynamic cross-boundary areas, important sites for organic carbon burial (Hedges and Keil, 1995), and for the decomposition of both terrestrial and marine particulate OM (Aller, 1998). In deltaic/estuarine systems and in particular in those subjected by highly episodic flood events, the magnitude, mobilization and quality of exchanged OM can highly depend upon the intensity and frequency of river discharge and drainage basin composition (Bonifácio et al., 2014; Tesi et al., 2011 and literature therein). Generally, a low river flow (dry season) is usually associated with strong contributions of marine production. Conversely, high river flow during the wet season is typically associated with a strong contributions of soil-derived OM and terrestrial plant debris carried by the river, mainly as result of soil erosion and river sediments resuspension (Boldrin et al., 2005; Yu et al., 2002). The geomorphologic architecture of river deltas, by playing an important role in depositional dynamics, is another factor affecting land-ocean OM exchanges (Syvitski et al., 2005; Tesi et al., 2011).

The condition and growth of benthic macroinvertebrates are dependent upon the quantity and quality of food resources assimilated over time, which can be assessed by stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. This

technique can provide time-integrated information about the source of food assimilated by organisms and about trophic community structures and dynamics (Layman et al., 2012). If estuarine, terrigenous, and marine food resources have their own distinct isotopic signatures their spatial subsidy and its contribution to secondary production can be assessed using stable isotopes in combination with mixing models (Phillips and Gregg, 2003). Moreover, taking species biomass and biomass-weighted isotope signatures into account provides the opportunity to investigate and identify dominant food web pathways, based on the structure and dynamics of species 'feeding relationship' (Grall et al., 2006; Quillien et al., 2016). The matching of stable isotope analysis and mixing models with qualitative studies of macrobenthic communities has been recently addressed as an effective strategy to assess and disentangle the effects of multiple environmental impacts in coastal marine ecosystems (Bongiorni et al., 2016; Mancinelli and Vizzini, 2014).

In this study, we aimed to investigate whether intense river flow-events and the generated strong inputs of soil-derived OM and terrestrial plant debris would provide important food subsidy for coastal macrobenthic community, shaping its structure and the main food web pathways. Here we focused on the Po River Delta (north Adriatic Sea), which is considered one of the most relevant transitional systems in Europe. The Po Delta plain present a high level of biodiversity due to the extensive range of habitats such as riverbeds, lagoons surrounded by salt marshes and mud flats, sandbars, coastal dunes, etc. The whole area comprises one of the largest wetland in the northern Mediterranean region and since 2015 has been designated as a Man and the Biosphere (MAB) reserve by UNESCO.

Previous studies have highlighted that the Po River can largely contribute to accumulate allochthonous OM in the area interested by its plume (Giani et al., 2009). A high contribution of terrestrial OM with respect to the riverine fraction, strongly indicate that seasonal flooding, although shorter in time, can carry a much higher load of detritic OM than that transported during long periods of minimum regime flow. Moreover, under both moderate and peak discharge regimes, the relative fraction of terrigenous organic carbon transported and discharged by the river decreases with distance from its main distributary mouth, Pila (Tesi et al., 2011).

In this study we therefore hypothesized that: i) allochthonous (riverine/terrestrial) OM sources transported by the Po River, following intense floods, would contribute to the diets of coastal benthic invertebrates (food subsidy); ii) differences in OM composition and availability along the river plume would significantly influence macrofauna communities' structures, isotopic composition and feeding groups; and iii) relative changes in macrofauna biomass composition would influence major energy pathways (i.e. the ways energy and nutrients are channelled) along the local food web. To test these hypothesis, nine coastal sites located at increasing distance from the main Pila mouth were compared in term of invertebrate communities structures, feeding groups, isotopic composition and biomass, and analysed together with potential deltaic food sources.

2. Material and methods

2.1. Study area and sampling

The Po River, with a drainage basin of 71,000 km² and a length of 673 km, is the most important river in Italy and one of the largest in Europe. It is characterized by an annual mean freshwater discharge

of $1525 \text{ m}^3 \text{ s}^{-1}$ (recorded at Pontelagoscuo gauging station) and by two annual floods ($>5000 \text{ m}^3 \text{ s}^{-1}$) associated with rainfall in autumn and snowmelt in spring (Boldrin et al., 2005). This river supplies over 50% of the fresh water to the northern Adriatic basin (Mediterranean Sea) via a large delta, which includes five distributary mouths, from north to south: Maestra, Pila, Tolle, Gnocca, and Goro (Degobbis et al., 1986; Fig. 1). Pila accounts for 61% of the total freshwater discharged in the delta whereas Maestra, Tolle, Gnocca, and Goro supply the remaining 3, 12, 16, and 8%, respectively (Syvitski et al., 2005). During normal flow conditions, fine-grained sediments in the Po River undergoes rapid deposition close to its mouths (sediment deposition rates amount to $\sim 6 \text{ cm year}^{-1}$ near the Pila distributary and $\sim 2 \text{ cm year}^{-1}$ in the southern portions of the prodelta; Frignani et al., 2005; Palinkas et al., 2005). Subsequently, the sedimentary plume is principally transported southward along the shelf due to the predominant cyclonic Western Adriatic Coastal Current and wind-induced resuspension events promoted by the north-easterly Bora wind.

Sampling was carried out between 15th and 19th of December 2014, in the Po Prodelta area, during a rapid-response survey that followed the two most relevant river floods occurred during the whole 2014 (maximum discharge rates registered at the Pontelagoscuo gauging station on 19th November and on 5th December, were ca. 8501 and $5930 \text{ m}^3 \text{ s}^{-1}$ respectively, ARPA Emilia, www.arpae.it). The river front was monitored in real time by satellite images and samples were collected in nine sampling sites at increasing distance from the main distributary mouth (Pila), along the river plume (Fig. 1). Bottom depth of sampling sites varied from 8 to 14 m, with the exception of three sites (C19, C22 and C23) at which depth ranged between 18 and 27 m. Hydrological condition of the area, as shown by CTD profiles, revealed a marked influence of the freshwater discharge which was visible in all sites, although decreasing from north to south (data not shown).

At each site, sediment samples were collected using a van Veen grab (0.4 m^2). Overall, six replicate grabs were collected at each site and sediment samples were sieved through $1000 \mu\text{m}$ mesh to retain the macrofaunal invertebrates. The macrofauna obtained from three grabs were immediately fixed with formaldehyde solution (4% v/v final concentration in seawater) for community structure analyses (diversity, abundance and biomass) while the other three grabs were used for stable isotopes analysis (SIA). Additional surface sediment samples were collected for the determination of sediment grain-size distribution, and

frozen for later measurements of stable isotopes, organic carbon (Corg), total nitrogen (TN), chlorophyll-*a*, and phaeopigments. At each sampling site, suspended particulate organic matter (SPOM) was collected using Niskin bottles at ca. 1 m below surface and 1 m above sea-bottom. Water sub-samples ($300\text{--}1000 \text{ ml}$) were filtered on pre-combusted ($450 \text{ }^\circ\text{C}$, 4 h) GFF filters (Whatman) and immediately frozen.

Potential estuarine food sources were collected within the Po River delta at three sites: Pila (along the main distributary channel), Porto Barricata (near Tolle distributary mouth) and Gorino (inside Goro lagoon, Fig. 1). Sites were chosen to represent much of the variability of the whole area (i.e. riverbanks, branches and saltmarshes). Bulk sediment organic matter (SOM) and SPOM samples were collected and treated as explained above. Macroalgae, plants and detritus samples were collected by hand at the edges of marshes and riverbanks or by nets, if floating on surface water. Both fragments of riparian/wetland vegetation and wood-derived detritus were observed drifting in several sites inside the delta, therefore potentially transported offshore by currents, and were considered as potential primary sources. Zooplankton samples were collected by horizontal tows of a WP2 net ($200 \mu\text{m}$ mesh size) and successively sorted from detritus. In order to obtain a pure isotopic signal of deltaic phytoplankton, a phytoplankton net ($20 \mu\text{m}$ mesh size) was vertically deployed at each delta site. Samples were decanted to remove fine particles and observed under a microscope; however, the low number and biomass of cells and high detritus abundances (Bongiorno pers. comm.) prevented further SIA. Replicated sediment cores were also collected at each site for isotopic microphytobenthos (MPB) determination. In the lab, MPB cells were light-stimulated to migrate onto filter papers (previously placed on cores surfaces). Also in this case, MPB biomass was extremely low compared to detritus to allow SIA. The low recovery of benthic microalgae were probably due to the low growth rates typically reported in the north Adriatic Sea during the late autumn-winter period; and likely related to the burial of MPB by high riverine input and sediment deposition (Blackford, 2002 and literature therein; Cibic et al., 2012).

All OM sources collected in the Po Delta were analysed separately for the three sampling sites, but were later pooled to obtain representative isotopic value of resources from the whole delta-area.

