



Article Linking Biodiversity and Functional Patterns of Estuarine Free-Living Nematodes with Sedimentary Organic Matter Lability in an Atlantic Coastal Lagoon (Uruguay, South America)

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Abstract: We examined the taxonomical and functional traits of free-living nematodes, focusing on their density by genus, maturity index (MI), and trophic diversity index (ITD) to determine whether these indices are sensitive to changes in the organic content of the sediment. Samples were collected in autumn and spring from 12 subtidal sampling stations in Rocha Lagoon, distributed between the outer (near the mouth) and the inner sector. We identified 26 genera, with higher abundance in the inner sector, likely due to increased organic matter and biopolymers. In spring, both sectors had sediments rich in fresh organic matter, dominated by deposit-feeding nematodes and showing low trophic diversity (high ITD values). In autumn, the inner sector maintained similar characteristics to spring sampling, while the outer one was dominated by older organic matter, predatory nematodes and higher trophic diversity. The MI showed low variation between sectors, suggesting a disturbed environment. Our findings support the use of ITD to assess other aspects of communities such as the response of trophic groups to the freshness of organic matter, while the MI seems less effective for assessing the ecological status of Rocha Lagoon. Understanding nematode biodiversity and functional traits is crucial for effective ecological quality assessments.

Keywords: Rocha Lagoon; benthic environment; soft sediment; environmental quality; biotic indices

1. Introduction

Biological distribution patterns remain one of the central issues in community ecology, especially in invertebrates [1–4]. Free-living nematode research is largely based on the description of a community's patterns through a taxonomic approach (e.g., species richness, abundance, and composition) and studies focusing on establishing relationships between the community and environmental variables [5,6]. However, the taxonomical composition can vary both spatially and temporarily and do not always reflect the ecological role that the species play in the ecosystem [7,8]. Moreover, changes in taxonomical composition do not necessarily imply changes in ecosystem stability [9,10].

In the current decade, functional trait-based approaches have been increasingly used to address several ecological-oriented questions, particularly to understand how different types of disturbances affect species' functional role [6,11–13] and related species/genera to functional diversity [14]. These biological traits consist of individually measurable properties that can be used comparatively among species/genera [15]. The biological trait analysis and the subsequent creation of functional groups (i.e., groups of species or genera with the same ecological function) has allowed us to obtain information on ecosystem functions [16], revealing additional relationships in the assemblages and environmental conditions [17].



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Free-living nematodes are of interest because they are, generally, the meiofauna dominant group and show a great diversity of species/genera. Benthic nematodes have a great diversification of nutritional requirements and contribute to energy flow in the sediment where they complete their entire life cycle [5,6,18,19]. We can obtain information of functional traits such as trophic group using mouth morphology [20] in addition to other traits associated with the life history strategy. These traits reflect evolutionary adaptations to persist in a particular environment [21,22]. Among the functional approaches in nematode studies, the "index of trophic diversity" (ITD) [18] emerged as a useful tool in environmental monitoring [6,23]. The ITD can reflect disturbance when a change in the food availability affects the trophic composition of the community. An increase in the ITD (associated with the dominance of a trophic group) usually indicates an increase in environmental stress [18]. Another generally used functional index is the maturity index (MI) [22], which is based on classifying nematodes according to their degree of resistance (colonizers) or sensitivity (persistent) to disturbances.

The benthic nematode abundance in estuaries responds to food availability [24,25], the state of degradation and energy value of sedimentary organic matter [11,26], salinity [27,28], and grain size [29,30]. However, little is known about the functional response of nematodes to environmental changes compared to classical ecological approaches. [6,12,13]. Specifically, it is still unclear if nematodes' functional attributes are determined by the same environmental variables as their taxonomical attributes [17]. A combined taxonomic and functional approach is an effective tool in ecological research [6,31], although many researchers agree that this relationship is still not fully established in the case of nematodes [32–35].

Our work aimed to establish the taxonomic diversity of nematodes (at the genera level) and to determine whether those functional attributes (feeding types and life strategies) are sensitive to changes in the organic content and biochemical composition of the sediment in an open/closed coastal lagoon of South America (Rocha Lagoon, Uruguay). Within this framework, relationships between taxonomic and functional diversity and abiotic and biochemical environmental features were explored. Our hypothesis was that the feeding types are strongly related to changes in the organic content and biochemical composition of the sediment of the estuarine lagoon and are hence useful for monitoring the status of the community in response to eutrophication.

2. Materials and Methods

2.1. Study Area and Sampling Design

Rocha Lagoon, Uruguay (34°39′47.42″ S, 54°13′47.36″ W), is a shallow, choked-type lagoon [36,37] with 72 km² in area and an intermittently open–closed connection with the Atlantic Ocean, driven by the alternation of the natural and artificial opening of the sand bar [38–40]. Its sand bar constitutes the most fragile component of the lagoon and influences the provision of most ecosystem services (e.g., water quality maintenance and flood control), and therefore plays a key role in preserving the balance of the socio-ecological system [41]. The lagoon supports one of the most important continental fisheries of the Uruguayan coast [42] and has suffered a rapid development of tourism as well as an intensification of land use on its margins [43,44].

