







## Article

# Characterization of the Meiobenthic Community Inhabiting the Zwin Coastal Lagoon (Belgium, the Netherlands) and the Role of the Sedimentary Environment

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## Abstract

Coastal waters are sensitive habitats that support high biodiversity and provide essential ecosystem goods. Changes in sedimentation regimes due to land-use and engineering activities in the coastal zone affect biodiversity and these habitats' ecological value. This study aims to characterize the meiobenthic communities inhabiting the Zwin tidal lagoon, located on the border between Belgium and the Netherlands, and to evaluate to what extent the sedimentological characteristics and the quantity and composition of organic matter influence the composition and distribution of meiofauna. The meiobenthic community showed traits of a well-established population dominated by nematodes, followed by copepods + *nauplii*. Notably, meiofauna rapidly colonized the area after its opening to the sea in February 2019 (two years before sampling), showing that even very weak tidal currents were sufficient to suspend and transport these animals to the new environment. Our results suggest that the Zwin lagoon is a productive system with high food quality (i.e., PRT/CHO  $\geq$  1), predominantly of marine origin. Major structural differences in communities were related to the sedimentary environments at the investigated stations and estimations of the quantity of food. The present findings confirm that sedimentary dynamics and depositional processes, through their influence on sediment properties (e.g., grain size) and organic matter's quantity and composition, shape meiofaunal communities and their vertical and horizontal distributions.

**Keywords:** meiofauna; tidal lagoon; Zwin Nature Park; anthropogenic activities; depositional environment



Academic Editor: Achim A. Beylich

Received: 9 August 2025

Revised: 5 September 2025

Accepted: 8 September 2025

Published: 9 September 2025

**Citation:** Baldrighi, E.; Alvisi, F.; Van Colen, C.; Grassi, E.; Catani, L.; Ape, F.; Vasapollo, C.; Manini, E.; Baguley, J.G.; Semprucci, F. Characterization of the Meiobenthic Community Inhabiting the Zwin Coastal Lagoon (Belgium, the Netherlands) and the Role of the Sedimentary Environment. *Water* **2025**, *17*, 2669. <https://doi.org/10.3390/w17182669>

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## 1. Introduction

Marine and coastal waters are sensitive habitats that support high levels of biodiversity and provide many essential ecosystem goods and services. In particular, the Belgian coastal zone hosts a complex of space- and resource-use activities with a myriad

of pressures [1]. The biodiversity found in coastal habitats is on the frontline of the current environmental change resulting from anthropogenic activities related to the expanding exploitation of coastal areas [2]. Changes in sedimentation regimes and suspended sediment concentrations resulting from changes in land-use and engineering activities in the coastal zone (e.g., dredging, aggregate extraction, beach nourishment) affect biodiversity and ecological value in coastal soft-sediment habitats [3]. Coastal lagoons, like estuaries, provide goods, services, and social benefits [4–6]. In coastal lagoons, the deposition of suspended sediments depends on interactions between geomorphological, hydrological, and biological factors [7]. Moreover, the role of the depositional environment has been recognized as a crucial factor for benthic organisms, who spend their entire life within or in strict contact with the sediments [8,9]. Larger, more mobile species, such as crustaceans and errant polychaetes, may escape unfavorable conditions, but sessile and less mobile organisms often succumb to induced stress [10,11]. The physico-chemical characteristics of sediment determine the environmental conditions that benthic organisms inhabit [12]. For instance, in a study conducted in the Po River lagoonal system [13], grain-size fractions and organic matter content were significant drivers of differences in macrofaunal bioturbation activity, diversity, and functional diversity. In [14], the authors reported how the complexity of the carbonate sediments characterizing Maldivian lagoons can deeply shape the structural and functional diversity of meiofauna nematodes. The results of altered sediment dynamics and changes in intertidal sediment properties can lead to drastic changes in the distribution, diversity, and biomass of benthic organisms [15,16], affecting higher trophic levels [17].

Meiofauna, a diverse group of microscopic organisms between 30–42  $\mu\text{m}$  and 1 mm in size inhabiting marine sediments, play a crucial role in nutrient cycling and ecosystem functioning [18]. This assemblage includes nematodes, copepods, kinorhynchs, and other small metazoans, which are particularly responsive to environmental disturbances, making them valuable biological indicators [19–21]. Meiofaunal activities modify a series of physical, chemical, and biological sediment properties. They often do so simultaneously by, for example, displacing sediment grains during burrow construction and displacing organic matter (OM) and microorganisms within the sediment matrix during feeding [9]. These modifications can directly or indirectly, and positively or negatively, affect various ecosystem services, including sediment stabilization, biogeochemical (nutrient) cycling, waste removal, and food web dynamics, at various spatial and temporal scales [22]. Understanding meiofaunal responses to changes in environmental conditions is thus essential for understanding the functioning of marine ecosystems and assisting in the proper management and conservation of a particular ecosystem service provided by the lagoons [6,23]. In this case, meiofauna can serve as a crucial early warning system for detecting ecosystem shifts and guiding conservation efforts [24].

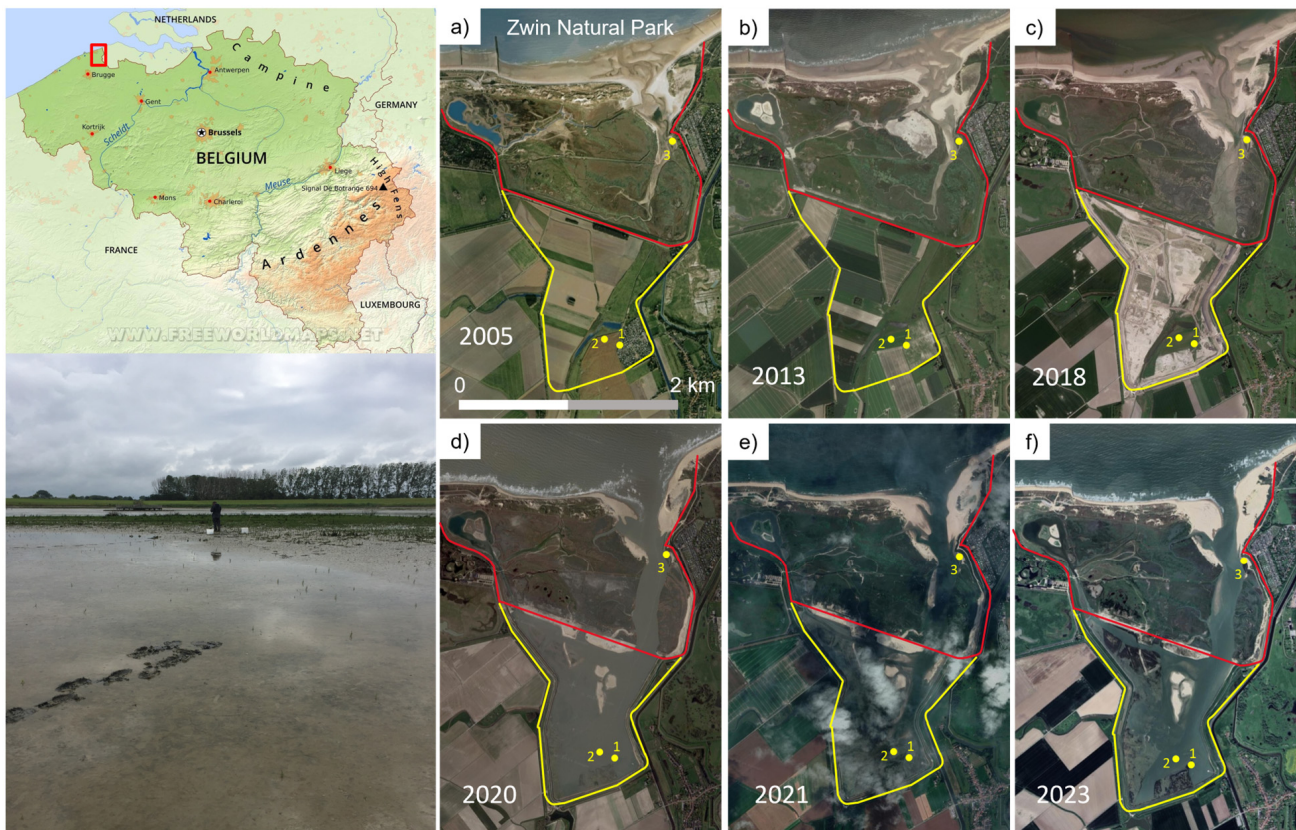
The Zwin Nature Park, located on the border between Belgium and the Netherlands, is a tidal lagoon that is included in the Ramsar list of wetlands of international importance and has been designated as a Natura 2000 area. Some studies have been dedicated to characterizing the macrobenthic populations inhabiting this area [17,25–27]. Macrofauna have been found to be largely affected by the sediment's physical properties, with higher biomass and diversity reported in finer sediments compared to those in coarser sediments [26]. Moreover, a strong relationship between macrobenthos–sediment interactions in structuring the nematode community after hypoxia has been reported [17]. However, no studies investigating the meiofaunal communities have been undertaken so far, thus leading to a clear lack of data on one of the most abundant and widespread benthic components, as well as the depositional environment.

This study aims to characterize the meiobenthic communities (i.e., abundance, diversity, composition, and spatial distribution) inhabiting the Zwin lagoon and to evaluate to what extent the sedimentological and depositional characteristics of the seafloor, along with the quantity and quality of food sources, influence meiofaunal composition and distribution. The main hypothesis tested is that sediment features and the quantity and quality of organic matter are reflected in the structure and spatial patterns of meiofaunal biodiversity. This is the first study investigating the meiobenthic community in this coastal lagoon, which is subject to continuous changes in sediment erosion and deposition dynamics due to natural aeolian and tidal transport, as well as anthropogenic activities [17]. The information provided here will serve as a tool to improve the management of the natural reserve.