2.2. Sediment grain-size, chemical parameters and pigments

Sediment subsamples ($10\text{--}15 \text{ g}$) for grain-size analysis were sieved at 2 mm and pre-treated with 10% hydrogen peroxide ($60 \text{ }^\circ\text{C}$ for 24 h), before being analysed with a Malvern Mastersizer 2000 equipped with Hydro 2000s (Malvern Instruments Ltd., Malvern, UK). Data were expressed as percentages of sand, silt and clay. Corg and TN were analysed contextually to stable isotopes with an Elemental Analyzer, as described below, and used to calculate the carbon to nitrogen (C:N) molar ratio. Corg and C:N were used as proxies of OM content and origin, respectively. Chloroplastic pigments (chlorophyll-*a* and phaeopigments) were analysed fluorometrically according to Lorenzen and Jeffrey (1980). Pigments were extracted with 90% acetone (24 h in the dark at $4 \text{ }^\circ\text{C}$). After centrifugation the supernatant was used to determine the chlorophyll-*a*, and acidified with 0.1 N HCl to estimate the amount of phaeopigments. The phaeopigments to chlorophyll-*a* ratio (Phaeo:Chl-*a*) was used as a proxy of freshness/degradation of phyto carbon (Dell'Anno et al., 2002).

2.3. Macrofauna samples processing

Samples for macrofauna were sorted using a stereomicroscope (Zeiss Discovery V.12, $8\times\text{--}100\times$ magnifications) and all animals were counted and identified to the lowest possible taxonomical level. For identification, the taxonomical keys listed in Morri et al. (2004) were used. Biomass of each taxon was measured by ash-free dry weight (AFDW), after combustion at $450 \text{ }^\circ\text{C}$ for 24 h.

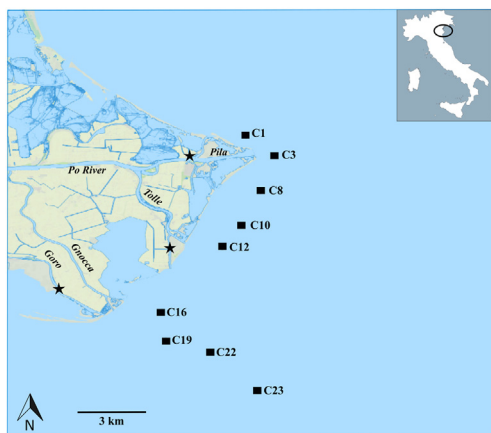


Fig. 1. Location of sampling sites along the coastal Po River Prodelta (black squares) and inside the delta (black stars). The four main Po River distributaries are depicted (from north to south: Pila, Tolle, Gnocca, Goro).

Abundance and biomass were converted to units per m². Feeding groups were defined as group of taxa sharing similar functional attributes, in order to understand the predominant trophic strategies related to the available food sources in the sampled area. One out of six different feeding groups was assigned to each taxa: suspension feeders (SF), surface deposit feeders (SDF), subsurface deposit feeders (SSDF), predators (P), omnivores (OMN); using as criteria the morphology of the feeding apparatus, the feeding mode, and the nature and origin of the food. Further, to have wider information on feeding modalities, a selective feeding description (i.e. obligate or facultative) was added. Traits for each taxon were derived from literature sources (i.e. Desrosiers et al., 2000; Jumars et al., 2015) and databases (i.e. MarLIN, 2006; Polytraits Team, 2016).

2.4. Stable isotopes measurements

Before SIA, sediment subsamples were oven dried (60 °C, 48 h) and sieved at 2 µm. Filters with SPOM and macrofauna specimens were dried in oven (60 °C, 48–72 h). Potential food sources (macroalgae, zooplankton, plants and detritus) were carefully sorted and cleaned from epiphytic organisms and sediments under a stereomicroscope and oven dried for further analyses. SIA were carried out on the whole body of macrofaunal organisms. Within each sampling site, several individuals of the same species (between 2 and 20) were pooled and homogenized to obtain sufficient biomass for a sample and to reduce the effect of possible intra-specific variability. To account for ontogenetic variations in diet for each taxon, only organisms of similar size were analysed. Invertebrates' δ¹³C were not corrected for lipid content due to several reasons: invertebrate C/N ratio was fairly low and constant, and was weakly related to δ¹³C values ($r = -0.22$); moreover, the little δ¹³C shift (1.3‰) obtained after correction (Logan et al., 2008) did not affect isotope signals or interpretations regarding animal diets. All samples (sediments, primary producers, and animals) were homogenized with clean mortar and pestle until obtaining a fine powder. Overall, prior to analyses, samples containing traces of carbonates (e.g. SOM, POM filters, seagrasses, and some invertebrate organisms containing carbonates) were divided into two subsamples, one of which was pre-treated with HCl (1 N) solution to remove carbonates and the other was not acidified and was used for δ¹⁵N analyses (Mateo et al., 2008). Bulk and acidified samples were weighed and placed into tin capsules to measure δ¹³C and δ¹⁵N and percentage of C and N in one run. The analyses were carried out on an Isotope Ratio Mass Spectrometer (Delta Plus, Thermo Scientific) coupled with an Elemental Analyzer Trace GQ (Thermo Fisher). The isotopic composition was denoted in delta (δ) notation, i.e. differences between the isotopic ratios in the samples and in international standards (Vienna Pee Dee Belemnite and Air for δ¹³C and δ¹⁵N, respectively) and expressed in ‰ (Coplen, 2011). The isotopic values were calculated against working in-house standards, which were calibrated against international reference materials: L-glutamic acid USGS 40 (IAEA International Atomic Energy Agency, Vienna, Austria) and sugar (IAEA-CH-6) for δ¹³C, and L-glutamic acid USGS 40 and potassium nitrate IAEA-NO3 for δ¹⁵N. Uncertainty of stable isotopic determinations was 0.3‰ for both δ¹³C and δ¹⁵N. The percentage of C and N were measured using as reference material atropine (Carlo Erba, Milano). The detection limit of the method for C and for N was 0.6 mmol and 0.9 mmol, respectively.

2.5. Data analysis

Biochemical parameters of Po River Prodelta sediments were compared among sampling sites by mean of One-way ANOVA. All analyses were carried out using the R software v 3.4.2 (R Core Team, 2017). Prior to all analyses, data were checked for normality and

homoscedasticity using Shapiro-Wilk's and Levene's test. When significant differences were observed, Student-Newman-Keuls (SNK) post hoc test was also performed. Multivariate multiple regression analyses were applied to identify sediment variables that best explain the variability in macrofauna species composition. The analysis was performed using the Distance-Linear Modelling (DistLM) on macrofauna abundance matrix. Data were square root transformed and Bray-Curtis similarity was applied. Environmental variables included proxies of sediment texture (% of sand and clay), OM origin (C:N), quantity (Corg), and quality (Phaeo: Chl-*a*). Prior to the analysis, data were normalized. The options "All specified" and R² were used as the selection procedure and criterion, respectively. A distance-based redundancy analysis (dbrDA) plot was prepared using all the tested variables. Differences in macrofaunal species and its stable isotopes values were tested among groups of sampling sites, previously distinguished throughout the dbrDA plot, by one-way PERMANOVA (Permutational Multivariate Analysis of Variance). Before the analysis, macrofauna community composition and stable isotopes data were square root and log (X + 1) transformed, whereas Bray-Curtis similarity and Euclidean distance dissimilarity were applied, respectively. All multivariate analyses: PERMANOVA test, DistLM analyses and dbrDA plot were performed using PRIMER 7 (PRIMER-E Ltd., Plymouth, UK).

In order to estimate the contribution of terrigenous and marine sources to the composition of prodelta organic matter pools (SOM and SPOM) and to the diets of benthic primary consumers, the Bayesian mixing model SIAR (Stable Isotope Analysis in R, v 4.2, Parnell et al., 2010) was applied. These models produce a range of feasible solutions given the available sources, while taking into account uncertainty and variation both in consumer and trophic enrichment factors. They also provide error terms that gives information on the variability that cannot be explained based on diet alone (residual error, Parnell et al., 2010). Data for the mixing model consisted in carbon and nitrogen isotopic ratios of single sample and mean ± standard deviation of organic sources. For each model, discriminatory power was retained by selecting the best sources and by pooling those with similar isotopic values (Phillips et al., 2014). Before running the SIAR models, all δ¹³C and δ¹⁵N data were plotted to check the inclusion of samples in the convex polygon formed by the selected sources (Phillips et al., 2014). The contribution was estimated for each prodelta sampling site/areas and benthic consumers feeding group, assuming this last as a simplified means to describe common resources exploitation by macrofauna (Bonsdorff and Pearson, 1999). Feeding groups can represent a helpful indicator of macrobenthic trophic structure, especially in case of difficulties in achieving reference species common among sampling sites (Arbi et al., 2018); as was the case of the present study.

Trophic enrichment factors (fractionation values) of +2.5‰ ± 2.5 for δ¹⁵N and 0.47‰ ± 1.23 for δ¹³C were used following Vander Zanden and Rasmussen (2001); and a fractionation equal to 0 was used for models run on organic C pools.

Finally, to test if differences in food sources along the Po River plume gradient would potentially influence pathways of trophic transfer, we weighted the isotope signature of every taxon funded in each sampled sites by its biomass (individual AFDW × abundance) and superimposed it to appurtenance to certain feeding groups. This produced a stable isotopes-biomass bubbles plots where the area of circles reflected the biomass of each species. Trophic pathways were analysed by focusing on: i) trophic groups that dominate the faunal biomass, assuming these were responsible for channeling most of the energy and nutrients through the web; and ii) the way animal biomass was distributed over the isotopic space. Finally, we tried to link those patterns to the influence of food subsidy. This analysis is based on the rationale that different macrofaunal taxa/feeding group, being capable of assimilating different type and variable proportion of OM (also in relation to its local availability and quality), would vary in composition and biomass, influencing OM and energy transfer along the local food web.