In taking into account that ecological processes vary with the scale of observation [45,46] and particularly how in this study area the great environmental heterogeneity determined complicated relationships between biota and the environment [47,48], samples were taken at three spatial scales, which included (i) two clearly differentiated zones (mouth or outer sector and inner sector, kilometer scale), (ii) sites within each sector (hectometer scale), and (iii) replicates at each site (meter scale). The outer sector is located from the mouth of the lagoon (sand bar has an intermittently open–closed connection with the Atlantic Ocean) to the line of dunes, while the inner sector extends from the projection in the water of the line of dunes toward the interior of the lagoon. The choice of these sectors is based on pre-existing information about hydrodynamic and morphodynamic characteristics; the

outer sector is characterized by sandy sediments and high hydrodynamics, while the inner sector is dominated by sand–muddy sediments characteristic of more protected environments [47,48]. In addition to previous knowledge that meiofaunal communities respond differently to these two environmental conditions [25], within each sector, 6 sites were chosen (Figure 1), where the sites in the outer sector were located in a transect parallel to the coastline (O1 to O6). Sites in the inner sector were randomly chosen in areas of known low energy [48], three in the central body of the lagoon (I1 to I3) and three in the area of the old sand bar (I4 to I6).



Figure 1. Map of the study area showing the sampling sites located in the inner (I1–I6) and outer (O1–O6) sectors of Rocha Lagoon.

In order to consider possible temporal variation in the nematode community and environmental variables, samples were carried out two times: November 2014 (spring) and April 2015 (autumn). Our decision to choose the seasonal timing was based on pre-existing information on the spatio-temporal variation in the trophic state of sediments evidenced by biopolymeric ratios [49], which reported the presence of fresh organic matter in the inner sector of the lagoon in autumn and a higher energetic value of sediments in spring compared to autumn, attributed to seasonal productivity differences.

2.2. Sample Collection and Analysis

Water salinity and temperature were measured in situ using a YSI® multi-parameter device (model 63). Cumulative rainfall recorded at the Rocha station 10 days before spring and autumn sampling was obtained from web database Meteomanz © (VMO index = 86565) [50]. Sediment samples and fauna were taken by autonomous diving because of the shallow habitats (<2 m). Sediment samples were collected for an analysis of the total organic matter (OM), photosynthetic pigments, biopolymers of the OM (three replicates for each analysis), and sediment size analysis (one replicate). Photosynthetic pigments (chl-a and phaeopigments) were analyzed according to Lorenzen (1967) [51], modified by Sündback (1983) [52] for sediments. The total organic matter (OM) was analyzed based on Byers et al. (1978) [53] and expressed as a percentage (%). The biochemical composition of the OM was analyzed following the protocols described by Danovaro (2010) [54]. Total protein (PRT) analysis was conducted according to Hartree (1972) [55], modified by Rice (1982) [56] to compensate for phenol interference. Total carbohydrates (CHO) were analyzed according to Gerchakov and Hatcher (1972) [57]. Total lipids (LIP) were extracted by ultrasonication with a mixture of chloroform–methanol (1:2 v/v) and analyzed following the protocol described by Marsh and Weinstein (1966) [58]. Blanks for each analysis were performed with precombusted

sediment (450 °C, 4 h). PRT, CHO, and LIP concentrations were expressed as bovine serum albumin, glucose, and tripalmitine equivalents, respectively. PRT, CHO, and LIP concentrations were converted to carbon equivalents assuming a conversion factor of 0.49, 0.40, and 0.75 μ g, respectively [59]. The sum of PRT, CHO, and LIP carbon equivalents was reported as the biopolymeric carbon (BPC) and used as a reliable estimate of the labile fraction of OM [60] and to classify the trophic status of the sediments. Also, the PRT: CHO and the CHO: LIP ratios were calculated and used as indicators of the status of biochemical degradation processes [26].

Meiofaunal samples (three replicates for site) were taken with a PVC corer (2.7 cm inner diameter, 6 cm depth) and preserved in 4% formaldehyde. In the laboratory, the content of each sample was washed between a 500 and a 63 µm sieve using filtered water to segregate macro- and meiobenthic organisms, respectively [61]. To extract the meiofauna from the sediment fraction, retained on the 63 μ m sieve, we applied a flotation technique using Ludox HS 40 colloidal silica (1.18 g cm⁻³) and centrifugation [18,62]. This process was repeated three times, whereby the supernatant Ludox containing the meiofaunal organisms was decanted and washed each time. The final washed and extracted sample was then preserved in 4% formaldehyde, and a small amount of Rose Bengal was added to facilitate identification. All nematodes extracted from each sample were counted under a stereomicroscope. A set of 100 nematodes was randomly picked from each sample and mounted on glass slides for genus identification under the microscope. Before permanently mounting in glass slides, nematodes were placed in a solution of glycerol-ethanol and allowed to evaporate in a desiccator so that the organisms remained in glycerin, facilitating the observation of their structures. Nematodes were identified until the genus level, using pictorial key identification [63–65] and the online identification keys/literature available in the NeMys database [66].