## 2. Materials and Methods

### 2.1. The Study Area

The Zwin (51°21' N, 3°22' E) is the largest fully marine salt marsh environment in Belgium, covering nearly 180 ha of Belgian territory, with 125 ha of lagoons, gullies, and salt marshes with a semidiurnal tidal regime (i.e., with high tides occurring every ~12 h for 25 min and low tides in between) and 55 ha of sand dunes and tidal sandy beaches, with an additional 27 ha extending into the Netherlands. The nature reserve 'Het Zwin' was the first Flemish nature reserve, founded in 1952. It is a nature reserve recognized as an international bird and habitat directive area included in the Ramsar list of wetlands of international importance, and it has been designated as a Natura 2000 protected area. The salt marsh is at the level of spring high water, with the tidal amplitude there being ca. 4.5 m [28]. The Zwin area consists of a tidal inlet with a channel (the Zwin proper), intertidal sand flats, and salt marshes. The tidal environments are fronted by a narrow dune facing an even narrower beach. Landwards, it is bordered by dikes. The area west of the tidal environment, separated from it by a low dike, lies at altitudes around 5 m. The Flemish regional nature and forest agency, which took over the management of the Zwin in August 2006, planned to restore the rich biodiversity of this internationally important Natura 2000 site by carrying out large-scale restoration of the ecological dynamics in the Zwin area in 2018–2019. The objectives, among others, were as follows: (1) Deepening and enlarging of the main gully of the Zwin estuary (access to the sea and the channel for tidal movements of water) to restore the tidal dynamics in the whole area. (2) Enlargement of the Zwin area by removing the international dike, allowing the tidal system to expand onto a further 120 hectares of former agricultural land (Figure 1). The enlargement and deepening of the Zwin gully immediately improved the water dynamics throughout the entire Zwin area. As a result of the tidal area's expansion in 2019, the rising tide now enters the area more easily and rapidly. Consequently, even the most remote western sections are flooded better, with a greater water volume contributing to the strength of the outgoing tide and reducing the sedimentation further; see [29] and the references therein.



**Figure 1.** Top left: geographical location of the studied area (i.e., red rectangle; NW:  $51^{\circ}21'55''$  N– $3^{\circ}20'33''$  E; SW:  $51^{\circ}20'26''$  N– $3^{\circ}21'22''$  E; NE:  $51^{\circ}22'24''$  N– $3^{\circ}22'17''$  E; SE:  $51^{\circ}20'48''$  N– $3^{\circ}23'17''$  E); bottom left: the ‘new’ mudflat area of the Zwin tidal flat (photo by Elisa Baldrigli, UNR); right: evolution of the study area from 2005 to 2023 (a–f). The ZW21 field work was carried out in June 2021 (e). Red line: the Zwin Tidal ‘old’ area; yellow line: the ‘new’ area following the expansion after 2019; yellow dots: sampling stations (aerial photos from Google Earth).

## 2.2. The Field Sampling Strategy

Sediment samples for meiofaunal characterization and geological investigation were collected the 28th of June 2021 in the Zwin Natural Park (Belgian North Sea) from the older tidal mudflat (i.e., Old Area = OA) and from the more recent tidal area (i.e., New Area = NA). For sedimentological and geochemical characterization of the investigated areas, PVC cores (25 cm in length, with an 8.0 cm internal diameter) were manually collected at three stations. Two stations were in the muddy area of the NA along the Southern side: one in the main tidal channel (St.1) and one in the upper mudflat (St.2). Both stations, sampled with two replicates, are emerged during low tide and flooded quickly after the gully is filled. However, St.1, located at a lower level than St.2, shows the direct influence of the tidal channel. The third station (St.3) was situated in the sandy area of the OA, specifically on a small beach along the eastern side. Sediment cores for the meiofauna investigation were collected (yellow dots in Figure 1) at the same stations. At each station, six PVC cores with a 3.6 cm internal diameter were collected manually. Of these cores, three were used for the meiofauna analysis, and three were used to assess the composition of organic matter (OM) and the Chlorophyll-*a* (chl-*a*) content at the time of sampling.

## 2.3. The Sedimentological Analysis

The depositional pattern in transitional areas can be very different in space and time [7]. To evaluate the relationship between recent depositional dynamics and vertical chemical–physical microstructures, the cores dedicated to the sedimentological analysis

were analyzed and accurately described considering both surficial and subsurficial sedimentary records up to a 20–25 cm depth. For comparison with the meiofauna and OM data and for statistical purposes, only the top 3 cm was subsequently considered (see Table S1).

At the UGent lab, each core was cut longitudinally, and the sedimentary record was cleaned with a sharp knife and photographed and its lithological (i.e., clay, silt, sand) and sedimentological characteristics described (i.e., layering and structures, colors, hydration, oxidation, etc.). For each station, half of the core was sub-sampled for grain size, total organic carbon (TOC), and total nitrogen (TN). Carbon and nitrogen stable isotopes were measured every 1 cm to allow for a higher level of detail and a tight correlation with meiofauna. The second half was sampled according to the sedimentological characteristics, with the top 4 cm distinguished between more oxidized and hydrated samples and more compact and reduced samples. Then, some more layers were sampled along the deeper record according to the layering to characterize the sedimentary environment better and eventually shed light on the present vs. past depositional dynamics of the area. All samples were dried at 55 °C for 48 h, and water content, porosity, and bulk dry density were determined according to [30].

#### 2.4. Grain-Size Analyses

Aliquots (i.e., 10–15 g) of homogenized dry sediment samples for each layer of the core dedicated to the sedimentological analyses were slightly disaggregated and oxidized using a 10% hydrogen peroxide solution for 48 h (Carlo Erba, Rodano, Italy). Analyses were performed through wet sieving with a 63 µm mesh to separate sand from mud and then through dry sieving of sand to separate the different fractions. Shells were separated from sand fractions by sieving with a 2 mm mesh. Data were expressed as the weight percentage of the fraction of the dry sediment (% d.w.).

#### 2.5. TOC, TN, and Stable Isotope Analyses

The aliquots (i.e., 3–5 g) of homogenized dry sediment samples for each layer of the core dedicated to the sedimentological analyses were ground in a ceramic mortar prior to the analyses. Total organic carbon (TOC), total nitrogen (TN),  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  were analyzed using an Elemental Analyzer–Isotope Ratio Mass Spectrometry (EA-IRMS) system, consisting of a Thermo Fisher DeltaQ mass spectrometer connected to a Thermo Fisher Scientific FLASH 2000 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA, USA). The measurements were carried out at the Institute of Polar Sciences of the National Research Council (CNR-ISP) in Bologna, Italy. Prior to the analysis, the sediment samples were treated with 1.5N HCl in silver capsules to eliminate inorganic carbon, following the method outlined by [31]. The TOC and TN concentrations in the sediments were expressed as the weight percentage of the element in the dry sediment (% d.w.), whereas  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were taken as parts per mil (‰) from the international standard VPDB (Vienna Pee Dee Belemnite). The TOC-to-TN ratio (TOC:TN) was calculated as the molar ratio. The estimate errors are  $<0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $<0.3\text{‰}$  for  $\delta^{15}\text{N}$  based on replicates of the in-house standard, whereas the variation coefficient for the TOC and TN is better than 4%.

#### 2.6. Organic Matter and Chlorophyll-*a* Analyses

Sediment cores for the OM and chl-*a* analyses were sliced every 0.5 cm down to 3 cm and frozen in storage at  $-20\text{ °C}$  until analysis. In the laboratory, chl-*a* and phaeopigments were determined using the standard procedures [32]. The sum of the chl-*a* and phaeopigment concentrations was referred to as chloroplastic pigment equivalents (CPE). The total phytopigment concentrations were converted into carbon (C) equivalents using a conversion factor of 40 [33] and expressed as  $\text{mgC g}^{-1}$ . Biopolymeric organic carbon (BPC) was calculated as the sum of the carbon equivalents of carbohydrates (CHO), proteins (PRT),

and lipids (LIP) [34]. The PRT-to-CHO ratio (PRT:CHO) was then calculated and used as a descriptor of the nutritional quality of sedimentary OM. A PRT:CHO ratio >1.0 indicates relatively high quality and high food availability [35].

### 2.7. Meiofaunal Analyses

Once in the laboratory, the sediment cores dedicated to the meiofauna were immediately sliced as for the OM analysis (i.e., 6 layers of 0.5 cm each, named L1, L2, L3, L4, L5, and L6) down to a 3 cm sediment depth, where meiofaunal organisms are typically more abundant, and sieved through a 1000  $\mu\text{m}$  mesh. A 32  $\mu\text{m}$  mesh was used to retain the smallest metazoan organisms. The retained fraction was centrifuged 3 times with Ludox HS40 (diluted with water to a final density of 1.18  $\text{g cm}^{-3}$ ); fixed in a 4% formaldehyde solution; and stained with Rose Bengal (0.5  $\text{g L}^{-1}$ ) [36]. Meiofaunal organisms were counted and identified to the higher taxonomic level (i.e., phylum and/or order) according to [37] under a stereomicroscope. The density (no. of individuals per 10  $\text{cm}^{-2}$ ) and taxon richness (n. taxa) of the communities were calculated.