3. Results

3.1. Environmental data and isotopic values of basal sources

In the investigated area, sediments were mainly represented by the finest fractions, as the percentage of silt, clay, and sand were on average 68 ± 3 , 28 ± 4 , and $4 \pm 3\%$, respectively. The sandy fraction decreased from north to south (11 and 1% at site C3 and C12, respectively) and from C16 to the more offshore and deepest sites (6 and 1% at site C16 and C23, respectively), while an opposite trend was observed for the percentage of clay. TN concentration in sediments ranged between 1.12 ± 0.04 and $1.62 \pm 0.01 \text{ mg g}^{-1}$ (at sites C8 and C16, respectively) and differed among sites ($p < 0.01$). The SNK post hoc test showed higher concentrations at sites C12, C16, and C22 and lower at C8 and C23 compared to other sites ($p < 0.01$). Corg concentration in sediments ranged between 9.96 ± 0.20 and $14.09 \pm 0.03 \text{ mg g}^{-1}$ (at C23 and C16, respectively) and varied significantly among sites (ANOVA, $p < 0.001$). Higher concentrations were found at site C16 (SNK test: $C16 > C22 > C1$ and $C3 > \text{others}$, $p < 0.01$). Sediments C:N molar ratio ranged between 8.62 and 10.59 (at C19 and C3, respectively), and values >10 (indicating a contribution of terrestrial derived OM, Hedges et al., 1997) were found at the northern sites C1, C3, and C8 and at the southern site C16. Chlorophyll-*a* concentration in sediments was generally low and ranged between 0.54 ± 0.01 and $2.84 \pm 0.01 \mu\text{g g}^{-1}$ at sites C23 and C16, respectively. Values differed among sites (ANOVA, $p < 0.001$) and the SNK test showed higher concentrations in the northern and central portion of the prodelta than in the southern and offshore sites ($C1\text{--}C16$ vs $C19$ and $C23$, $p < 0.01$). Phaeopigment concentrations in sediments ranged between 10.50 ± 0.03 and $27.55 \pm 0.19 \mu\text{g g}^{-1}$ at sites C3 and C10, respectively. Concentrations differed among sites (ANOVA, $p < 0.001$), and were generally higher in the central and southern prodelta sites than in the northern ones ($C10\text{--}C16$ and $C19\text{--}C23 > C1\text{--}C3$, SNK test, $p < 0.01$).

The $\delta^{13}\text{C}$ of prodelta SOM ranged between -22.42 and -28.87% at sites C23 and C16, respectively and its average value was similar to that of bottom SPOM (Fig. 2). The $\delta^{15}\text{N}$ of prodelta SOM ranged between 1.75 and 3.74‰ at sites C1 and C23, respectively and its average value resulted similar to that of surface SPOM and ^{15}N enriched compared to

bottom SPOM (Fig. 2). River delta SPOM was ^{13}C depleted compared to the prodelta SPOM, while $\delta^{13}\text{C}$ values of SOM were quite conserved across the investigated river delta and prodelta areas. The $\delta^{15}\text{N}$ signatures of the river delta SPOM were enriched in ^{15}N compared to that of the prodelta (Fig. 2).

The isotopic signatures of organic sources quite well distinguished OM sources collected in this study (Fig. 2). Stable isotopes values of the macroalgae *Ulva* spp. and *Gracilaria* spp. collected in the Po River delta were similar and were pooled prior to be used in the mixing models. Similarly, both fringing vegetation such as the common reed (*Phragmites*, C3-pathway) and terrestrial detritus (consisting mainly of fragments of wood and aged leaves) displayed similar low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures, and therefore were pooled and named hereafter as detritus/C3-plants (Fig. 2). Detritus/C3-plants $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were clearly distinct from other unidentified river delta plants material, which displayed typical C4-pathways values (hereafter named C4-grass). Values of marine sources (phytoplankton, SPOM and zooplankton) were obtained from samples collected in the northwestern Adriatic waters (Giani et al., 2009; Berto pers. comm., Fig. 2). Since isotopic ranges of marine organic sources clustered in isotopic space, only marine phytoplankton was considered as a better representative of marine end-members. The SIAR mixing model for prodelta OM pools was run considering five end-members potentially contributing to nitrogen and organic carbon composition (marine SPOM, riverine/deltaic SPOM, terrigenous detritus/C3-plants, C4-grasses and macroalgae). Despite we could not completely exclude the occurrence of sediment resuspension in the area, this was considered of minor importance as compared to particle deposition along the river plume and SOM was not included as potential source in mixing model of SPOM pools. SIAR results showed that on average, $>40\%$ of the composition of prodelta SPOM at surface was represented by detritus/C3-plants, and an even higher contribution of this source was observed at the bottom water layer (average 59%, data not shown). Detritus/C3-plants was also the first contributing source to the composition of prodelta sediments (range between 23 and 64% at sites C23 and C16, $CI_{95\%}$: 3–41 and 44–82, respectively, Table A1), and was followed by riverine/deltaic SPOM ($>30\%$ at the northern-central sites C3, C10 and C12). The contribution of marine phytoplankton to sediments slightly increased with increasing distance from the Pila mouth reaching its maximum in the most offshore sampling site C23 (21%). It is worth mentioning that the highest contribution of macroalgae to the prodelta sediments was observed at site C16 (14%, Table A1).

3.2. Macrobenthic community structure

Macrofaunal abundance in the Po River Prodeltà ranged between $83 \pm 75 \text{ ind. m}^{-2}$ at site C23 and $5333 \pm 3409 \text{ ind. m}^{-2}$ at site C8. The highest biomass value was measured at site C8 ($9.99 \pm 6.70 \text{ g m}^{-2}$) while the lowest at site C12 ($0.38 \pm 0.50 \text{ g m}^{-2}$). Biomass decreased from the northern to the southern prodelta sites. Polychaetes were by far the most dominant group (60% of the total abundance), followed by molluscs (38%), crustaceans (7%), echinoderms (2%) and other groups (anthozoans, sipunculids and nemertines, $<1\%$).

Suspension feeders (SF, 52.1%) dominated the macrofauna communities and were followed by surface deposit feeders (SDF, 26.5%), subsurface deposit feeders (SSDF, 19.3%) and predators (P, $<2\%$). Omnivores (OMN) remained the least represented group ($<1\%$) in the whole community. At site C1 the community was dominated by SDF (46.7%) due to the high presence of the bivalves *Chamelea gallina* and *Nucula nucleus*. At increasing distance from Pila, sites C8 and C10, SF dominated (81.6 and 32.9%, respectively) mainly due to the presence of the polychaete *Owenia fusiformis* and

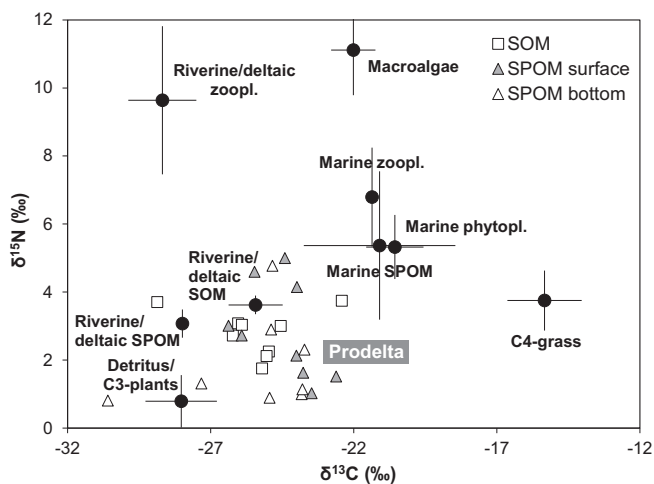


Fig. 2. Dual stable-isotope plot of SOM and SPOM in the Po Prodeltà and mean (\pm SD) of potential organic sources: Riverine/deltaic SOM and SPOM, Marine and Riverine/deltaic zoopl. (zooplankton), Marine phytopl. (phytoplankton), Macroalgae (*Ulva* spp. and *Gracilaria* spp.), Detritus/C3-plants (mainly wood detritus and *Phragmites*). Source data were not corrected for fractionation as this was considered equal to 0.

the bivalve *Corbula gibba* (site C8). Instead, the southernmost and offshore sites were characterized by a higher abundance of SSDF. The polychaete *Sternaspis scutata* was numerically dominant at these sites reaching up to 74.7% of the whole community at site C19. DistLM analysis ($R^2 = 0.70$) showed that four environmental variables (% of sand and clay, and C:N and Phaeo:Chl-*a* ratio) were significant drivers of the macrofaunal community composition. Sediment C:N ratio explained the highest variability in the macrofauna communities (28%, Table 1, Pseudo-F = 2.77, $p < 0.01$).

The first dbRDA plot axis (dbRDA1) captures 44% of the fitted and 31% of the total variation of the macrofauna community composition, while the second (dbRDA2) captures 23% of the fitted and 16% of the total variation (Fig. 3). As depicted by the dbRDA plot, the tested environmental variables split the sampling sites into three groups: a northern group (sites C1, C3 and C8) which corresponded to the area surrounding the main Pila distributary mouth, a central group (sites C10, C12, C16) located at increasing distance from the main Pila distributary and in proximity to a secondary river distributary (Tolle), and a southern group (sites C19, C20 and C23) located at a further distance from the coastline and from Pila (Fig. 3). Differences among these three groups in terms of macrofauna community composition were also supported by the PERMANOVA main test (Pseudo-F = 2.52, $df = 2$, $p < 0.01$).