2.3. Structure of Nematode Assemblages and Biological/Functional Traits

The richness (as the number of genera) and abundance of nematodes per genus (as individuals per 10 cm²) were determined for each sample, and then nematode genera were classified according to two functional traits:

(i) Life history strategies: each genera identified was classified according to its life strategy on the spectrum of colonizer–persister (c-p score) [21,22]. The scale is defined from extreme colonizers (c-p score = 1) to extreme persisters (c-p score = 5). The maturity index (MI) of the community was calculated using the following formula [22]:

$$MI = \Sigma (v_{(i)} \times f_{(i)})$$

where $v_{(i)}$ = the c-p value of genus i, and $f_{(i)}$ = the relative frequency of genus i.

(ii) Trophic groups: nematode genera were assigned to feeding types according to Wieser's (1953) classification based on the morphology of the buccal cavity–selective deposit feeder (1A), nonselective deposit feeder (1B), epigrowth feeder (2A), and omnivore/predator (2B). This classification was used to calculate the index of trophic diversity (ITD) [18], calculated as

ITD =
$$\Sigma \theta^2$$

where θ is the percentage contribution of each trophic group according to Wieser (1953) [20]. ITD values range between 0.25 (high trophic diversity: the 4 groups have a representation of 25%) and 1.0 (low trophic diversity: a single trophic group dominates at 100%).

2.4. Statistical Analysis

Multi- and univariate techniques were used for data analysis using the softwares PRIMER 6.0.2 [67], STATISTICA 10.0 from StatSoft, and R (R Development Core Team, 2020) [68].

We performed 2-way ANOVAs to establish statistical differences in water variables (temperature, salinity, pH, and depth) between sectors and time.

To establish taxonomic and functional patterns, we selected all genera with abundances greater than 30 individuals (in at least one of the sectors), total abundance, ITD, MI, and trophic groups (1A, 1B, 2A, 2B) for additional analysis. The responses of nematodes (taxonomic and functional structure) to the sediment attributes (OM, granulometry, biopolymers, chl-a, and phaeopigments) and nematode assemblages–taxonomic (richness and abundance per genera) and functional structure (MI and ITD) to consider estuarine sectors. The data were analyzed separately by sampling time, with sites nested within sectors. The glmm on gamma distribution failed to converge; we then fitted models based on the Gaussian distribution (R package: R Development Core Team, 2020) [68]. For sediment fractions, however, we had only a single replicate sample per site; here, a site represents a replicate unit, and we did not run mixed modeling.

Also, the distribution of environmental variables along the estuary were visualized by performing principal component analysis (PCA) based on previously standardized environmental data with all samples from both sampling times (data from autumn and spring).

Non-metric multidimensional scaling (n-MDS) using the Bray–Curtis similarity measure was performed to order the sampling sites according to nematofauna attributes: (i) the relative abundance of trophic groups and (ii) $\log x + 1$ genus abundance, for each one of the two sampling times. The n-MDS was performed using 999 permutations.

3. Results

3.1. The Environment

The abiotic variables measured in situ in both times (November 2014 and April 2015) are shown in Table 1. None of the sampled sites exceeded two meters of depth; however, greater depths were recorded at all sites in spring (non-significant differences). The water temperature showed seasonal values typical of Southern Hemisphere temperate latitudes. In both samplings, the temperature did not exceed 25 °C, with significantly higher values in spring than in autumn (F (1.20) = 4.96, *p* < 0.05). Water pH showed marine water conditions both in spring and autumn, with higher values in the outer sectors than in the inner ones (F (1.20) = 6.11, *p* < 0.05). In addition, homogeneous salinity values were recorded in all sampling sites in spring, while in autumn, significantly higher values were observed in the outer sectors (F (1.20) = 21.04, *p* < 0.01). The sand bar remained open in both sampling; in spring, the sand bar was opened artificially a few days before the sampling. Approximately one month before the autumn sampling, the sand bar was naturally opened by wind action. The accumulated rainfall recorded at the Rocha station 10 days before the spring sampling was 58 mm, while in autumn, it was 13 mm (Meteomanz © 2005–2023, VMO index = 86565) [50].

Table 1. Water column environmental variables recorded in situ for both sampling times: spring and autumn, respectively. O1-O6: outer sites; I1-I6: inner sites.