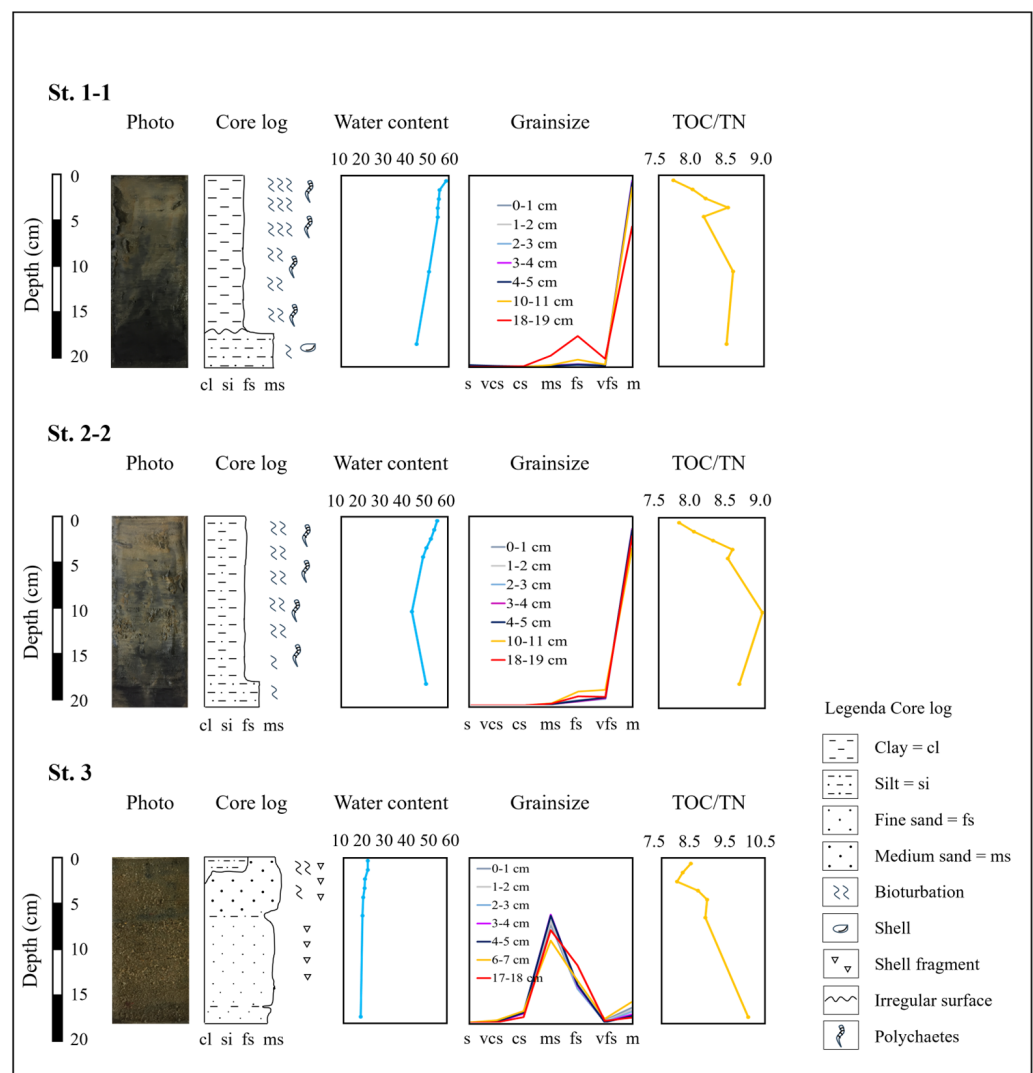
### 2.8. Statistical Analyses

Differences between stations as well as along the vertical distribution of total meiofauna abundance, the number of taxa, and meiofauna community composition were tested through a PERMANOVA (9999, number of random unrestricted permutations of raw data) analysis considering two factors as the main sources of variance: 'station' (i.e., fixed, three levels; St.1, St.2 and St.3) and 'layer' (i.e., random and nested in 'station', six levels; L1 to L6). The data were first square-root-transformed to give more relevance to less abundant taxa in the analysis [38], and then, the original matrix was converted into a Bray–Curtis similarity matrix. Where significant differences were obtained by the main test, a pairwise test was performed, and as there was a limited number of unique permutations, the  $p$  values were obtained from Monte Carlo tests [39]. A Permutational Multivariate Analysis of Dispersion (PERMDISP) test was applied to assessing whether differences among the sampling stations (between-group) were due to real differences in benthic community composition and not to differences in the multivariate dispersion of replicates (within group) among their respective centroids. A SIMPER analysis (cut-off: 80%) was used to identify the meiofaunal taxa that contributed to the dissimilarity among stations and sediment layers. Non-Metric Multidimensional Scaling (nMDS) was then used to visualize the differences in meiofaunal community composition among stations and layers. A PERMANOVA was also used as a univariate analysis (a robust ANOVA) of meiofaunal total abundance, the total number of taxa, and environmental variables after converting the original data matrix into the Euclidean distance. A principal component analysis (PCA) with the Euclidean distance was performed to highlight differences in environmental variables among stations and/or sediment layers. The purpose of the PCA is to create new multivariate variables that are a combination of the original variables. Each PC is uncorrelated with the others and accounts for a percentage of the total variance in the dataset. To assess which environmental variable most influenced the distribution of the meiofaunal abundance, diversity, and community structure (i.e., identification of higher taxa at the phylum and/or order level), a DistLM (Distance-Based Linear Model) was generated, after checking for highly correlated variables (a correlation cut-off of 0.8), which were excluded from the analysis. The following environmental variables were used: PRT, CHO, LIP, BPC, PRT:CHO, chl-*a*, phaeopigments, TOC, TN,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , TOC:TN, and grain size. This analysis was performed on normalized and transformed ( $\log x + 1$ ) environmental variables using a sequential stepwise selection procedure [38]. All multivariate analyses were performed using the software PRIMER v.7 with the PERMANOVA [38,40].

### 3. Results

#### 3.1. Environmental Variables

Regarding the depositional environment at the different locations, evidence of hypoxic/anoxic conditions was found only in the muddy cores from the NA, as previously suggested by direct visual inspection of the study areas and as is supported by the available data and maps (Figure 1). A slight indication of such conditions was detected only in the uppermost part of the St.3 core from the OA. The NA of the Zwin national park has a large variety of depositional environments typical of low-gradient muddy dynamic tidal flats that are also reflected in the sampled sedimentary records. Regarding the three stations sampled for the sedimentological analyses (Figure 2), the first two, namely St.1, sampled in the lower tidal mudflat in correspondence with the main tidal channel, and St.2, in the upper part of the tidal mudflat emerged during low tide, show very similar profiles, with only slight differences in grain size and OM content (Table 1).



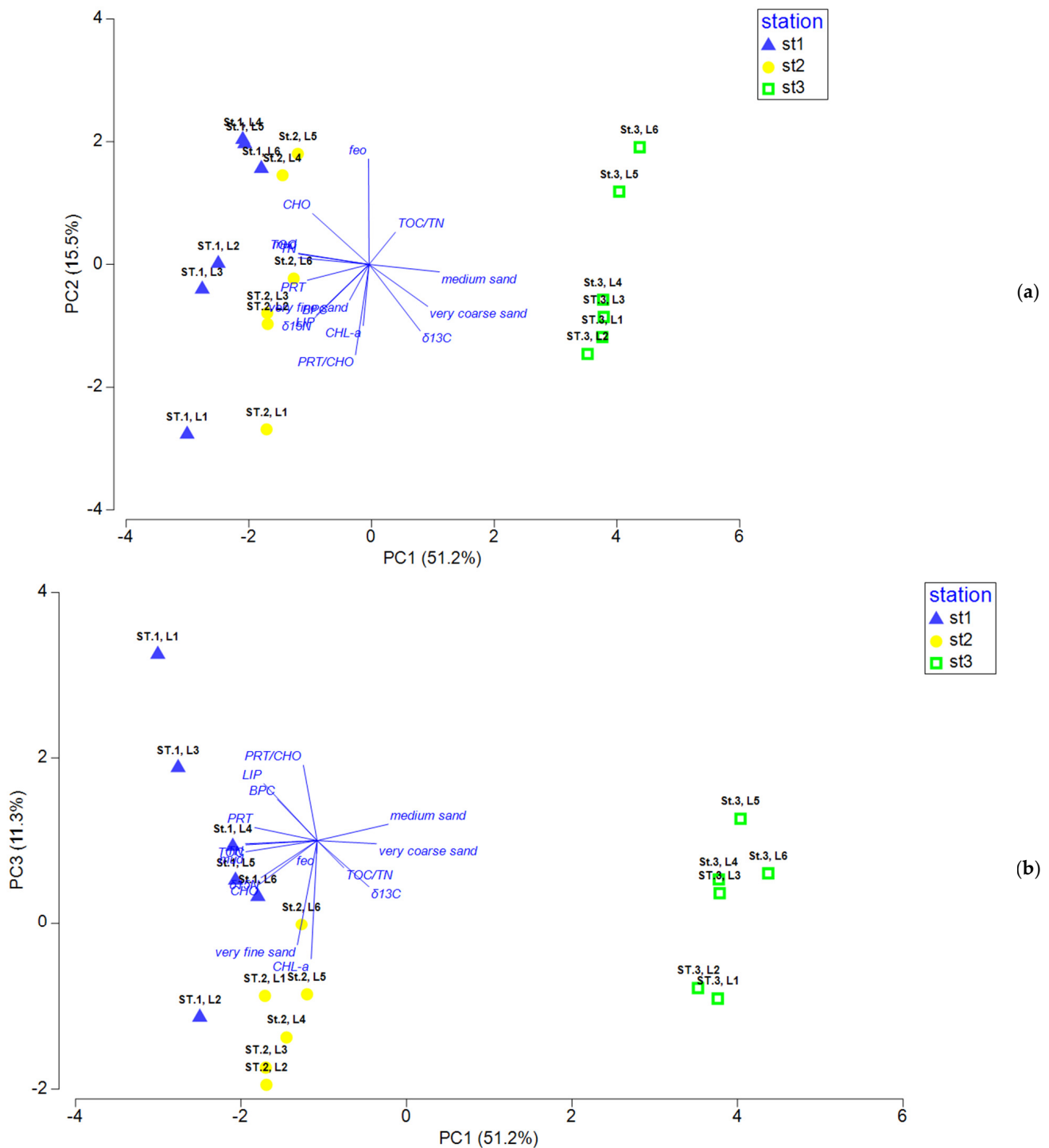
**Figure 2.** Lithological and sedimentological characteristics of the studied cores: Core log (cl = clay, si = silt, fs = fine sand, ms = medium sand); water content (% wet weight); grain size (horizontal scale: s = shell, vcs = very coarse sand, cs = coarse sand, ms = medium sand, fs = fine sand, vfs = very fine sand, m = mud; vertical scale: concentration in % dry weight); TOC/TN (molar ratio).

**Table 1.** Sediment features reported from the investigated stations. Abbreviations: BDD = bulk dry density; TOC = total organic C; TN = total N. Where available, all replicas are shown.