3.3. Isotopic composition of macrobenthic organisms

Isotopic analyses of macrobenthic consumers in the Po River Prodelta area were obtained from 56 invertebrate taxa (24 molluscs, 15 polychaetes, 10 echinoderms, 5 crustaceans and 2 anthozoans). The average values of stable isotopes signals in macrobenthic organisms were $-19.22 \pm 2.35\%$ ($\delta^{13}\text{C}$) and $7.37 \pm 2.07\%$ ($\delta^{15}\text{N}$). The $\delta^{13}\text{C}$ values of invertebrate consumers ranged between -14.49% and -25.02% (the Echinodermata *Amphiura filiformis*, site C10 and the bivalve *Spisula subtruncata*, site C3). Consumers' $\delta^{15}\text{N}$ values ranged between 3.12 (*Amphiura chiajei* at site C23, if excluding 1.74% measured in the amphipod *Gammarus* sp.) and 12.56% (the bivalve *Nucula nucleus*, site C10). Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of macrobenthic organisms showed significant differences among groups of sites located at increasing distance from the Pila distributary mouth (sites C1–C8, C10–C16, and C19–C23, PERMANOVA: Pseudo-F = 1.2 and 1.3, $df = 2$, $p < 0.05$, for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively).

Differences in the $\delta^{13}\text{C}$ signatures of primary consumers analysed for each feeding group reflected the marine–terrestrial origin of potential food source. Suspension feeders' $\delta^{13}\text{C}$ signature was more ^{13}C -depleted ($-22.61 \pm 3.49\%$) at site C3 in front of the Pila mouth and gradually became more positive at increasing distance from the Pila distributary mouth ($-20.55 \pm 1.46\%$ and

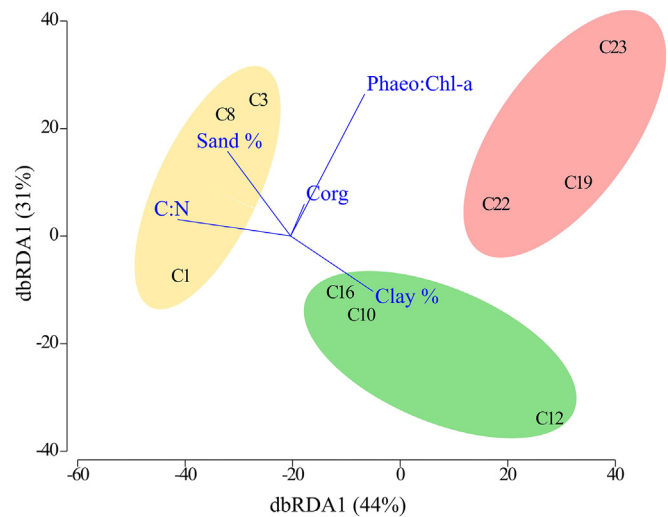


Fig. 3. dbRDA ordinations of the DistLM model which describe the relationship between the macrobenthic community composition and environmental variables in the Po Prodelta sediments. C org (organic carbon), C:N (carbon to nitrogen ratio), Phaeo:Chl-*a* (phaeopigments to chlorophyll-*a* ratio).

$-20.27 \pm 1.68\%$ at sites C1 and C8, and up to $17.10 \pm 1.02\%$ at central sites, Fig. 4, Table A2). At the southernmost sites, the signal was again ^{13}C depleted reaching $-20.03 \pm 2.61\%$ all over the area. Similarly, the average $\delta^{13}\text{C}$ signature of surface deposit feeders was more ^{13}C depleted at site C3 ($-22.00 \pm 2.18\%$), if compared to the other sites, and values became more positive at increasing distance from the Pila distributary mouth ($-19.91 \pm 2.34\%$ and $-18.12 \pm 1.52\%$ at sites C1 and C8, Fig. 4, Table A2). Comparatively, $\delta^{13}\text{C}$ values of SSDF appeared to be more homogeneous. Contrarily to $\delta^{13}\text{C}$, values of macrobenthic $\delta^{15}\text{N}$ did not show clear trends.

3.4. Contributions of food sources to primary consumers and analysis of trophic pathways

The dual-isotope plots of primary consumers and their potential food sources (Fig. 5) showed that most animals were included in the convex hull formed by the identified sources, once they were corrected for fractionation; however, values that did not fit the hull were excluded. Mixing models were run considering the three groups of prodelta sites previously identified by statistical analysis. In order to reduce the model-output redundancy, related sources such as detritus/C3-plants and riverine/deltaic SPOM were pooled (see Fig. 2). Prodella SOM was considered as potential food source, and hence included as model end member but only for deposit feeders. Although the mixing model showed some differences in the relative contribution of food sources to the diet of primary consumers, it included a high level of uncertainty, as indicated by the large credibility intervals that often included zero at their lowest limit (Parnell et al., 2008, Table 2). As the sources were well distinct in the isotopic space, the broad dispersion of consumers in the dual isotope plot could imply the use diverse resources and/or feeding plasticity. SIAR results indicated that despite multiple autochthonous and allochthonous food sources (including deltaic-terrestrial detritus and C4-grass) contributed to the diet of all primary consumers, C4-grass was the main contributing food source for all feeding groups and in the entire prodelta, reaching up to 44–57% of the macrofaunal diet at the central sites. At the northern sites, in the case of SF and SDF (Table 2), different allochthonous (detritus-C3/estuarine SPOM and C4-grass) and autochthonous sources, equally contributed to

Table 1

Output of the DistLM analysis on macrofauna community composition in the Po River Prodella. Reported are the results of the Marginal Tests. SS: Sum of square. Prop.: percentage of variance explained by each variable; p values having statistical significance are highlighted in bold.

Marginal tests				
Variable	SS (trace)	Pseudo-F	p	Prop.
C:N	6794.6	2.7697	0.005	0.283
Phaeo:Chl- <i>a</i>	5548.1	2.1085	0.011	0.231
Corg	2785.9	0.92071	0.523	0.116
Sand %	5060	1.8733	0.037	0.211
Clay %	2785.9	0.92071	0.018	0.257
res.df: 7				
Total SS (trace): 23967				

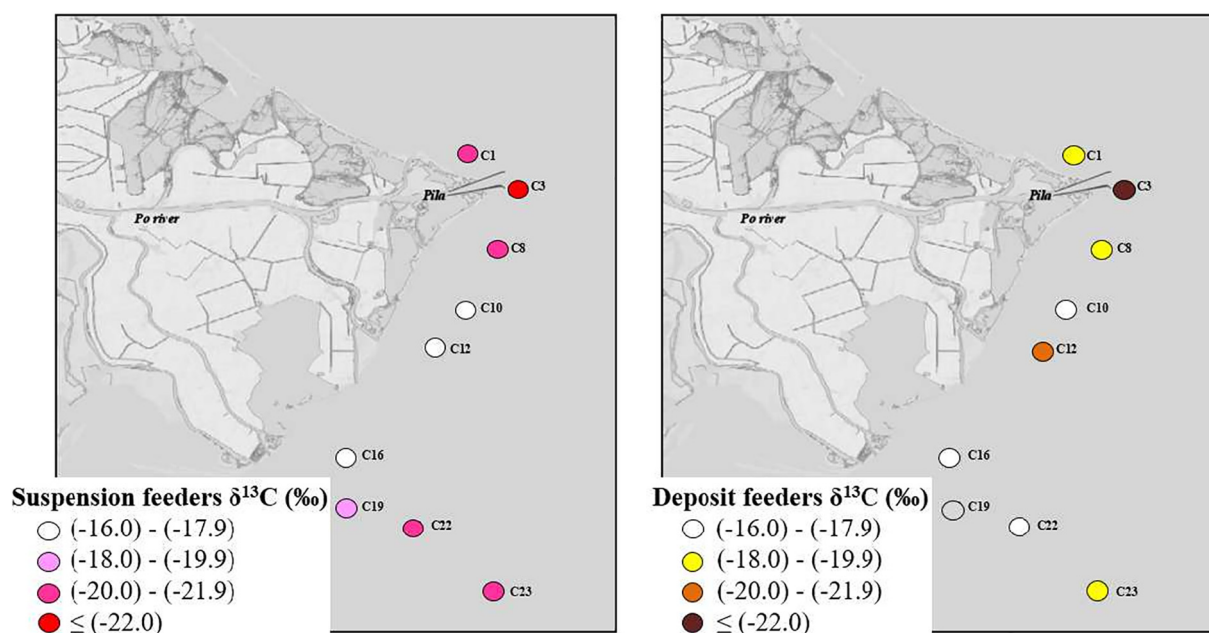


Fig. 4. Mean $\delta^{13}\text{C}$ (‰) values of suspension feeders and surface deposit feeders in the Po River Prodelta sites.

organisms' diets. At the southern sites, bulk SOM contribution to SSDF diets was high, probably reflecting the ingestion and assimilation of bulk sediments. Overall, the dual-isotopes plots confirmed all these results (Fig. 5).