		Spring	Autumn							
Sites	Depth (m)	Temperature (°C)	Salinity	pН	Depth (m)	Temperature (°C)	Salinity	pН		
O1	1	22.1	7.8	8.23	0.3	20.4	24.3	8.84		
O2	1	21.7	7.9	8.35	0.6	20.6	25.1	8.67		
O3	1	23.3	8.4	8.59	0.3	22	26	8.42		
O4	1.2	23.1	8.2	8.59	1.6	20.9	26	8.01		
O5	1	22.5	7.7	8.39	0.2	20.1	19.7	8.58		
O6	0.7	23.3	8	8.5	0.3	20.8	19.4	8.56		
I1	1.8	21.4	7.4	8.08	1.7	18.8	17.2	8.2		
I2	1.8	21.6	7.2	8.06	1.6	18.5	17.1	8.26		
I3	1.6	21	6.4	8	1.6	18.5	17.1	8.25		
I4	1.2	21.3	7.6	8.37	0.3	22.9	16.5	8.3		
I5	1	22.3	8.2	8.49	0.5	23	16.9	8.54		
I6	0.7	22.6	8.2	8.43	0.3	24.1	17.2	8.32		

The inner sector showed higher values of OM, Chl-a, phaeopigments, PRT, CHO, LIP, mud, fine sand, and gravel than the outer sector (Table 2, Figures 2–4). These differences between sectors were consistent in both times, except for the case of Chl-a, which in autumn showed similar average values among sectors (Figure 3). Also, in autumn, fine sand showed a higher proportion in the inner sector, while in spring, it presented similar values in both sectors (Figure 2). The outer sector showed higher values of coarse sand in both times (Table 2, Figure 2).



Figure 2. Grain size characteristics in sites of the inner (I) and outer (O) sectors of Rocha Lagoon, for both sampling times: (**a**) spring; (**b**) autumn.





Figure 3. Organic matter and photosynthetic pigment content in sediments of sites located in the outer (O1–O6) and inner (I1–I6) sectors of Rocha Lagoon for both sampling times. Error bars are standard deviations. (a) Organic matter. (b) Phaeopigments. (c) Chlorophyll a.

				1						
			Spi	Autumn						
Mode	el	Estimate	Std Error	t Value	Pr(> t)	Estimate	Std Error	t Value	Pr(> t)	
ОМ	Intercept Sector	0.009142 0.057063	0.007571 0.011086	1.208 5.147	$\begin{array}{c} 0.227 \\ 2.64 \times 10^{-7} *** \end{array}$	0.007983 0.030412	0.007302 0.010326	1.093 2.945	0.27427 0.00323 **	
Chl-a	Intercept Sector	3.830 16.849	3.088 4.457	$\begin{array}{c} 1.24 \\ -3.78 \end{array}$	0.214812 0.000157 ***	8.309 4.204	2.149 3.039	3.866 1.383	0.000111 *** 0.166633	
Phaeopig	Intercept Sector	1.019 24.017	3.320 4.856	$0.307 \\ 4.946$	$\begin{array}{c} 0.759 \\ 7.56 \times 10^{-7} \ *** \end{array}$	2.977 12.139	2.513 3.555	1.184 3.415	0.236310 0.000637 ***	
PTR	Intercept Sector	1.0065 2.6729	0.3300 0.4854	3.050 5.507	$\begin{array}{c} 0.00229 \; ^{**} \\ 3.65 \times 10^{-8} \; ^{***} \end{array}$	0.8762 1.7048	0.2899 0.4099	3.023 4.159	$\begin{array}{c} 0.0025 \ ^{**} \\ 3.2 \times 10^{-5} \ ^{***} \end{array}$	
СНО	Intercept Sector	0.8438 0.9905	0.2412 0.3545	3.498 2.794	0.000469 *** 0.005210 **	1.1689 0.8342	0.2677 0.3786	4.367 2.204	$\begin{array}{c} 1.26\times10^{-5}\text{ ***}\\ 0.0275\text{ *} \end{array}$	
LIP	Intercept Sector	0.1891 1.0033	0.1581 0.2303	1.196 4.356	$\begin{array}{c} 0.232 \\ 1.33 \times 10^{-5} *** \end{array}$	0.3026 1.0558	$0.1709 \\ 0.2417$	1.771 4.369	$\begin{array}{c} 0.0766 \\ 1.25 \times 10^{-5} \ *** \end{array}$	
BPC	Intercept Sector	0.8211 2.6098	0.1936 0.2738	4.242 9.533	$\begin{array}{l} 6.86\times10^{-5}~^{***}\\ 3.71\times10^{-14}~^{***}\end{array}$	1.1238 1.9609	0.2925 0.4137	3.842 4.740	$\begin{array}{c} 0.000122 \ ^{\ast\ast\ast}\\ 2.14 \times 10^{-6} \ ^{\ast\ast\ast}\end{array}$	
Gravel	Intercept Sector	522.4 512.2	108.5 108.6	$4.814 \\ -4.718$	$\begin{array}{c} 2.99 \times 10^{-5} *** \\ 3.97 \times 10^{-5} *** \end{array}$	522.4 512.2	108.5 108.6	$\begin{array}{c} 4.814\\-4.718\end{array}$	$\begin{array}{c} 2.99 \times 10^{-5} \ *** \\ 3.97 \times 10^{-5} \ *** \end{array}$	
Mud	Intercept Sector	13.980 	1.873 1.897	7.462 -6.185	$\begin{array}{c} 1.17\times10^{-8}~^{***}\\ 4.96\times10^{-7}~^{***}\end{array}$	35.357 31.979	5.304 5.328	$6.666 \\ -6.002$	$\begin{array}{c} 1.19\times 10^{-7} \; *** \\ 8.56\times 10^{-7} \; *** \end{array}$	
Coarse Sand	Intercept Sector	0.4152 4.9929	0.3451 1.3928	4.971 3.585	$\begin{array}{c} 1.87\times 10^{-5} ***\\ 0.00105 ** \end{array}$	1.4084 2.9553	0.3021 0.9837	4.661 3.004	$\begin{array}{c} 4.7\times10^{-5} \ ^{***}\\ 0.00497 \ ^{**}\end{array}$	
Medium Sand	Intercept Sector	4.604 4.796	1.104 2.509	4.172 1.911	0.000197 *** 0.064417	5.387 4.747	1.002 2.135	5.376 2.223	$\begin{array}{c} 5.58\times10^{-6}\text{ ***}\\ 0.0329\text{ *} \end{array}$	
Fine Sand	Intercept Sector	7.873 -2.611	2.011 2.418	$3.915 \\ -1.080$	0.000412 *** 0.287906	$13.490 \\ -9.897$	2.304 2.385	$5.854 \\ -4.151$	$1.33 \times 10^{-6} *** \\ 0.00021 ***$	
Medium grain size	Intercept Sector	$0.0020259 \\ -0.0004943$	0.0002110 76.074	9.603 -1.869	$3.26\times10^{-11}~^{***}_{0.0702}$	0.0020465 0.0017483	0.0002901 0.0006112	7.055 2.861	$\begin{array}{c} 3.81\times 10^{-8} \text{ ***} \\ 0.00718 \text{ **} \end{array}$	
Homogeneity	Intercept Sector	0.0035063 -0.0026019	0.0003920 0.0004049	$8.944 \\ -6.426$	$\frac{1.88 \times 10^{-10}}{2.42 \times 10^{-7}} $	$0.58567 \\ -0.40652$	0.07701 0.08053	$7.605 \\ -5.048$	7.76×10^{-9} *** 1.49×10^{-5} ***	