Station	From	To	Water Content	Porosity	BDD	Shells	Very Coarse Sand	Coarse Sand	Medium Sand	Fine Sand	Very Fine Sand	Mud	TOC	TN	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TOC/TN
	cm	cm	%	%	$\text{g cm}^{-3}$	% d.w.	% d.w.	% d.w.	% d.w.	% d.w.	% d.w.	% d.w.	% d.w.	% d.w.	‰	‰	Molar Ratio
St.1-1	0	1	58.85	77.68	0.55	0.00	0.24	0.16	0.72	1.52	0.96	96.40	2.06	0.31	−22.33	8.66	7.69
	1	2	55.71	75.38	0.61	0.00	0.00	0.00	0.36	0.99	0.63	98.03	1.99	0.29	−22.57	8.24	7.97
	2	3	55.41	75.16	0.61	0.00	0.00	0.00	0.41	0.90	0.55	98.14	1.95	0.28	−22.58	8.27	8.15
	3	4	54.90	74.77	0.62	0.00	0.00	0.15	0.54	1.08	0.61	97.62	2.23	0.31	−22.81	8.23	8.48
	4	5	54.97	74.82	0.62	0.89	0.44	0.09	0.35	0.98	0.53	96.72	2.11	0.30	−22.57	8.16	8.13
	10	11	50.68	71.44	0.71	0.00	0.00	0.00	0.83	3.63	1.15	94.40	1.87	0.26	−23.11	7.94	8.55
	18	19	44.86	66.45	0.83	0.00	0.00	0.21	5.81	16.12	4.08	73.77	1.65	0.23	−23.06	7.54	8.46
St.1-2	0	2	54.58	74.52	0.63	0.00	0.00	0.00	0.52	1.14	0.93	97.41	1.95	0.29	−22.41	9.33	7.97
	2	4	52.99	73.29	0.66	0.00	0.00	0.00	0.45	1.01	0.68	97.86	1.97	0.29	−22.54	9.17	8.02
	4	5	54.17	74.21	0.64	0.00	0.00	0.07	0.60	0.90	0.45	97.98	1.98	0.28	−22.56	9.08	8.14
	10	11	49.50	70.47	0.73	0.00	0.00	0.00	2.11	8.03	1.25	88.62	1.84	0.26	−22.74	8.94	8.15
	18	19	46.79	68.16	0.79	0.00	0.12	0.25	5.74	16.21	2.87	74.81	2.08	0.29	−22.95	9.18	8.42
St.2-1	0	2	50.43	71.24	0.71	0.00	0.00	0.00	0.69	2.07	3.66	93.59	1.71	0.25	−22.38	9.52	7.98
	2	4	47.65	68.90	0.77	0.00	0.00	0.00	0.58	2.58	4.45	92.39	1.77	0.25	−22.49	9.29	8.19
	4	5	46.05	67.51	0.80	0.00	0.00	0.00	0.66	3.22	4.80	91.32	1.82	0.26	−22.55	9.40	8.24
	10	11	37.31	59.16	1.01	0.13	0.13	0.00	0.98	9.33	13.25	76.17	1.05	0.15	−22.89	9.49	8.48
	18	19	41.73	63.55	0.90	0.00	0.14	0.00	1.43	5.08	1.72	91.64	1.89	0.26	−22.38	8.83	8.38
St.2-2	0	1	54.75	74.65	0.63	0.00	0.00	0.00	1.00	2.68	3.98	92.34	1.73	0.26	−21.83	8.50	7.78
	1	2	53.32	73.55	0.65	0.00	0.00	0.00	0.77	2.01	3.48	93.74	1.83	0.27	−22.26	8.41	7.99
	2	3	51.80	72.34	0.68	0.00	0.00	0.00	0.54	2.11	3.47	93.87	1.99	0.28	−22.42	8.05	8.27
	3	4	49.70	70.64	0.73	0.00	0.00	0.00	0.64	2.06	3.73	93.57	1.91	0.26	−22.71	7.82	8.55
	4	5	48.16	69.34	0.76	0.00	0.00	0.00	0.64	2.34	4.18	92.84	1.85	0.25	−22.57	8.07	8.48
	10	11	43.00	64.74	0.87	0.00	0.00	0.00	1.06	7.35	8.27	83.32	1.60	0.21	−22.95	7.92	8.98
	18	19	49.53	70.49	0.73	0.00	0.00	0.00	0.96	4.81	4.43	89.80	2.05	0.28	−22.79	8.15	8.65
St.3	0	1	21.20	39.57	1.51	0.25	1.47	7.00	59.70	20.79	1.55	9.25	0.44	0.06	−21.84	8.16	8.32
	1	2	21.24	39.63	1.50	0.00	0.98	6.79	61.89	21.54	1.10	7.72	0.48	0.07	−21.76	7.86	8.08
	2	3	19.93	37.74	1.55	0.00	0.47	6.06	65.40	20.73	0.69	6.64	0.32	0.05	−22.01	7.32	7.92
	3	4	19.72	37.42	1.56	0.15	0.42	5.63	65.72	22.41	0.57	5.10	0.26	0.04	−22.03	8.08	8.53
	4	5	18.95	36.27	1.59	0.00	0.76	6.24	65.09	23.18	0.44	4.29	0.26	0.04	−22.31	5.01	8.80
	6	7	18.60	35.74	1.60	0.46	1.66	7.23	49.90	25.61	2.49	12.64	0.27	0.04	−22.62	7.85	8.75
	7	18	17.71	34.38	1.64	0.00	0.42	3.61	56.35	35.00	1.35	3.27	0.16	0.02	−22.80	5.85	10.01

Oxidized and hydrated mud ranging in color from light gray to hazelnut brown was found in the upper 5–7 cm of the cores (96.4–98.1% d.w. in St.1 and 91.3–93.9% d.w. in St.2), likely due to the presence of several polychaeta galleries, approximately 0.5 cm wide and several centimeters long. Between a 7 and 15 cm sediment depth, the record becomes progressively gray, with vertical galleries of polychaetes still oxidized and hydrated. The mud content is in the range of 88.6–94.4% d.w. and 76.2–83.3% d.w. for St.1 and St.2, respectively. Then, it becomes increasingly darker gray to black and compact down to the bottom of the cores, where the mud content ranges within 73.8–74.8% d.w. and 89.8–91.6% d.w. for St.1 and St.2, respectively. In the upper part, the sand content ranges from 1.9 to 3.60% d.w. at St.1 and from 6.1 to 8.7% d.w. at St.2. Higher values were progressively recorded toward deep layers (8.4–26.2% d.w.). At St.3, the sedimentary record is characterized by rather homogeneous medium- (49.9–65.7% d.w.) to fine-grained (20.7–35.0% d.w.) sand, predominantly hazelnut-colored, with small shell fragments and some irregular darker muddy patches in the upper 4–5 cm, with the mud content decreasing from 9.3 to 4.3% d.w. with depth and at a depth of 6–7 cm (mud content: 12.6% d.w.). The distribution pattern of the TOC concentrations in the muddy stations was characterized by values ranging from 2 to 2.2% d.w. and from 1.7 to 2% d.w. in the surface sediments (0–5 cm) of St.1 and St.2, respectively (Table 1). At an intermediate depth (10–11 cm), the ranges were around 1.9% d.w. and 1.4% d.w. at the two stations, respectively. At a depth of 18–19 cm, ranges of 1.7–2.1% d.w. and 1.9–2.1% d.w. were found. As for TN, average values around 0.2–0.3% d.w. at all depths in both muddy stations were detected (Table 1). At St.3, total organic carbon (TOC) ranged from 0.5% to 0.2% d.w., and total nitrogen (TN) ranged from 0.1% to 0.02% d.w., decreasing from the top to the bottom of the core. The TOC:TN ratio in the surface sediments ranged from 7.7 to 8.5 at both muddy stations, with the lowest values observed in the 1–2 cm layers. With an increasing depth, the values ranged from 8.1 to 8.5 at St.1 and from 8.4 to 9.0 at St.2. At St.3, the TOC:TN ratios varied between 7.9 and 8.8 in the upper 5 cm, with the lowest value in the 2–3 cm layer, and reached 8.7 and 10.0 in the intermediate and deeper layers, respectively (Table 1). The  $\delta^{13}\text{C}$  values (Table 1) in the surface sediments at both muddy stations ranged from  $-22.8$  to  $-22.4$ ‰. At intermediate and deep layers, the values ranged from  $-23.1$  to  $-22.7$ ‰ at St.1 and from  $-23.0$  to  $-22.9$ ‰ at St.2. At St.3, the surface  $\delta^{13}\text{C}$  values ranged from  $-22.3$  to  $-21.8$ ‰, while intermediate and deep layers showed values of  $-22.6$ ‰ and  $-22.8$ ‰, respectively. As for  $\delta^{15}\text{N}$  (Table 1), surface sediments (0–5 cm) showed values ranging from 8.2 to 9.3‰ at St.1 and from 7.8 to 9.5‰ at St.2. Intermediate layers showed ranges of 7.9–8.9‰ and 7.9–9.5‰, while deep layers ranged from 7.5 to 9.2‰ and 8.2 to 8.8‰ at St.1 and St.2, respectively. At St.3, the  $\delta^{15}\text{N}$  values in the surface sediments ranged from 5.0 to 8.2‰, with intermediate and deep values of 7.9‰ and 5.9‰, respectively.

OM quality (i.e., PRT/CHO) and quantity as the concentration of proteins, carbohydrates, and lipids (i.e., total BPC) and chl-*a* sediment content are reported in Table S2. Overall, the quantity of OM decreased from St.1 to St.2 and St.3 (avg. BPC 7.5 mgC g<sup>-1</sup> vs. 5.7 mgC g<sup>-1</sup> vs. 4.3 mgC g<sup>-1</sup>, respectively). However, the quality of the OM remained comparable among stations (avg. PRT/CHO: 2.2 to 2.5) (Table S2). Phytopigments, chl-*a* (the 'fresh' fraction), and phaeopigments (the degraded fraction), collectively referred to as chloroplastic pigment equivalents (CPE), are commonly used as proxies for estimating primary production in the system. St.2 was characterized by the highest chl-*a* content (avg. 2.4 µg g<sup>-1</sup>) compared to that in all of the other stations, but the phaeopigments were comparable at all stations (avg. from 17.2 µg g<sup>-1</sup> to 19.2 µg g<sup>-1</sup>), and they constituted the majority of the phytopigments. Overall, a lower quantity and quality of OM and phytopigments were reported in the deepest sediment layers (Table S2). The multivariate characteristics of the sediments were investigated using the PCA (Figure 3a,b).