By weighting the mean isotope signature of every taxon in the food web by their respective mean biomass per square meter, major trophic pathways were visually identified (Fig. 6). Near the Pila mouth (sites C1 and C3), most of the macrofaunal biomass was channelled into SF and SDF feeding groups (in particular the biomass of the bivalves *Pharaonella astula*: $1.05 \pm 1.44 \text{ g m}^{-2}$ and *Corbula gibba* and of the polychaete *O. fusiformis*: $1.05 \pm 0.35 \text{ g m}^{-2}$). At site C3 the subsurface deposit feeder *H. filiformis* reached $0.85 \pm 0.28 \text{ g m}^{-2}$. At both sites the communities appeared well structured, with consumers biomass spread quite evenly over feeding groups and species. At site C8 the major trophic pathway was directed to SF due to the highest dominance in terms of abundance and biomass of the polychaete *O. fusiformis* ($2.99 \pm 2.35 \text{ g m}^{-2}$), which made up 29.9% of the total biomass. Interestingly, the suspension feeder *C. gibba* displayed a more negative $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ at site C8 compared to sites C1 and C19 where its biomass was lower. At increasing distance from the Pila mouth SSDF generally dominated the community biomass due to the polychaete *S. scutata* (maximum at site C19: $0.84 \pm 0.22 \text{ g m}^{-2}$, 35.3%, Fig. 6). In particular, at the southern sites C19 and C22 the community appeared to be simplified and more limited in the occupancy of δ -space.

4. Discussion

In this study, we assessed provision of food subsidies from the Po River Delta system to coastal benthic consumers. Comparing the prodelta invertebrate community among a set of sites at increasing distance from the main river mouth, we identified differences in macrobenthic community structure, isotopic composition and feeding groups. Our findings showcase the capability of primary consumers in a coastal food web to incorporate multiple autochthonous and allochthonous food sources, including deltaic wetland detrital matter.

4.1. Organic matter sources

Organic matter exported to the sea through river estuaries is usually composed by a complex mix of continental (e.g. vascular land plant debris, soil-derived matter), and marine material (e.g. advective inputs of marine autochthonous primary production, Boldrin et al., 2005; Cresson et al., 2012; Giani et al., 2009). Quantity, quality and composition of riverine OM fluxes are determined by seasonal productivity and by intensity and frequency of river discharge. In the case of multichannel delta systems like the one under study, OM exchange is deeply influenced by the delta/prodelta morphological architecture, which plays an important role in depositional dynamics (Bonifácio et al., 2014; Tesi et al., 2008, 2011 and literature cited). All these factors, together with local habitat characteristics (presence of shallow flats and vegetation type) crossed by each distributary channel before reaching the sea, contribute to control estuarine OM supplies (Goñi et al., 2009).

In the Po Delta area, flood events ensure a highly episodic and rapid supply and deposition of land-derived material (Tesi et al., 2008). A significant settling of coarse particles occur in front of Pila (the main distributary) mouth and a thick, turbid plume is formed and transported further seaward into the central prodelta area (Milligan et al., 2007; Tesi et al., 2011). In agreement with these observations, and with previous studies (Tesi et al., 2011 and literature therein), the prodelta sediments collected in the present study showed a prevalent riverine/terrigenous origin. In particular ^{13}C depleted isotopic values and C:N ratios above 10 were found in sediments near Pila and Tolle distributaries mouths (sites C3 and C16). The isotopic values and the mixing model indicated that land-derived detritus (in particular woody and C3-plants detritus) was the source mainly contributing (40–60%) to both suspended and sediment organic carbon pools in all δ sampling sites. This result is consistent with the presence of δ extensive reed swamps (approximately 2500 ha) dominated by *Phragmites australis*, bordering the lower ends of the main Po River channels (Scarton et al., 2002), and with the dominance in

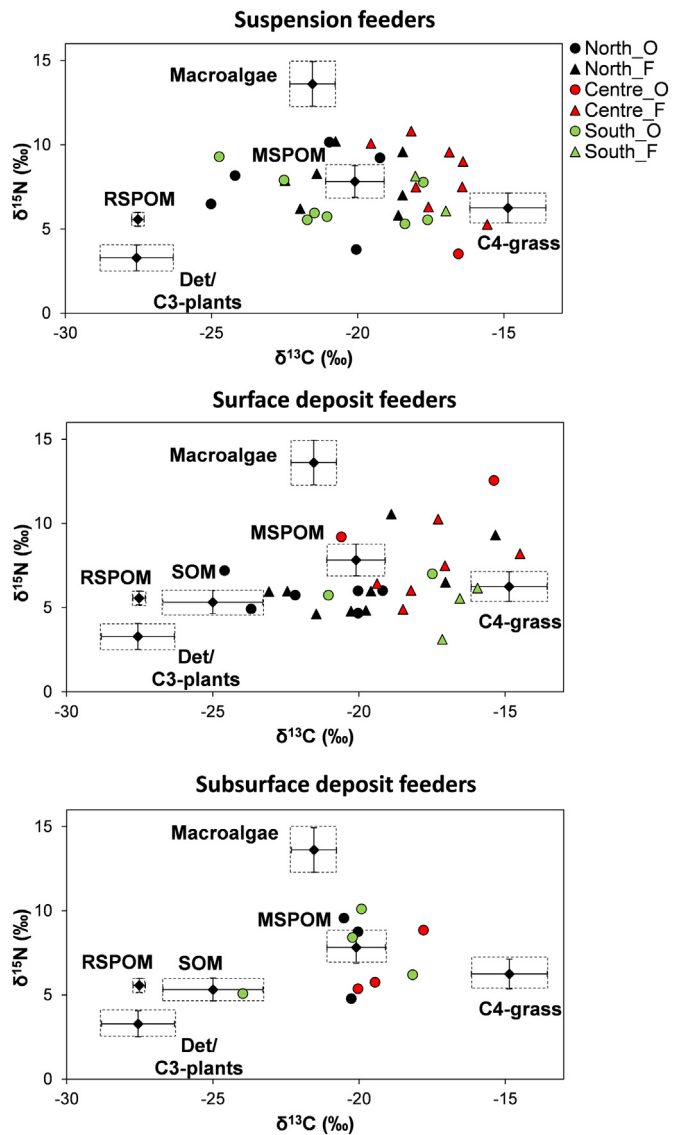


Fig. 5. Dual stable-isotope plots of potential basal food sources corrected for predicted fractionation, and values of primary consumers feeding groups (including selective feeding): obligate (O, circles), facultative (F, triangles). Different colours of symbols depict different prodelta areas: northern sites (black), central (red), southern (green). RSPOM (Riverine/deltaic SPOM), SOM (Sediment Organic Matter), Det/C3-plants (Detritus/C3-plants) and MSPOM (Marine SPOM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperate European wetlands of C3-vegetation (e.g. Teeri and Stowe, 1976). Moreover, this result clearly indicates the effective penetration of the river plume into the prodelta area, despite some differences among sampling sites were highlighted. Near and downstream Pila, the relatively high contribution of riverine SPOM to prodelta sediments, almost even out that of terrigenous origin (Table A2); probably reflecting the high freshwater discharge intensity and the morphology of this river mouth (Tesi et al., 2011). At the southernmost sites, in relation to the major distance from Pila (and hence from its influence), the δ contribution of the autochthonous marine source (marine SPOM) to the sediment pool was observed to increase. This is also consistent with the hypothesis of a selective trapping, in the δ central prodelta of transported coarse material, because of the geomorphologic setting of this outlet characterized by

an estuary-like mouth (Tesi et al., 2011). Moreover, the relatively high contribution of C3-plants and macroalgae in sediments at site C16 could be connected to the proximity of this area with the Scardovari lagoon, the widest in this delta system, which host a relatively rich community of seaweeds and macrophytes (Sfriso et al., 2016).

4.2. Prodelta macrobenthic community structure

Many studies have investigated the influence that rivers flows have on macrofaunal community structure through experimental approaches and spatial or temporal analyses (e.g. Ambrogi et al., 1990; Hermand et al., 2008; Occhipinti-Ambrogi et al., 2005; Thrush et al., 2003, 2004). At a large scale, physical environmental factors, mainly sediments grain-size and bottom depths, determine broad patterns of benthic organisms distribution (Hermand et al., 2008; Occhipinti-Ambrogi et al., 2005). In the investigated coastal area, macrofauna species composition was significantly related to the grain-size distribution, as significant differences were highlighted between the northern sampling sites (sandier) and the southern ones (more clay). According to previous studies (Ambrogi et al., 1990; N'Siala et al., 2008), species such as *Corbula gibba*, *Heteromastus filiformis*, *Owenia fusiformis* and *Pharaonella astula* were found to be dominant in the area near Pila distributary mouth whereas species inhabiting sediments with small grain-size particles (i.e. *Sternaspis scutata*, *Turritella communis*, *Amphiuira chiajei* and *Oostergrenia digitata*) prevailed in the southern prodelta area. However, at smaller scales, other factors such as quantity and quality of food supply are known to influence macroinvertebrate distribution (Thrush et al., 2004). On the base of macrofaunal species composition, three groups of Po Prodelta sites were clearly distinguished (Fig. 3) and correlated, rather than to OM quantity, to a successional gradient of sediment grain-size and food sources quality and origin (Phaeo: Chl-*a* ratios and C:N, Table 1). At sites close to Pila mouth (sites C1 and C3), characterized by high input and deposition of riverine/terrestrial OM, SDF were numerically dominant. The high abundance and biomass of the opportunistic polychaete *H. filiformis* found in this study and in general near other river estuaries (Hermand et al., 2008; Savage et al., 2012; Thrush et al., 2003), indicated that these organisms can efficiently exploit transient food supplies, like those linked to river flood events. At a very small spatial scale, these semi motile burrowing detritivore organisms, are indeed able to modify their feeding behaviour, and rather than ingest bulk sediment, can selectively feed on fresh OM thus reaching high densities with a patchy distribution (Cruz-Rivera and Hay, 2000; Thrush et al., 2004). Similar opportunistic behaviour is reported for the SF *O. fusiformis* and *C. gibba*. These species reached high density at site C8 where supply of relatively fresh OM and high hydrodynamic conditions (as suggested by the grain-size distribution and the Phaeo:Chl-*a* ratio) coexist leading to less extreme terrestrial OM deposition. Being filter feeders these species might preferentially thrive under moderate OM fluxes and deposition, since high amounts of particles can clog their feeding structure, interfere with particle selection, and require the use of energy to clear away unwanted particles (Ellis et al., 2002). At the central prodelta sites (C10–C16) the macrofaunal community was characterized by a higher structural variability behaving as a land-sea transition ecotone (Attrill and Rundle, 2002; Occhipinti-Ambrogi et al., 2002) between the northern prodelta area (more influenced by the river) and the more “marine” southern area. The southernmost and deepest group of sampling sites (C19–C23) was characterized by the presence of SSDF, in particular the polychaete *S. scutata* and the echinoderm *Oostergrenia digitata*. These species are common in estuarine/deltaic area as they typically belong to the Mediterranean VTC (*Vaseux Terrigène Côtière*, biocoenosis of terrigenous mud), above all *S. scutata* (Hermand et al., 2008 and references therein). Moreover, high abundances of these organisms were found in the Po Prodelta (similarly to other studies, e.g. Desrosiers et al., 2000; Hermand et al., 2008) in conjunction