Table 2. Glmm and Glm results for distribution patterns of physical–chemical parameters. Significance levels are as follows: * < 0.05; ** < 0.01; *** < 0.001. The parameters analyzed with Glmm are shown in black and the parameters analyzed with Glm are shown in red.



Figure 4. Concentrations of biopolymers in sediments of sites in the inner (I) and outer (O) sectors of Rocha Lagoon for the two sampling times. Error bars are standard deviations. (**a**) Spring. (**b**) Autumn.

The PRT: CHO ratio was >1 in the spring sampling in both sectors (except in sites O6 and I1) and also in the autumn sampling in the inner sector (excepting site I2), while in the outer sector, it was < 1. The CHO: LIP ratio was >> 1 in both sectors for both samplings (except I4 in spring and I1 in autumn). In both samplings, BPC showed higher values in the inner sector than in the outer (Tables 2 and 3).

SPRING										AUTUMN								
Sites	Sites BPC (mg C g^{-1})			PRT/CHO		CHO/LIP		BPC (mg C g^{-1})		PRT/CHO		CHO/LIP						
O1	1.32	±	0.2	1.67	\pm	0.73	4.31	±	0.69	1.04	±	0.02	0.88	\pm	0.04	6.28	\pm	0.14
O2	0.23	\pm	0.01	2.09	\pm	0.2	4.39	\pm	2.49	1	\pm	0.28	0.51	\pm	0.02	4.56	\pm	2.3
O3	0.68	\pm	0.03	1.74	\pm	0.21	3.83	\pm	0.63	0.17	\pm	0	0.7	\pm	0.03	4.36	\pm	1.87
O4	0.06	\pm	0.01	1.31	\pm	0.05	4.88	\pm	3.67	1.25	±	0.27	0.52	\pm	0.17	0.52	\pm	0.17
O5	0.68	\pm	0.01	1.44	\pm	0.42	4.05	\pm	1.98	1.05	\pm	0.19	0.77	\pm	0.05	2.75	\pm	0.3
O6	1.96	\pm	0.01	0.95	\pm	0.03	4.52	\pm	0.15	2.22	\pm	0.18	1.05	\pm	0.06	2.96	\pm	0.33
I1	3.43	\pm	0.19	2.18	\pm	0.14	1.38	\pm	0.31	3.97	\pm	0.13	2.31	\pm	0.47	0.89	\pm	0.33
I2	4.02	\pm	0.12	1.66	\pm	0.18	2.1	\pm	0.89	3.59	\pm	0.24	0.5	\pm	0.03	1.76	\pm	0.21
I3	3.13	\pm	0.01	1.99	\pm	0.24	1.59	\pm	0.01	3.68	±	0.18	1.19	\pm	0.19	1.82	\pm	0.29
I4	3.67	\pm	0.12	5.1	\pm	1.29	0.72	\pm	0.21	2.62	\pm	0.48	2.66	\pm	0.86	1.42	\pm	0.69
15	4.82	\pm	0.87	1.88	\pm	0.2	1.35	\pm	0.62	3.13	\pm	0.25	1.41	\pm	0.03	1.15	\pm	0.21
I6	1.51	\pm	0.27	0.93	\pm	0.08	13.76	±	3.18	1.52	\pm	0.09	0.97	\pm	0.07	3.9	\pm	0.24