**Figure 3.** The PCA outputs for the environmental data of all stations and layers. (a) Ordination of sampling stations using the first and second principal components and (b) ordination of sampling stations using the first and third principal components. In brackets, the percentage of variability explained along each axis is given. Abbreviations: LIP = lipids; PRT = proteins; CHO = carbohydrates; BPC = biopolymeric carbon; chl-*a* = chlorophyll-*a*; fae = phaeopigments; TOC = total organic carbon; TN = total nitrogen.

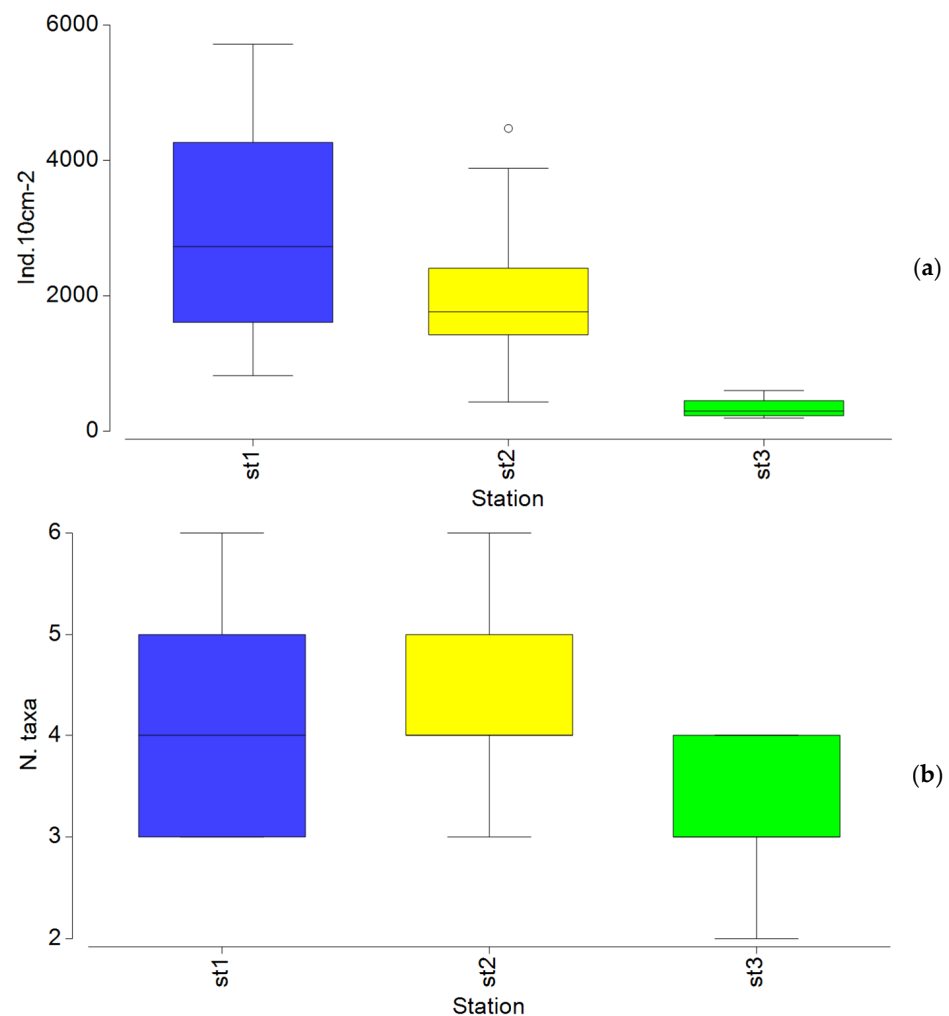
PC1 accounted for 51.2% of the total variance in the sediment characteristics across the stations. Grain size (higher % of sand at St.3) and the quantity (PRT, CHO, LIP, and TOC) and quality (TN) of OM (higher at St. 1 and St.2) loaded strongly on the PC1 axis (Table S3). Deeper layers were separated from shallower layers along PC2 (15.5% of the total variance explained), with the quality of the OM (PRT/CHO and PHAEO) loading strongly on this

axis. (Table S3 and Figure 3a). Along PC3 (11.3% of the total variance explained), a higher chl-*a* content and a higher percentage of very fine sand loaded strongly. This was especially evident at St.2 and in the top 1 cm of St.3, which separated these stations from St.1 (Table S3; Figure 3b). PC1, PC2, and PC3 accounted for a total of 78% of the variability between stations and layers. Although PC4 and PC5 had eigenvalues greater than one, they only accounted for 8.1% and 6.2% of the total variance, respectively, and are not considered further here.

### 3.2. The Meiofaunal Community

#### 3.2.1. Meiofaunal Abundance and Diversity

The mean total meiofaunal abundance in the first 3 cm of the sediment layer ranged from  $1865.6 \pm 250.7$  ind.10 cm<sup>-2</sup> at St.3 to  $18,253.1 \pm 6517.3$  ind.10 cm<sup>-2</sup> at St.1 (Table S4, Figure 4a). Meiofaunal abundance peaked between L3 (1–1.5 cm) and L4 (1.5–2 cm) at St.1 and at L2 (0.5–1 cm) at St.2, while at St.3, the total meiofaunal abundance decreased with an increasing sediment depth (Table S4). However, the PERMANOVA analysis reported significant differences in the meiofaunal abundance only between stations (Table 2); the PERMDISP test did not show any significant dispersion around centroids, confirming that the differences among the sampling stations were due to a real difference in meiobenthic total abundance (Pseudo-F = 11.24, P(perman) = 0.062).



**Figure 4.** Box plots showing (a) total meiofaunal abundance and (b) the number of higher taxa across all stations in the top three-centimeter layer. Minimum and maximum values and standard deviations are shown. White circle indicates outlier value.

**Table 2.** PERMANOVA results and pairwise tests for meiofaunal abundance and number of higher taxa. In bold are significant  $p$  values. Abbreviations: df = degree of freedom; SS = sum of squares; MS = mean of square; P(MC) = Monte Carlo test; st = station; la = layer; Res = residual. Bold numbers are significant P(MC) values.

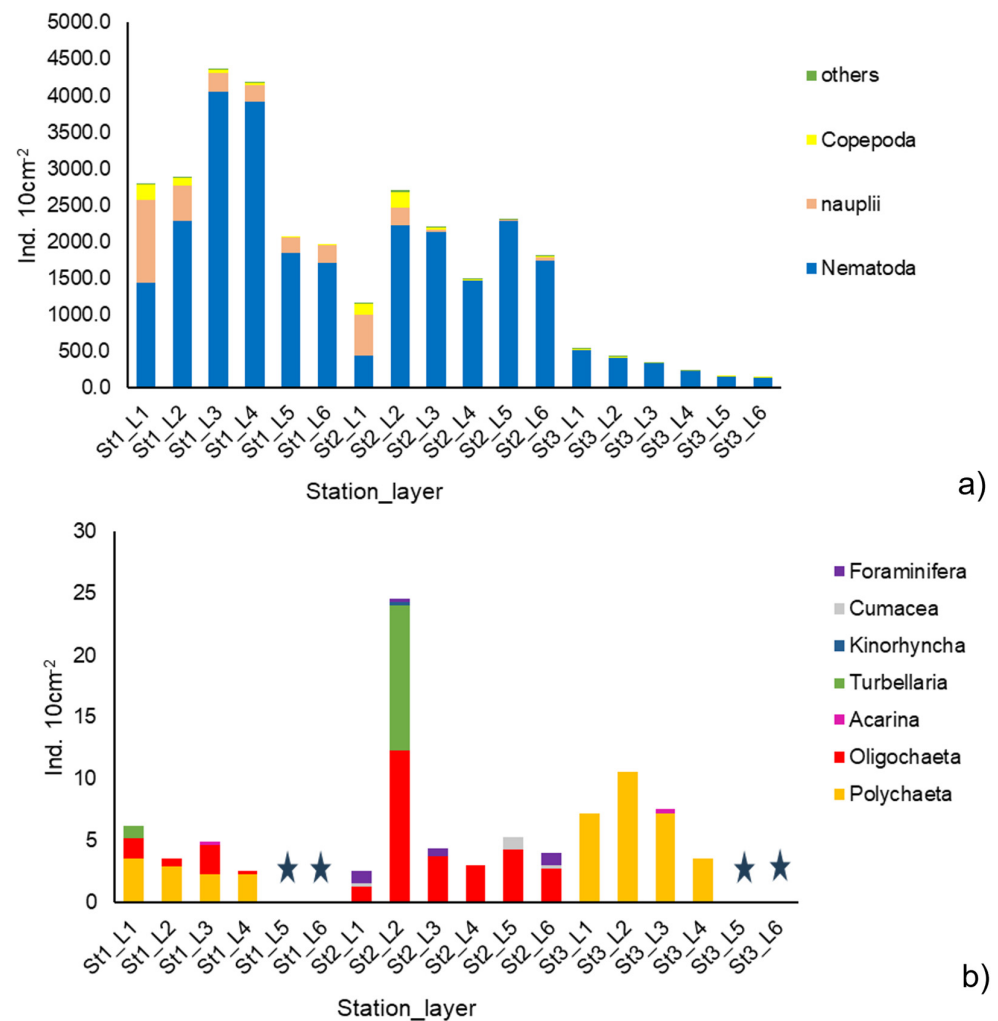
Total Abundance					
Source	df	SS	MS	Pseudo-F	P(MC)
st	2	11,699	5849.40	38.64	<b>0.001</b>
la(st)	15	2271	151.40	1.37	0.211
Res	36	3986.7	110.74		
Total	53	17,957			
PAIRWISE TESTS					
Groups	P(MC)				
st1, st2	<b>0.049</b>				
st1, st3	<b>0.001</b>				
st2, st3	<b>0.001</b>				
N. taxa					
Source	df	SS	MS	Pseudo-F	P(MC)
st	2	0.70	0.35	5.07	<b>0.028</b>
la(st)	15	1.03	0.07	2.21	<b>0.023</b>
Res	36	1.12	0.03		
Total	53	2.84			
PAIRWISE TESTS					
Groups	P(MC)	Groups (St1)	P(MC)	Groups (St3)	P(MC)
st1, st2	0.381	L1, L5	<b>0.013</b>	L1, L5	<b>0.019</b>
st1, st3	0.104	L1, L6	<b>0.009</b>		
st2, st3	<b>0.002</b>	L2, L5	<b>0.014</b>		
		L2, L6	<b>0.010</b>		
		L3, L5	<b>0.012</b>		
		L3, L6	<b>0.021</b>		
		L4, L5	<b>0.012</b>		
		L4, L6	<b>0.011</b>		