with low chlorophyll and high phaeopigments concentrations, proxies for highly degraded plant OM.

4.3. Delta resource subsidies to coastal food webs and trophic pathways

In this study, we mainly analysed the contribution of potential food sources to the diet of dominant macrobenthic primary consumers. Indeed, these organisms, due to the scarce or limited ability to move, are forced to use locally available resources, thus reflecting organic enrichment conditions (Pearson and Rosenberg, 1978). The SIAR model outputs indicated that in the period investigated, nearly 40–60% of primary consumers food intake was of allochthonous origin (riverine/deltaic SPOM and detritus/C3-plants and C4-grass). Macrofauna isotopes variability reflected the consumption and assimilation of a dynamic mixture of food sources entering the prodelta area. SF and SDF consumers showed more negative $\delta^{13}\text{C}$ values near the main river distributary compared to southern sites (C10, C12, and C16, Fig. 5), probably reflecting as suggested by the SIAR model, the composition of freshly transported or deposited OM; in this case, an even mix of the more and less ^{13}C -depleted allochthonous food sources (riverine/deltaic SPOM and detritus/C3-plants and C4-grass, respectively). In contrast, at increasing distance from the main distributary mouth, a higher contribution of C4-grass was reflected in a less depleted consumers' signal.

A major contribution of land derived OM to consumers' diets is in contrast with other studies in which riverine primary production was found to be the major estuarine supply source for coastal marine food web (Claudino et al., 2015; Savage et al., 2012). Such differences can be ascribed either to the sampling season or to the relative local productivity, which in this case was low (as indicated by the general low chlorophyll-*a* concentrations). Other factors could be: the estuaries morphological architecture (typical estuarine features vs multichannel-delta settings in this study), which could be responsible for transport/settlement of different detritus sizes; and the type and extension of vegetated habitats crossed by rivers. In the Po Prodelt, the contribution of C4-plants to the diet of the primary consumers resulted to be higher than that of C3-plants, notwithstanding the relatively lower contribution of C4-grass to both SPOM and SOM pools. While it is not possible to speculate on the preferential assimilation of C4- with respect to C3-plant sources by macrofaunal organisms, other factors could be responsible for the large variability of C - N stable isotopes within OM pools, likely confounding the relative contribution of these food sources to consumers' diet. These include for example: plant biomass colonization and transformation by fungal and bacterial decomposers; different microbial degradation pathways (e.g. denitrification, methanogenesis); differential C isotopes fractionations of C3- and C4-plants' carbohydrates by fungi; and changes in

plant $^{13}\text{CO}_2$ discrimination with fluctuation of soil moisture, salinity etc. (Cloern et al., 2002 and literature therein). In particular two parameters could help to explain the isotopic signatures (close to that of C4-plants) of the assimilated food-sources: i) the ingestion with food material of associated microbes, having biomass characterized by a more positive $^{13}\text{C}/^{12}\text{C}$ ratio compared to terrigenous sources; and ii) the variety and nature of both consumers' and their associated microflora digestive enzymes. For example, the ability of detritivores to hydrolyse carbohydrates more abundant in vascular plants and more enriched in ^{13}C compared to proteins, have been shown to largely depends on variety and nature of their digestive enzymes (see Créach et al., 1997 and literature therein). Nonetheless, a variety of digestive associations between marine detritivores and their gut-resident microbes have been recorded, including enzymatic degradation of refractory compounds such as structural polysaccharides (e.g. Harris, 1993). Anyway, since it is difficult to define the role of microorganisms in the diet of macrobenthic organisms as well as to decipher animal assimilation processes, these interpretations should be taken with caution. In addition, the high contribution of C4-grass to consumers' diets could have been also overestimated in our study because microphytobenthos (MPB), a more labile food source for consumers, was not included in the model. The $\delta^{13}\text{C}$ of MPB, typically ranging between -12 and -20‰ , can be very similar to that of C4-grass (Dias et al., 2016; Riera et al., 1996; Savage et al., 2012) making the discrimination between these two sources very difficult. Studies on MPB in the North Adriatic Sea are consistent with a strong benthic microalgal growth constrain during winter months and a significant light shading effect at 15 m depth and below (Blackford, 2002 and literature therein). Moreover, Cibic et al. (2012) reported low abundances of benthic diatoms in relation to an exceptional runoff of the Isonzo River (water discharge was five-fold lower than that of the Po River in this study) and sediments were observed to completely cover the benthic diatom community. Considering the above statements, the low Chlorophyll-*a* concentrations found in the Po Prodelt sediments, and microscopic observations of samples, we suggested that MPB, and thus its contribution as food source, was very low in this area and at the time of sampling.

Combination of the biomass structure of the macrobenthic community with stable isotopes values was made in Fig. 6. To our knowledge, such approach applied to a large number of species has been presented only in few studies (Grall et al., 2006; Quillien et al., 2016). This analysis showed that in the northern sites (C1 and C3) most of the primary consumers biomass (hence assumed to be responsible for channelling energy, nutrients through the food web) was concentrated in the polychetae *O. fusiformis* and *H. filiformis* (this last only at site C3) and in the bivalves *P. astula* and *C. gibba*. The appurtenance of these species to

Table 2

Output of SIAR mixing model showing the mean percentage contribution (95 % confidence intervals) of potential food sources to benthic primary consumers diet for north, centre and south-prodelta areas. MSPOM (Marine SPOM), RSPOM/C3 det (pooled Riverine/deltaic SPOM and detritus/C3-plants) and SOM (Sediment Organic Matter). SF (suspension feeders), SDF (surface deposit feeders) and SSDF (subsurface deposit feeders), nd (not determined).

Feeding group	Area	MSPOM	RSPOM/C3 det	C4-grass	Macroalgae	SOM
SF	North	25 (0-48)	25 (11-38)	25 (7-41)	25 (11-39)	nd
	Centre	20 (0-43)	5 (0-12)	57 (38-74)	18 (1-34)	nd
	South	27 (1-50)	27 (11-42)	36 (18-54)	10 (0-22)	nd
SDF	North	19 (0-37)	21 (2-38)	33 (18-48)	5 (0-13)	22 (0-43)
	Centre	23 (0-47)	8 (0-20)	44 (23-64)	14 (0-30)	11 (0-26)
	South	21 (0-40)	19 (0-36)	27 (1-50)	13 (0-29)	20 (0-39)
SSDF	North	23 (0-47)	12 (0-25)	30 (16-45)	20 (1-37)	14 (0-31)
	Centre	22 (0-48)	9 (0-22)	45 (29-62)	9 (0-23)	14 (0-31)
	South	9 (0-29)	4 (0-10)	35 (18-51)	8 (0-20)	45 (28-64)