Table 3. Biopolymeric carbon (BPC), protein-to-carbohydrate ratio (PRT/CHO), and carbohydrate-tolipid ratio (CHO/LIP) in both sampling times: spring and autumn, respectively. O1–O6: outer sites; I1–I6: inner sites. Mean values and standard deviation.

PCA performed with both water and sediment variables together showed that the water variables explained only a small proportion of the observed patterns and were associated with axis 2 (the axis with a low eigenvalue). Salinity was partially associated with both axes with the same eigenvectors. For this reason, the water variables were excluded, and only the sediment variables were included in the analysis. For this analysis, the first two PCA axes based on sediment variables explained 80.4% of the total variance (Figure 5, Table S1). PC1 explained over 68%; it showed a positive correlation with OM, PRT, mud, and BPC and a negative correlation with coarse sand. PC2 explained over 12.4%; it showed a negative correlation with CHO and medium and fine sand (Figure 5, Table S1). The ordination diagram shows a separation of the inner and outer sectors in both samplings, except for site I6 (located on the old sand bar), which shows similar characteristics to the outer sites in both times. In addition, the site most distant to the sand bar (O6) in spring was separated from the other outer sites.



Figure 5. Principal component analysis of the inner (I, I+) and outer (O) sectors of Rocha Lagoon for both sampling times based on environmental and biochemical variables. OM: organic matter, C sand: %coarse sand; M sand: %medium sand; F sand: %fine sand; BPC: biopolymeric carbon; PRT: total proteins, CHO: total carbohydrates. Oa: outer autumn, Ia: inner autumn; Os: outer spring; Is: inner spring; I+: inner sites in old sandbar.

3.2. The Nematofauna

A total of twenty-six genera of free-living nematodes were recorded for the first time in Rocha Lagoon. Twenty-five genera were recorded in the outer sector, with *Enoplolaimus, Mesacanthion, Mesorhabditis, Monhystera, Prismatolaimidae sp1, Diplogastridae sp2, Paracyatholaimus,* and *Pomponema* exclusively recorded in this sector. In the inner sector, twenty-one genera were determined, with *Halalaimus, Kosswigonema*, and *Meloidogyne* exclusively recorded in this sector (Table S2). In spring, the most abundant genera in the outer sector were *Theristus* (37.4%), *Sabatieria* (16.1%), and *Neochromadora* (13.3%), while in the inner sector, *Theristus* (26.3%), *Pseudochromadora* (16.4%), and *Sabatieria* (15.8%) predominated. On the other hand, in autumn, the outer sector was dominated by *Neochromadora* (38.6%), *Viscosia* (32.1%), and *Paralinhomoeus* (10%), while in the inner sector, *Viscosia* (22.7%), *Neochromadora* (20.6%), and *Theristus* (15.5%) were dominant (Figure 6).



Figure 6. Proportion of the most abundant genera (%) discriminated by time and sector.

Significant differences in the number of individuals were observed among sectors for 3 of the 12 genera recorded. *Oxytomina* were significantly more abundant in the inner sites in both sampling times (Table 4, Figure 7). Variation among sectors depending on sampling time were observed in the abundance of *Anonchus*. The genus *Anonchus* was more abundant in the inner sector than the outer in autumn, while in spring, non-individuals were registered (Figure 7). *Neochromadora* was more abundant in the outer sector than the inner in spring (Figure 7). *Neochromadora* was more abundant in the outer sector than the sectors were found in the genera *Anoplostoma, Daptonema, Leptolaimus, Paralinhomoeus*, and *Theristus*.

Table 4. Glmm results for distribution patterns of biotic parameters. Significance levels are as follows: * < 0.05; ** < 0.01; *** < 0.001.