A total of 10 taxa were identified: Nematoda, Copepoda (adults + *nauplii*), Polychaeta, Oligochaeta, Halacaridae, Ostracoda, Platyhelminthes, Kinorhyncha, Cumacea, and Foraminifera (Table S4). The total richness ranged from  $4 \pm 1$  ( $\pm$ SD) to  $7 \pm 1$  ( $\pm$ SD) at St.3 and St.2, respectively (Figure 4b). Considering changes along the sediment's vertical profile, the diversity dropped in the last two sediment layers (L5 and L6) (Table S4). The PERMANOVA analysis reported significant differences in the number of taxa among stations and among sediment layers at St.1 and St.3 (Table 2); the PERMDISP test did not show any significant dispersion around centroids, confirming that the differences were due to a real difference in the number of taxa among stations (Pseudo-F = 0.09, P(permutation) = 0.912) and layers (Pseudo-F = 0.32, P(permutation) = 0.928). In detail, pairwise tests detected differences ( $p = 0.002$ ) between St.2 and St.3 and between surface layers L1–L4 and the deepest sediment layers L5 (2–2.5 cm) and L6 (2.5–3 cm) ( $p \leq 0.02$ ) (Table 2).

### 3.2.2. Meiofaunal Community Composition

Nematodes were the predominant meiofaunal component at all stations and across sediment layers. They were followed by copepods and their *nauplii* and by annelids (i.e., Polychaeta and Oligochaeta), whereas the other groups were sporadically detected (Figure 5a,b). The only exception was recorded at St.2 L1 (0–0.5 cm), where a higher abundance of copepods + *nauplii* ( $706 \text{ ind.}10 \text{ cm}^{-2}$ ) was detected compared to that of nematodes ( $442 \text{ ind.}10 \text{ cm}^{-2}$ ) (Table S4).

The taxonomic composition of the meiofaunal communities varied significantly ( $p = 0.001$ ) between stations and sediment layers (Table 3); the PERMDISP test did not show any significant dispersion around centroids, confirming that the differences among the sampling stations (Pseudo-F = 4.39,  $P$  (perm) = 0.070) and among layers (Pseudo-F = 0.13,  $P$  (perm) = 0.992) were due to a real difference in meiobenthic composition. In detail, the pairwise tests reported changes in the community composition among all stations; within each station, the meiofaunal community changed significantly along the vertical profile from the top 2 cm to the deeper layers (Table 3). At St.1, significant changes were reported mainly between L3 and L4 and the deepest layers, while at St.2 and St.3, the meiofaunal communities changed between L1, L2, and L3 and the deepest sediment layers (Table 3). The nMDS graphs (Figure 6) clearly showed major separation between St.3 and all of the other stations and a separation between the top 1 cm (L1 and L2) and all deeper sediment layers at St.1 and St.2.



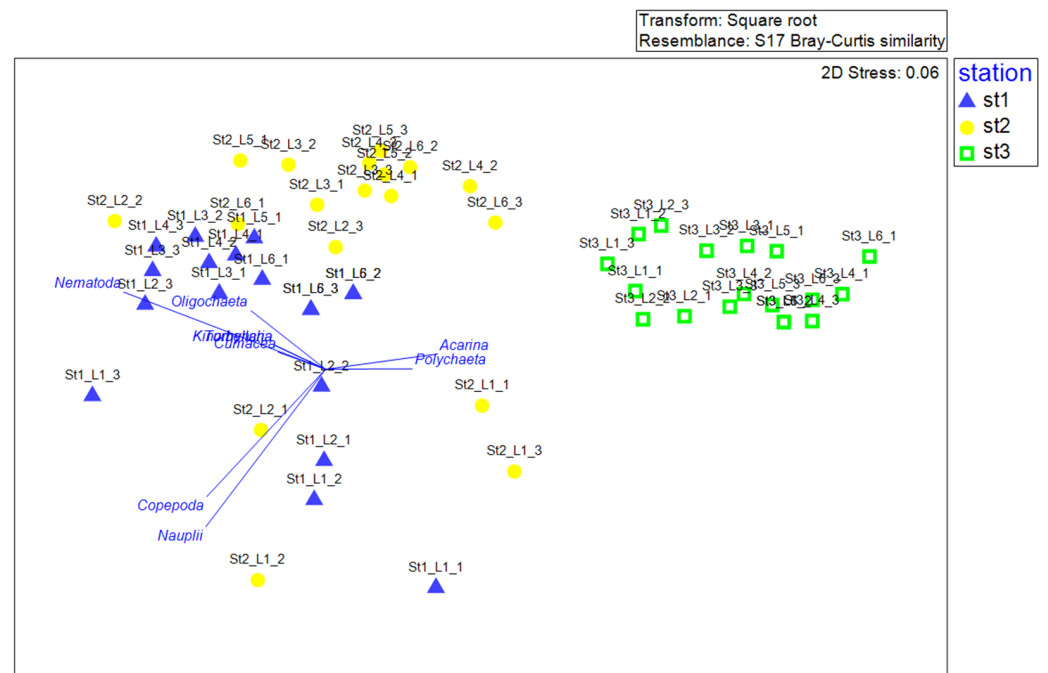
**Figure 5.** Bar plots showing the meiofaunal community composition characterizing all stations and layers. (a) A bar plot showing the most represented taxa (ind. 10 cm<sup>-2</sup>) of nematodes, copepods, and their nauplii; (b) a bar plot showing the contribution of less represented taxa (others). Blue stars indicate stations/layers where only nematodes and copepods + nauplii were reported.

Among stations, the SIMPER test (Table S5) disclosed the highest dissimilarity percentage between St.1 and St.3 (58%), while among layers, the highest dissimilarity occurred between L1 and L6 (36%). In all cases, the most represented taxa of nematodes, nauplii, and/or copepods contributed to the dissimilarity among stations and layers (Table S5

and Figure 6). However, when the SIMPER test was run again without considering the three dominant taxa, other meiofaunal groups were detected to determine the dissimilarities in the meiofaunal communities between stations and along the vertical sediment profile (Table S5 and Figure 6). In this case, the dissimilarity percentages ranged from 60% (St.1 vs. St.3) to 100% (St.2 vs. St.3), mostly due to Polychaeta, Oligochaeta, Cumacea, and Halacaridae (Table S5). As for the differences among layers, the highest dissimilarity percentages were reported between the shallowest layers and the deepest layers: from 69% (L2 vs. L5) to 73% (L1 vs. L5 and L2 vs. L6). Taxa such as Polychaeta, Oligochaeta, Halacaridae, Platyhelminthes, Cumacea, and Foraminifera contribute most to the high dissimilarity (Table S5 and Figure 6).

**Table 3.** PERMANOVA results and pairwise tests for meiofaunal community composition. In bold are significant *p* values. Abbreviations: df = degree of freedom; SS = sum of squares; MS = mean of square; P(MC) = Monte Carlo test; st = station; la = layer. Bold numbers are significant P(MC) values.

Meiofauna Community Composition					
Source	df	SS	MS	Pseudo-F	P(MC)
st	2	31,458	15,729	23.76	<b>0.001</b>
la(st)	15	9930.60	662.04	3.93	<b>0.001</b>
Res	36	6071.90	168.67		
Total	53	47,460			
PAIRWISE TESTS					
Groups	P(MC)	Groups (St1)	P(MC)	Groups (St2)	P(MC)
St.1, St.2	<b>0.025</b>	L3, L5	<b>0.020</b>	L1, L3	<b>0.022</b>
St.1, St.3	<b>0.001</b>	L3, L6	<b>0.018</b>	L1, L4	<b>0.015</b>
St.2, St.3	<b>0.001</b>	L4, L6	<b>0.023</b>	L1, L5	<b>0.019</b>
				L2, L4	<b>0.046</b>
Groups (St3)	P(MC)	Groups (St3)	P(MC)		
L1, L3	<b>0.019</b>	L2, L4	<b>0.026</b>		
L1, L4	<b>0.009</b>	L2, L5	<b>0.020</b>		
L1, L5	<b>0.001</b>	L2, L6	<b>0.014</b>		
L1, L6	<b>0.002</b>	L3, L6	<b>0.036</b>		



**Figure 6.** The nMDS ordination plot based on meiofaunal communities, comparing the meiofauna composition among stations. The taxa that contribute most to the station and layer grouping are superimposed onto the graph. All replicates are shown.