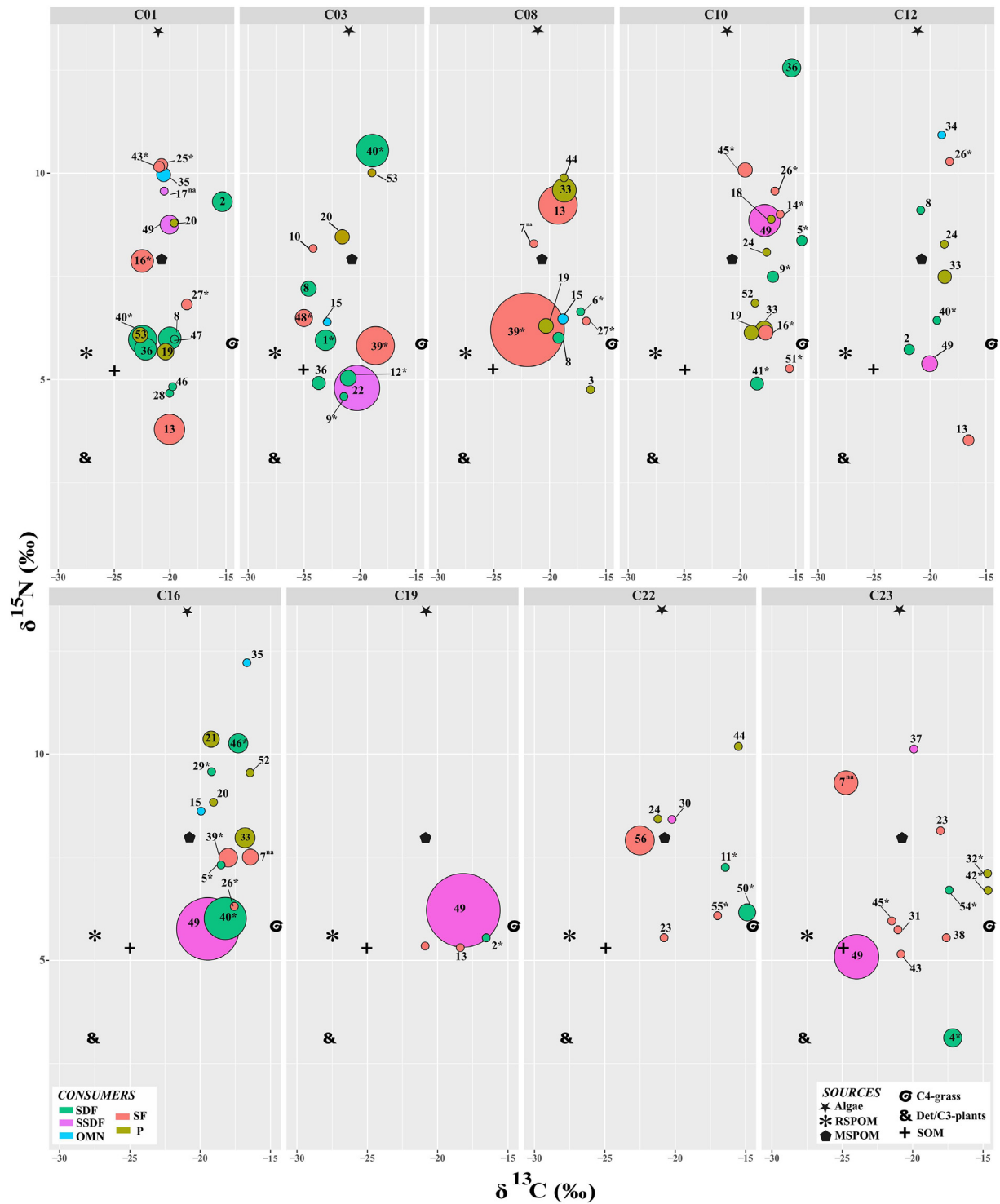


Fig. 6. Stable C-N isotope bi-plots of macrofaunal consumers' weighted by biomass per square meter (filled circles). Macrofaunal feeding groups are indicated with different colours. The facultative feeding of taxa is indicated with an asterisk (na: not available). Stable isotopes values of food sources, corrected for predicted fractionation, are depicted with different shapes. Algae (macroalgae), RSPOM (Riverine/deltaic SPOM), SOM (Sediment Organic Matter), Det/C3-plants (Detritus/C3-plants), MSPOM (Marine SPOM). Each macrofaunal consumer species is denoted by a number: 1 = *Abra alba*; 2 = *Acrocnida brachiata*; 3 = *Aceteon tornatilis*; 4 = *Amphiura chiajei*; 5 = *Amphiura filiformis*; 6 = *Antalis vulgaris*; 7 = *Anthozoa* nd.; 8 = *Aricidea* sp.; 9 = *Atlantella distorta*; 10 = *Barbatia barbata*; 11 = *Brada villosa*; 12 = *Chamelea gallina*; 13 = *Corbula gibba*; 14 = *Cylichna cylindracea*; 15 = *Diopatra neapolitana*; 16 = *Dosinia lupinus*; 17 = *Echinodermata* nd.; 18 = *Eulima glabra*; 19 = *Euspira nitida*; 20 = *Glycera* sp. 21 = *Glycera unicornis*; 22 = *Heteromastus filiformis*; 23 = *Hiatella arctica*; 24 = *Labioleanira yhleni*; 25 = *Lanice conchilega*; 26 = *Leptopentacta elongata*; 27 = *Leptopentacta tergestina*; 28 = *Loripinus fragilis*; 29 = *Lumbrineridae* nd.; 30 = *Maldane glebifex*; 31 = *Musculus subpictus*; 32 = *Necallianassa truncata*; 33 = *Nephtys hystricis*; 34 = *Nereidae* nd.; 35 = *Nereis lamellosa*; 36 = *Nucula nucleus*; 37 = *Oestergrenia digitata*; 38 = *Ostrea edulis*; 39 = *Owenia fusiformis*; 40 = *Pharaonella astula*; 41 = *Phascolosoma (Phascolosoma) strombus*; 42 = *Pisidia longimana*; 43 = *Pitar rudis*; 44 = *Processa* sp.; 45 = *Sabella pavonina*; 46 = *Scoletoma impatiens*; 47 = *Sipunculus (Sipunculus) nudus*; 48 = *Spisula subtruncata*; 49 = *Sternaspis scutata*; 50 = *Tellimya ferruginosa*; 51 = *Thyone fusus*; 52 = *Tritia mutabilis*; 53 = *Tritia reticulata*; 54 = *Turritella communis*; 55 = *Upogebia tipica*; 56 = *Virgularia mirabilis*.

SF, SDF and SSDF feeding groups suggested the importance of both particulate and sedimentary OM as food sources. At these sites, the evenly spread of macrofauna biomass over primary feeding groups and species, and the wide occupancy of the isotopic space, indicated diversified trophic pathways and suggested that benthic organisms were able to consume different food sources, including well-balanced mixed pools of ^{13}C enriched and depleted allochthonous plant sources. Such effect could be explained by both species adaptation to efficient exploitation of terrigenous resources (Quijón et al., 2008) and to the supply of high quality food for consumers as suggested by the higher proteins concentrations (Nasi, pers. comm.) and lower Phaeo:Chl-*a* ratios. Conversely, at southernmost sites, the macrofauna community biomass narrower the occupancy of isotopic space and its structure suggested a simplified food web, exclusively concentrated on a single trophic pathway due to the dominance of the motile burrowing detritivore *S. scutata*. Although these sampling sites still receive terrestrial inputs transported by the main plume and by secondary distributaries discharge, the degraded and low quality of SOM (high phaeopigments and low chlorophyll contents) could be the reason for the lower macrofauna assimilation and therefore for the low biomass observed.

Several studies have highlighted the influence of river floods on macrofauna community composition (e.g. Akoumianaki et al., 2012; Bonifácio et al., 2014; Salen-Picard et al., 2003). For example, the conceptual model proposed by Rhoads et al. (1985) predicts that macrobenthic consumers' diversity and abundance would increase along depositional gradients from the river delta front to more distal areas. This would be mainly due to: the high sedimentation rates and instability near rivers mouths, and the increase of benthic macrofauna further offshore because of moderate organic enrichment. However, similarly to what observed in our study, during river flow peaks, which are typically associated with strong contributions of soil-derived POM and plant debris, a negative correlation between species abundance and distance from the river outflow occur. This effect could likely reflect species' capacity to exploit diversified allochthonous/land derived food sources and to tolerate transient period of high sediment instability and sedimentation (Akoumianaki et al., 2012 and literature therein).

More difficult is to predict which could be the effect on the longer term of the hydrographical regime of the Po River (and its subsidy) on the macrobenthic food web stability and trophic pathways, being our study limited to a single sampling time following intense flood events. Studies carried out in the coastal area close to the Po River have highlighted a general tendency toward the reduction of opportunist/tolerant species in favour of more sensitive ones; a trend probably related to the reduction of river inputs and frequency of extreme floods, as a consequences of climatic changes (Occhipinti-Ambrogi et al., 2005; N'Siala et al., 2008 and literature therein). However, whether these

predicted conditions would favour on the long term the occurrence of communities with a higher degree of structural complexity is still to be addressed. This should be investigated also considering other important factors, such as for example the increase in frequency and extent of dystrophic events (in particular summer hypoxic/anoxic conditions driven by thermal stratification of water, Russo et al., 2002), and not last, the influence of riverine/deltaic food sources subsidy and the presence of extended and well preserved deltaic wetlands.

5. Conclusions

This study highlight the importance of land derived matter, in particular deltaic wetland, as potential food sources for benthic primary consumers in coastal areas, following intense seasonal river floods. Factors like, delta morphological setting, habitat complexity and river flow dynamics seems to be responsible for carbon flow and food supply to coastal food webs and for shaping macrofaunal trophic diversity. Our results suggest that in condition of low in situ productivity but intense river floods, coastal invertebrates might be adapted toward a more efficient exploitation of allochthonous food sources, in particular, detritus from riverbanks and salt marshes transported by intense river runoff. This further stimulates and recalls the need to develop and integrate ecosystems and seascape approaches, in order to reinforce management and protection strategies targeting interconnected terrestrial and marine ecosystems.

Although this study provides a snapshot, being limited to a single flood event-response sampling, it suggests the existence of a strong trophic connectivity between deltaic and coastal systems and the capacity of macrofaunal to respond and adapt to the detrimental effect of increased turbidity and sedimentation.

Studies integrating different intensity and duration of flood events' as well as river-flow variability on a longer temporal scale will be particularly valuable in unravelling changes in food supplies and impacts on coastal food webs. Such studies could be extremely relevant in those areas around the world that will be most affected by alteration in rivers' discharge due to climate change.