			S	pring		Autumn						
Model		Estimate	Std Error	t Value	Pr(> t)	Estimate	Std Error	t Value	Pr(> t)			
Anonchus	Intercept Sector	-	-	-	-	0.6611 10.6512	1.6709 2.3630	0.396 4.507	$\begin{array}{c} 0.692 \\ 6.56 \times 10^{-6} \ *** \end{array}$			
Anoplostoma	Intercept Sector	2.558 1.409	1.955 2.792	1.308 0.505	0.191 0.614	0.6611 0.8815	0.5272 0.7455	1.254 1.182	0.210 0.237			
Daptonema	Intercept Sector	2.355 1.832	1.232 1.765	1.911 1.038	0.056 0.299	1.983 3.159	$1.474 \\ 2.084$	1.346 1.516	0.178 0.130			
Leptolaimus	Intercept Sector	$2.3015 \\ 0.4898$	1.2519 1.7789	1.838 0.275	0.066 0.783	$3.967 \\ -1.175$	1.911 2.702	$2.076 \\ -0.435$	0.0379 * 0.6636			
Neochromadora	Intercept Sector	7.313 -7.019	1.748 2.518	$4.183 \\ -2.788$	$\begin{array}{c} 2.87 \times 10^{-5} \ ^{***} \\ 0.00531 \ ^{**} \end{array}$	47.233 - 4.921	16.953 23.975	$2.786 \\ -0.205$	0.00534 ** 0.83736			
Oxystomina	Intercept	0.1129	1.1060	0.102	0.9187	0.2204	1.5063	0.146	0.88369			

			S	pring	Autumn						
Mode	1	Estimate	Std Error	t Value	Pr(> t)	Estimate	Std Error	t Value	Pr(> t)		
	Sector	4.0741	1.5879	2.566	0.0103 *	6.1704	2.1302	2.897	0.00377 **		
Pseudochromadora	Intercept Sector	6.665 24.040	9.743 14.066	0.684 1.709	$0.4939 \\ 0.0874$	3.820 16.381	8.148 11.523	0.469 1.422	0.639 0.155		
Paralinhomoeus	Intercept Sector	0.5877 18.4377	7.1725 10.1435	0.082 1.818	0.9349 0.0735	$11.973 \\ -1.910$	7.935 11.222	$1.509 \\ -0.170$	0.131 0.865		
Sabatieria	Intercept Sector	11.405 18.198	9.507 13.939	1.200 1.306	0.230 0.192	1.249 10.284	5.567 7.873	0.224 1.306	0.823 0.191		
Theristus	Intercept Sector	-	-	-	-	8.301 23.580	10.867 15.368	0.764 1.534	0.445 0.125		
Terschellingia	Intercept Sector	$0.5345 \\ 25.9834$	$\begin{array}{c} 10.7780 \\ 15.8434 \end{array}$	$\begin{array}{c} 0.05\\ 1.64\end{array}$	0.960 0.101	0.1469 12.9284	5.7743 8.1662	0.025 1.583	0.980 0.113		
Viscosia	Intercept Sector	$2.42520 \\ 0.07233$	$1.54081 \\ 2.24429$	1.574 0.032	$0.115 \\ 0.974$	39.520 7.125	19.451 27.507	2.032 0.259	0.0422 * 0.7956		
Total abundance	Intercept Sector	59.52 119.57	37.57 55.10	1.584 2.170	0.113 0.030 *	121.42 84.48	41.52 58.72	2.924 1.438	0.00345 ** 0.15029		
Richness	Intercept Sector	7.2090 0.2355	$0.8050 \\ 1.1610$	8.955 0.203	${<}2 imes 10^{-16}$ *** 0.839	7.2222 2.1111	0.9207 1.3021	7.844 1.621	$\begin{array}{c} 4.36\times 10^{-15} \ ^{***}\\ 0.105 \end{array}$		
MI	Intercept Sector	2.74843 0.09707	0.05854 0.08279	46.95 1.17	$<\!$	2.42332 0.32539	0.08976 0.12694	26.999 2.563	$\substack{<\!2\times10^{-16}\ ***\\0.0104\ *}$		
ITD	Intercept Sector	0.37083 0.01264	0.02621 0.03787	14.149 0.334	${<}2 imes 10^{-16}$ *** 0.739	$0.50440 \\ -0.08595$	0.03082 0.04359	$16.364 \\ -1.972$	$\substack{<\!2\times10^{-16}\ ***\\0.0486\ *}$		

Table 4. Cont.

Several genera presented a different pattern between the inner sectors of the main lagoon (I1, I2, I3) and the inner sectors of the old sandbar (I4, I5, I6). Such is the case of *Pseudochromadora, Sabatieria*, and *Terschellingia*, which present higher abundances in the old bar (Figure 7).

In addition, time differences were observed (not statistically tested), and *Viscosia* showed higher abundances in autumn than in spring (Figure 7). The total abundance of nematodes was higher in autumn than in spring, and in both samplings, there was higher abundance in the inner sector than in the outer one; in spring this difference was significant (Figure 8a). The richness did not show significant differences between sectors (Table 4, Figure 8b).

An nMDS ordination plot (based on a similarity matrix of the genera) for the autumn sampling showed that the inner sites, located in the central body of the lagoon, had a very different nematode assemblage respect compared to the outer and inner sites located in the old sandbar (Figure 9a). In addition, in the spring sampling, the inner sites located in the old sandbar of the lagoon showed a very different nematode assemblage with respect to the others (Figure 9b).