## 4. Discussion and Conclusions

### 4.1. Environmental Characterization of the Zwin Natural Park

The muddy sedimentary records from St.1 and St.2 represent the relatively calm depositional environment of the internal tidal plain, characterized by the slow and constant accumulation of material during tidal cycles. At St.1, the direct influence of the tidal channel resulted in the significant deposition of highly hydrated and oxidized mud. Bioturbation, mainly due to burrowing polychaetes (personal observation), occurred below a 10–15 cm depth, where the sediments turned blackish, indicating increasing hypoxic conditions (Figure 2). Such bioturbation caused mixing of the superficial sediments and promoted oxygen and water penetration into deeper layers [26,41]. St.2 showed a slightly higher concentration of medium–fine sand than that at St.1 and the presence of greater oxidation along the polychaete burrows and across the upper 15 cm. Below this depth, St.2 appeared very similar to St.1 (Figure 2). The presence of mud and fine sand at both stations favored the accumulation and preservation of OM (TOC: avg. 1.83 +/− 0.2; TN: avg. 0.26 +/− 0.03) [17]. In contrast, St.3, located on a dynamic sand flat with longer emersion periods during low tide, did not favor OM accumulation (TOC: avg. 0.31 +/− 0.1; TN: avg. 0.04 +/− 0.02), despite the surface sediments (0–3 cm) still showing relatively fresh marine OM concentrations (i.e., TOC/TN: avg. 8.11 +/− 0.2). In addition to isotopic ratios, the carbon-to-nitrogen (TOC/TN) ratio has been employed as a metric to evaluate the relative contributions of marine and terrestrial OM in certain ecosystems [42,43]. The overall distribution patterns in the surface and subsurface sediments of the TOC and TN concentrations at the three stations were closely correlated ( $r^2 = 0.993$ ), while the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values remained relatively stable (i.e., avg.  $-22.51\text{‰}$  +/− 0.3 and  $8.26\text{‰}$  +/− 1.0, respectively) despite differences in the TOC and TN concentrations, suggesting consistent quality and variable quantity of OM among stations (St.1 > St.2 > St.3). The use of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic ratios, along with TOC/TN ratios, provides a robust framework for tracing OM sources and understanding their contributions to sedimentary carbon storage [43]. In our case, when the TOC/TN ratio (TOC/TN: avg. 8.3 +/− 0.4) was considered with respect to the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, almost all samples showed a marine origin of POC [41,42], even if a slight increase with depth was recorded in the first two parameters, probably due to the loss of the freshest OM component with burial. Differently,  $\delta^{15}\text{N}$  showed a more or less constant decreasing trend with depth, particularly in the first 3 cm, suggesting the progressive use/consumption of the fresh component of the OM. Typically, the  $\delta^{13}\text{C}$  values for marine phytoplankton average  $\sim -20.5\text{‰}$  and the  $\delta^{15}\text{N}$  values in marine POM average  $7\text{‰}$ , while the TOC/TN ratios of marine sources typically range from 4 to 8, while terrestrial plant material often exhibits values greater than 12 [43]. The biochemical composition of sedimentary OM provides insight into its origin, quality, and availability [44]. OM degradation affects both its long-term burial [45] and benthic community metabolism [46]. The sum of PRT, CHO, and LIP (i.e., the BPC content) is a good indicator of OM's nutritional value [46], while the PRT/CHO ratio reflects its quality [47]. Phytopigments and BPC values reflect trophic conditions in marine sediments [48], and the Zwin lagoon data confirmed a high OM quality at all stations, with a lower concentration at St.3. It is known that the sediment deposition rate can influence sedimentary OM accumulation and that fine-grained components commonly show a high content in OM compared to that in coarse sediments [19,49], which may explain the generally low values of the latter at St.3. Comparing Zwin's trophic status (i.e., phytopigments and BPC contents) to that of other productive coastal and shallow systems worldwide [48,50] (Table 5) suggests that this lagoon is a productive system with a high food quality (i.e., PRT/CHO  $\geq 1$ ; [50]).

**Table 5.** A comparison of phytopigments, biopolymeric C sediment contents, and total meiofauna abundance (as ind./10 cm<sup>2</sup>) between different tidal systems and the present study. Abbreviation: Adr. Sea = Adriatic Sea; Tot. meioF. = total meiofaunal abundance.

Site	Depth (m)	chl- <i>a</i> (µg/g)	Phaeo (µg/g)	CPE (µg/g)	BPC (mgC/g)	PRT/CHO	Tot. meioF.
Goro lagoon, Adr. Sea *	1.5	1.7 ± 0.6	12.3 ± 2.2	14.1 ± 3.2	1.4 ± 0.3	0.9 ± 0.3	2713 ± 347
Lesina lagoon, Adr. Sea *	0.8	23.3 ± 1.7	20.2 ± 5.6	41.0 ± 4.3	8.1 ± 1.2	0.3 ± 0.03	1273 ± 490
Marsala lagoon, Sicily *	1.0	3.5 ± 0.6	3.1 ± 1.2	6.6 ± 1.8	6.5 ± 3.4	1.0 ± 0.1	50 ± 27
Caribbean Seagrass **	0.5	1.4 ± 0.2	8.7 ± 1.5	10.1 ± 0.7	1.77 ± 0.42	0.9 ± 0.3	1268 ± 731
Caribbean Mangrove **	0.5	4.8 ± 0.1	92.6 ± 5.0	97.4 ± 3.2	19.89 ± 0.89	0.5 ± 0.3	2474 ± 117
Caribbean Reef **	3.0	2.7 ± 2.8	34.7 ± 5.9	37.4 ± 3.9	1.79 ± 0.15	0.3 ± 0.2	2871 ± 1307
Red Sea Seagrass **	0.5	0.2 ± 0.1	16.4 ± 4.7	16.6 ± 2.7	0.54 ± 0.06	1.2 ± 0.1	1475 ± 166
Red Sea Mangrove **	0.5	0.1 ± 0.0	13.4 ± 1.4	13.5 ± 0.5	0.18 ± 0.02	4.0 ± 0.3	343 ± 41
Red Sea Reef **	2.0	0.4 ± 0.1	49.9 ± 8.0	50.3 ± 6.5	0.41 ± 0.07	6.7 ± 0.4	488 ± 253
Celebes Seagrass **	0.5	2.2 ± 1.0	20.4 ± 8.9	22.6 ± 6.4	7.17 ± 0.45	0.4 ± 0.3	1604 ± 267
Celebes Mangrove **	0.5	0.7 ± 0.3	4.0 ± 1.9	4.7 ± 0.8	2.35 ± 0.19	1.1 ± 0.2	627 ± 192
Celebes Reef **	5.0	1.0 ± 0.3	5.8 ± 1.1	6.8 ± 0.5	0.90 ± 0.08	0.6 ± 0.1	706 ± 271
St.1, Zwin park #	0.5	0.9 ± 0.1	7.6 ± 1.1	8.5 ± 1.1	8.7 ± 2.1	5.5 ± 1.0	2785 ± 2187
St.2, Zwin park #	0.5	3.3 ± 1.6	13.4 ± 7.5	16.7 ± 9.1	7.6 ± 1.1	4.3 ± 0.9	1151 ± 1093
St.3, Zwin park #	0.5	2.8 ± 0.6	8.8 ± 2.2	11.5 ± 2.6	5.2 ± 0.4	1.9 ± 0.5	544 ± 53

Source: \* [48]; \*\* [46]. # Present study = values reported here are from the top 1 cm for comparison with other studies.

#### 4.2. The Meiofaunal Communities Inhabiting the Zwin Natural Park: An Anthropogenically Created Lagoon

The present study represents the first effort to characterize the meiofaunal communities inhabiting the Zwin Natural Park and serves as a pilot for future research. Meiofauna are frequently overlooked in biodiversity assessments, resulting in a lack of understanding regarding their ecological status and the potential impacts of anthropogenic pressures [51]. However, their high species richness and rapid response to environmental changes make them promising indicators for ecological and biomonitoring studies, which is particularly important in the context of increasing human-induced stress [52,53]. To effectively use meiofauna for this purpose, it is first necessary to identify the taxa present and to understand how shifts in community composition and biotic interactions influence ecosystem functioning [54]. The meiofaunal abundance values reported in this study are consistent with those observed in other coastal and lagoonal environments in Belgium and worldwide [50,51,55,56] (see also Table 5). Although vertical variations in abundance were observed within the sediment profile, significant differences emerged between sampling stations (i.e., St.1 > St.2 > St.3). This decreasing trend reflects differences in depositional environments. The higher energy and wave mixing effect at St.3 is reflected in the accumulation of sand and a lower quantity and quality of OM compared to that at St.1 and St.2. These latter stations, more sheltered from a direct marine influence but subject to regular tidal inputs and affected by the recent enlargement of the tidal flat, favor the accumulation of sediments and fresh OM. Similarly, the meiofaunal diversity and abundance also declined at St.3 in comparison to those at the other stations. An overall decrease in the number of taxa moving deeper into the sediment layers was reported, particularly at St.1 and St.3, where nematodes and copepods + nauplii dominated the deepest layers. These trends can be ascribed to changes in sediment composition (coarse vs. muddy sediment) and to the active movement of meiofauna toward sediment layers that offer more favorable conditions [57,58]. However, at St.2, the number of taxa characterizing the deeper layers was comparable to that in the upper layers (L1–L3), possibly due to emersion at low tide and the downward migration of the organisms into deeper layers [56]. It has also been proven that individual meiofauna can redistribute within the sediments during the tidal cycle through sediment resuspension and hydrodynamic forces [59,60]. Some benthic organisms, such as harpacticoid copepods, can even appear temporarily in the water column, either passively, due to erosion, or because they have moved actively [61]. The meiofauna community composition in the Zwin lagoon was dominated by taxa commonly found in lagoons and tidal environments, such as nematodes, followed by adult copepods and their