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Table A1

Output of the SIAR mixing model showing the mean percentage contribution (95% confidence intervals) of potential OM sources to SOM pools. MSPOM (Marine SPOM), RSPOM (Riverine/deltaic SPOM).

	Mean relative contribution (CI = 95%) to SOM				
	MSPOM	RSPOM	C4-grass	Detritus/C3-plants	Macroalgae
C1	10 (0–26)	16 (0–35)	13 (0–25)	57 (37–76)	4 (0–10)
C3	11 (0–25)	34 (3–61)	7 (0–15)	42 (19–68)	6 (0–14)
C8	12 (0–31)	22 (0–43)	15 (1–27)	47 (26–69)	4 (0–11)
C10	12 (0–27)	36 (5–65)	7 (0–15)	37 (12–63)	7 (0–17)
C12	13 (0–28)	34 (3–60)	7 (0–16)	38 (15–63)	7 (0–17)
C16	4 (0–12)	15 (0–38)	2 (0–6)	64 (44–82)	14 (3–25)
C19	17 (0–36)	27 (1–48)	15 (1–28)	35 (15–57)	6 (0–14)
C22	12 (0–29)	20 (0–40)	14 (1–26)	50 (29–71)	4 (0–11)
C23	21 (0–40)	20 (0–39)	27 (13–42)	23 (3–41)	9 (0–19)

Table A2

Average (\pm sd) of $\delta^{15}\text{N}$ (‰), $\delta^{13}\text{C}$ (‰), and C:N of benthic macrofauna-feeding groups (suspension feeders, SF; surface deposit feeders SDF; subsurface deposit feeders, SSDF; predators, P; omnivores, OMN) collected in the Po River Prodelt: Pol (Polychaeta), Biv (Bivalvia), Ech (Echinodermata), Gast (Gasteropoda), Ant (Anthozoa), Scaph (Scaphopoda), Decap (Decapoda), Sip (Sipunculidea), nd (not determined).

Site	Feeding guilds	$\delta^{15}\text{N}$	sd	$\delta^{13}\text{C}$	sd	C:N	sd	Species
C1	SF	7.81	2.65	-20.55	1.46	5.90	1.00	<i>Lanice conchilega</i> (Pol); <i>Corbula gibba</i> ; <i>Dosinia lupinus</i> , <i>Pitar rudis</i> (Biv); <i>Leptopentacta tergestina</i> (Ech)
	SDF	6.07	1.53	-19.91	2.34	5.99	0.40	<i>Aricidea</i> sp., <i>Scoletoma impatiens</i> (Pol); <i>Loripinus fragilis</i> , <i>Nucula nucleus</i> , <i>Pharaonella astula</i> (Biv); <i>Acrocnida brachiata</i> , <i>Sipunculus nudus</i> (Ech)
	SSDF	9.17	0.57	-20.28	0.34	5.39	0.53	<i>Sternaspis scutata</i> (Pol); <i>Echinodermata</i> nd. (Ech)
	OMN	9.96	nd	-20.57	nd	5.67	nd	<i>Nereis lamellosa</i> (Pol)
	P	6.85	1.69	-20.89	1.58	5.62	0.15	<i>Glycera</i> sp. (Pol); <i>Tritia reticulata</i> , <i>Euspira nitida</i> (Gast)
C3	SF	6.83	1.22	-22.61	3.49	5.79	0.72	<i>Owenia fusiformis</i> (Pol); <i>Barbatia barbata</i> , <i>Spisula subtruncata</i> (Biv)
	SDF	6.34	2.28	-22.00	2.18	6.42	0.64	<i>Aricidea</i> sp. (Pol); <i>Abra alba</i> , <i>Chamelea gallina</i> , <i>N. nucleus</i> , <i>Atlantella distorta</i> , <i>P. astula</i> (Biv)
	SSDF	4.79	nd	-20.27	nd	6.04	nd	<i>Heteromastus filiformis</i> (Pol)
	OMN	6.40	nd	-22.94	nd	7.21	nd	<i>Diopatra neapolitana</i> (Pol)
	P	9.24	1.10	-20.27	1.87	5.72	0.62	<i>Glycera</i> sp. (Pol); <i>T. reticulata</i> (Gast)
C8	SF	8.33	1.52	-20.27	1.68	5.75	0.87	<i>O. fusiformis</i> (Pol); <i>C. gibba</i> (Biv); <i>L. tergestina</i> (Ech); <i>Anthozoa</i> nd. (Ant)
	SDF	6.26	1.52	-18.12	1.52	5.80	0.27	<i>Aricidea</i> sp. (Pol); <i>Antalis vulgaris</i> (Scaph)
	OMN	6.47	nd	-18.80	nd	5.67	nd	<i>D. neapolitana</i> (Pol)
	P	7.60	2.47	-18.45	1.63	6.27	0.54	<i>Nephtys hystricis</i> (Pol); <i>Acteon tornatilis</i> , <i>E. nitida</i> (Gast); <i>Processa</i> sp. (Decap)
	SF	8.01	2.16	-17.22	1.52	6.94	4.10	<i>Sabella pavonina</i> (Pol); <i>D. lupinus</i> (Biv); <i>Thyone fusus</i> (Ech); <i>Cylichna cylindracea</i> (Gast); <i>Leptopentacta elongata</i> (Ech)
C10	SDF	8.29	3.18	-16.36	1.75	5.39	0.83	<i>N. nucleus</i> , <i>A. distorta</i> (Biv); <i>A. vulgaris</i> (Scaph); <i>Amphiura filiformis</i> (Ech); <i>Phascolion (Phascolion) strombus</i> (Sip)
	SSDF	8.86	nd	-17.80	nd	5.54	nd	<i>S. scutata</i> (Pol)
	P	7.23	1.21	-18.07	0.74	5.59	0.46	<i>Labiolelanira yhleni</i> , <i>N. hystricis</i> (Pol); <i>Tritia mutabilis</i> , <i>E. nitida</i> , <i>Eulima glabra</i> (Gast)
	SF	7.18	5.15	-17.37	1.14	5.06	1.00	<i>C. gibba</i> (Biv); <i>L. elongata</i> (Ech)
	SDF	7.12	1.84	-20.61	1.24	5.76	0.34	<i>Aricidea</i> sp. (Pol); <i>P. astula</i> (Biv); <i>A. brachiata</i> (Ech)
C12	SSDF	5.38	nd	-20.04	nd	4.57	nd	<i>S. scutata</i> (Pol)
	OMN	11.31	nd	-18.66	nd	5.34	nd	<i>Nereidae</i> nd. (Pol)
	P	7.89	0.56	-18.71	0.02	4.88	0.32	<i>L. yhleni</i> , <i>N. hystricis</i> (Pol)
	SF	7.10	0.68	-17.34	0.82	6.77	2.59	<i>O. fusiformis</i> (Pol); <i>L. elongata</i> (Ech); <i>Anthozoa</i> nd. (Ant)
	SDF	7.86	2.17	-18.01	0.64	5.64	0.30	<i>S. impatiens</i> (Pol); <i>P. astula</i> (Biv); <i>A. filiformis</i> (Ech)
C16	SSDF	5.76	nd	-19.46	nd	5.23	nd	<i>S. scutata</i> (Pol)
	OMN	10.42	2.55	-18.31	2.31	5.67	0.40	<i>D. neapolitana</i> , <i>N. lamellosa</i> (Pol)
	P	9.24	0.87	-18.33	1.35	6.07	1.23	<i>Glycera</i> sp., <i>Glycera unicornis</i> , <i>Lumbrinidae</i> nd., <i>N. hystricis</i> (Pol); <i>T. mutabilis</i> (Gast)
	SF	5.31	nd	-18.39	nd	5.47	nd	<i>C. gibba</i> (Biv)
	SDF	5.55	nd	-16.55	nd	nd	nd	<i>A. brachiata</i> (Ech)
C19	SSDF	6.21	nd	-18.17	nd	5.38	nd	<i>S. scutata</i> (Pol)
	SF	6.51	1.24	-20.41	2.99	6.09	0.69	<i>Hiattella artica</i> (Biv); <i>Upogebia typica</i> (Decap); <i>Virgularia mirabilis</i> (Ant)
	SDF	6.59	0.60	-16.72	1.10	5.76	1.27	<i>Brada villosa</i> (Pol); <i>Tellinmya ferruginosa</i> (Biv)
	SSDF	8.42	nd	-20.23	nd	5.32	nd	<i>Maldane glebifex</i> (Pol)
	P	9.35	1.29	-18.58	3.75	4.81	0.10	<i>L. yhleni</i> (Pol); <i>Processa</i> sp. (Decap)
C23	SF	7.08	1.54	-20.11	2.84	5.31	0.42	<i>S. pavonina</i> (Pol); <i>H. artica</i> , <i>Musculus subpictus</i> , <i>Ostrea edulis</i> , <i>P. rudis</i> (Biv); <i>Anthozoa</i> nd. (Ant)
	SDF	4.43	1.85	-19.10	2.76	6.27	0.86	<i>Turritella communis</i> (Gast); <i>Amphiura chiajei</i> (Ech)
	SSDF	7.61	3.56	-21.95	2.87	4.94	0.28	<i>S. scutata</i> (Pol); <i>Oestergrenia digitata</i> (Ech)
	P	7.09	0.10	-14.85	0.00	6.03	0.93	<i>Necallianassa truncata</i> , <i>Pisidia longimana</i> (Decap)

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