*nauplii* [50,55,62]. Nematodes are considered the most adaptable meiofaunal group, capable of surviving in a wide range of environmental conditions [63,64]. The high abundance of copepods and their juvenile stages reported at all stations is also unsurprising since it has been reported that some copepods can survive stressful conditions [65]. The most sensitive taxa, on the other hand, are rare, often masked by the more abundant ones, and even disappear [66,67]. The presence of these less represented taxa (i.e., Polychaeta, Oligochaeta, Halacarida, Platyhelminthes, Cumacea, and Foraminifera), however, greatly contributed to the differences in the community composition between stations and along the vertical profile, otherwise wholly or partially masked in the analysis of the more abundant groups [68]. This behavior probably reflects the adaptation capacity of the meiofauna community to very specific depositional conditions, even at a small vertical and horizontal spatial scale of centimeters, typical of the tidal lagoon environments [60,69]. Some other taxa that are thought to be less tolerant, such as Kinorhyncha, Halacarida, and Cumacea [48,70–73], were found only at certain stations and sediment depth(s), underlining their preference for specific sediment conditions and/or avoidance of predation and competition pressure from other animals [72,73]. Platyhelminthes, usually characterizing beach and tidal sediments and recognized as voracious predators but flexible in their diet [51,52], were found only at St.2 L2. Since they can also prey on nematodes and other meiofaunal taxa [74], our findings suggest that they may have followed the nematodes toward the surface layer during low tide. Nematodes in fact showed some of the highest abundance in the same layer (i.e., L2–St.2). Members of the harpacticoid family Cletodidae are known to show high resistance (survival time) and high resilience (rapid reproduction) to anoxia [75]. Concerning benthic foraminifera, they are prevalent members of the meiobenthic community, and in soft sediments, the majority of them are infauna [76,77], and they are not often included in general benthos studies [78]. Commonly, metazoan meiofauna and soft-shelled foraminifera are extracted from sediment through centrifugation with Ludox [36]. However, with this procedure, most hard-shelled foraminifera remain in the sediment. In light of this, it is worth noting their presence specifically at St.2, even at deeper layers. Indeed, foraminifera have been found living at depths of 30 to 35 cm, suggesting that the most common benthic foraminifera inhabiting soft sediments operate near the lower limit of the oxic zone, with substantial populations often residing in suboxic or even anoxic sediments [79]. The Zwin lagoon's meiofaunal diversity, distribution, and community composition were highly variable across stations and sediment layers. We suggest that these characteristics are the results of the availability of several different sedimentary environments evolving dynamically in space and time. A rich meiobenthic community can in fact cope with rapid environmental changes even at a small spatial scale (i.e., among sediment layers) [80,81] and to changes in the quantity and biochemical composition of sediment OM under different trophic conditions [46]. Moreover, tides and the local morphodynamic conditions they induce may deeply influence the vertical distribution of meiofaunal organisms in response to temporal variability in physical and chemical (e.g., water content, light intensity, temperature, oxygen levels, salinity) parameters and ecological conditions (e.g., prey movement and competition) [54]. In fact, meiofauna may actively migrate to avoid harsh conditions and return to the surface when the interstitial environmental conditions improve [82,83].

In the case of the Zwin lagoon, it is interesting to note how meiofauna rapidly colonized and spread throughout the studied area after it was opened up in February 2019 (two years prior to sampling). Considering that meiofaunal organisms are generally poor swimmers, their dispersion usually occurs through passive suspension in the water column due to external forces (wave or currents, tides, bioturbation) [84]. Once in the water column, meiofaunal organisms may be carried long distances by oceanic currents [85]. Flooding of the Zwin lagoon by seawater from the North Sea in 2019 represented the

most reasonable and feasible way for adult and juvenile meiofauna to colonize these new habitats. Regular tidal cycles can also cause sufficient mixing to provide, mix, and disperse meiofauna [84]. During the colonization process, usually, harpacticoid copepods are known to be the pioneers, as active swimmers compared to other taxa, followed by nematodes, amphipods, polychaetes, and other meiofaunal organism [84,86]. However, in other cases, nematodes are reported to be the fastest and most abundant colonizers thanks to their rapid reproduction time [67,81,84,87] over a very short time scale (i.e., a few days to 9 months). No time series for meiofauna samples are available for the Zwin lagoon, and the first meiofauna sampling in this area, which occurred two years after it was opened up to the sea, is presented in this study. We can conclude that the meiofaunal community showed the characteristics of a typical lagoon area's meiofaunal population, dominated by nematodes and secondarily by copepods with their *nauplii*. Major structural differences in the meiofaunal communities were related to the depositional processes and sedimentary environments characterizing the investigated stations and, among them, the estimated quantity of organic matter. At the Zwin lagoon, meiofaunal colonization was quick and abundant, and even very weak tidal currents were sufficient to suspend and transport these animals to the new environment.

#### 4.3. The Influence of the Depositional Environment on the Meiobenthos

A previous study by [17] explored the relationship between sediment types and macrofauna in the Zwin Natural Park. Its species response models showed that the highest biomass of macrobenthic organisms occurred in organically enriched cohesive muddy sediments, with a marked decline in coarse sediments and in areas where sediment coarsening occurred over time. In contrast, the macrobenthos biomass increased in sheltered, shallow intertidal habitats, acting as sinks for fine sediments. The authors concluded that the physical properties of the sediment strongly influence the occurrence and biomass of microbenthic species. Similarly, changes in sedimentation regimes and sediment transport dynamics resulting from land-use and engineering activities can affect the functioning of shallow soft-sediment coastal habitats such as the Zwin lagoon. In this study, sedimentological variables (e.g., lithology and organic matter's quantity and composition) again emerged as key factors influencing meiofaunal abundance and diversity [9,23]. Sedimentary characteristics and hydrodynamics strongly affect the availability and accessibility of food for benthic organisms (e.g., [19,40]). The spatial differences in environmental conditions, as detected by the PCA, were reflected in the nMDS analysis of meiofaunal community composition. The clear separation of St.3 from the other stations and the grouping by sediment depth layers, both in terms of meiofaunal structure and the environmental characteristics, were supported by the DistLM results. These are like those reported in other ecosystems, e.g., [83,88,89]. Since the quantity and quality of organic matter drive the vertical sediment distribution of meiofauna, the high subsurface densities observed at St.1 and St.2 are likely attributable to the extensive quantity of relatively fresh marine phytodetritus [90,91]. The observed reduction in meiofaunal abundance and diversity moving from muddy shelter stations (St.1 and St.2) to the more exposed sandy environment at St.3 was therefore unexpected. Changes in the depositional environment can significantly affect meiobenthic communities, with cascading effect(s) on higher trophic levels and essential ecosystem functions [22]. Therefore, changes in meiobenthic communities may directly affect ecosystem functioning through biomass production or sediment reworking or indirectly by modifying the structure of other benthic size classes (see the review by [22]).

In conclusion, the hypothesis that depositional and sedimentological features, including OM quantity, composition, and quality, can influence the structure and distribution of the meiofaunal community is once again confirmed. Meiobenthos represents

a multifunctional group with a tight network of biotic interactions within and beyond its own size class [9,22]. The loss of or a decline in peculiar species or functional groups, such as basal organisms in food webs, can provoke a cascade of effects, with consequences for interacting species and ecosystem functions [92]. Therefore, anthropogenic activities that alter depositional dynamics, sedimentation regimes, and suspended sediment concentrations may affect the complex relationships between marine biodiversity, the surrounding environment, and the ecological functions that they sustain.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/w17182669/s1>, Table S1: Sedimentological parameters characterizing the three sampling stations and used for comparison with biological data. Abbreviations: BDD = bulk dry density; cs = coarse sediment; Ms = medium sediment; Fs = fine sediment; TOC = total organic carbon; TN = total nitrogen. Table S2: Organic matter content and phytopigment concentrations into the sediment characterizing the three sampling stations and at all sediment layers (L1–L6). Abbreviations: PRT = proteins; CHO = carbohydrates; LIP = lipids; BPC = biopolymeric C; Chl-a = chlorophyll-a; PHAEO = phaeopigments; CPE = chloroplastic pigment equivalents, std = standard deviation. Table S3: Principal Component Analysis of the environmental data involving all stations and layers. Eigenvalues for the PCs and loadings for each variable. Abbreviations: Eigenv. = Eigenvalues, Var. = variation, Cum. Var. = cumulative variation. Very cs = very coarse sand, ms = medium sand, very fs = very fine sand. Table S4: Abundance as ind./10 cm<sup>2</sup> of meiofaunal taxa and meiofaunal diversity as total number of higher taxa reported at all sampling stations and sediment layers (L1–L6). Table S5: SIMPER test output on meiofaunal community composition considering the contribution to dissimilarities between stations and layers of (A) all meiofauna groups and (B) less represented groups (the first four taxa which contributed most to the dissimilarities are reported). Abbreviations: Diss/SD = standard deviation; Contrib% = contribution to dissimilarity; Cum. = cumulative %.

**Author Contributions:** Conceptualization: E.B., C.V.C. and F.A. (Francesca Alvisi); methodology: E.B., C.V.C. and F.A. (Francesca Alvisi); validation: E.B., C.V.C., F.A. (Francesca Alvisi), E.G., F.A. (Francesca Ape), F.S., C.V., J.G.B. and E.M.; formal analysis: E.B., F.A. (Francesca Alvisi), E.G., F.A. (Francesca Ape), L.C., C.V. and E.M.; investigation: E.B., C.V.C. and F.A. (Francesca Alvisi); resources: E.B., C.V.C., F.A. (Francesca Alvisi), F.A. (Francesca Ape), F.S., C.V. and E.M.; data curation: E.B. and F.A. (Francesca Alvisi); writing—original draft preparation: E.B., C.V.C., F.A. (Francesca Alvisi), E.G., F.A. (Francesca Ape), F.S., C.V., J.G.B. and E.M.; writing—review and editing: E.B., C.V.C., F.A. (Francesca Alvisi), E.G., F.A. (Francesca Ape), F.S., C.V., J.G.B. and E.M.; project administration: E.B., C.V.C. and F.A. (Francesca Alvisi); funding acquisition: E.B., C.V.C. and F.A. (Francesca Alvisi). All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by European Union’s Horizon 2020 research and innovation program under grant agreement no. 730984. This study was supported by the project MeBOX, funded by the Assemble<sup>+</sup> program (contract number: ASSEMBLEPLUS202011906).

**Data Availability Statement:** The original contributions presented in this study are included in the article and Supplementary Materials. Further inquiries can be directed to the corresponding author.

**Acknowledgments:** Sampling was carried out using infrastructure funded by EMBRC Belgium—FWO international research infrastructure I001621N. We would like to thank B. Beuselinck of UGent for his help during the field work and T. Tesi of CNR-ISP for assistance with the TOC, TN, and stable isotope analyses.

**Conflicts of Interest:** The authors declare no conflicts of interest. The funders had no role in the design of this study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

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