ITD values showed a significant sector variation, whit higher values in outers sites than inners in autumn sampling (Figure 10). We observed differences among sectors depending on the sampling time in the deposit feeder, epigrowth feeder, and predators/omnivores. The epigrowth feeder showed greater abundances in the outer sector in both sampling times. However, in autumn, the nonselective and selective deposit feeder nematodes showed greater abundances in the inner sector, while in spring, there were no significant differences between sectors. The predators/omnivores showed greater abundances in the inner sector in spring (Figure 11). Also, we observed variation among sectors depending on the sampling time in the MI values. The MI showed equal values between sectors in spring, but in autumn, it showed greater values in the inner sector compared to the outer sector. The increase in MI (to values of 3) indicates a lack of disturbance effects (Table 4, Figure 10). In addition, ITD values showed temporal variation (not statistically tested), with higher values in autumn than spring. Lower ITD values imply a greater trophic diversity in spring (Figure 10). Differences in ITD values were due to changes in the deposit feeder and epigrowth feeder abundances, with a higher abundance of these two groups in autumn than in spring, and a higher selective deposit feeder abundance in spring than in autumn (Table 4, Figure 11).



Figure 7. Abundance (mean and SD) of the main genera in sediments from the inner (I) and outer (O) sites of Rocha Lagoon for both sampling times. Error bars are standard deviations.



Figure 8. Mean and SD of total abundance of nematodes (**a**) and richness of genera (**b**) from the inner (I) and outer (O) sites of Rocha Lagoon for both sampling times. Error bars are standard deviations.



Figure 9. nMDS diagram of the analysis performed on the nematode genus matrix (**left**) and on the trophic group matrix (**right**) for autumn sampling (**top**) and spring sampling (**bottom**): (**a**) genera/autumn; (**b**) genera/spring; (**c**) trophic groups/autumn; (**d**) trophic groups/spring.



Figure 10. Mean and SD of trophic diversity index (ITD) and maturity index (MI) of nematode assemblages in sediments from the inner (I) and outer (O) sites of Rocha Lagoon for both sampling times. Error bars are standard deviations.



Figure 11. Mean and SD abundance of feeding types (%) of nematode assemblages in sediments from the inner (I) and outer (O) sites of Rocha Lagoon for both sampling samplings. Error bars are standard deviations. Deposit feeder (**1A**), nonselective deposit feeder (**1B**), epigrowth feeder (**2A**), and omnivore/predator (**2B**).

The nMDS ordination plot (based on the similarity matrix of trophic groups) in the autumn sampling suggests that inner sites had a different trophic assemblage compared to the outer sites. In addition, some inner sites (those from the old sandbar) were grouped with the outer sites (Figure 9c). In the spring sampling, three groups of sites were observed, evidencing three different trophic assemblages (Figure 9d).

4. Discussion

4.1. Environmental Patterns

Higher depths and homogeneous salinity values across the lagoon in spring, which could be related to the level of rainfall before the sampling date and the fact that the sandbar had only been open for only a few days, impeded the outflow of water into the ocean. In autumn, the higher salinity in the outer sector could be related to the length of time the sandbar had been open (approximately one month), and its natural opening was due to the persistence of southeast winds. Several authors have already emphasized that an intermittent connection with an ocean constitutes a structuring factor of coastal lagoons, e.g., [39,69]. At the beginning of the intrusion, the southern region of the lagoon has waters of similar salinities; surely, this would be the scenario in the spring season. In the case that the intrusion continues, a saline gradient is generated, separating the southern region (with marine characteristics) from that located near the streams (northern region, which exhibits a predominance of limnetic conditions). This would be the scenario recorded in the autumn sampling. If conditions favorable to intrusion persist (winds from the south and open sand bar), the intrusion can reach the northern region of the lagoon, which can present estuarine characteristics [39]. Similarly, the lagoon becomes homogeneous again once the connection is cut, and the horizontal salinity gradient tends to disappear, leaving a remnant of it that lies in the difference between the mouth and the inner part or head of the lagoon that receives freshwater inputs from the continent [40]. The temporal patterns in temperature were attributed to normal seasonal variation, which is consistent with previous studies [25,70].

Sediment differences between sectors were already reported in previous studies [25,46,48]. The inner sector of Rocha Lagoon, dominated by mud and fine sands, is therefore a more sheltered region, less exposed to the force of the ocean and wind, generating a lower-energy

environment, containing higher sedimentary organic matter, Chl-a, and phaeopigments. The presence of gravel in the inner sector has already been observed in previous studies [25,47,48], highlighting that this fraction corresponds to the presence of biogenic clasts (shells), indicating an accumulation of this type of material.

The organic biopolymers (CHO, PRT, and LIP) studied were used to assess the degree of organic matter degradation, nutritional value, and trophic status of the benthic environment [71]. The present study determined in both samplings a higher proportion of PRT, CHO, and LIP in the inner sector of the lagoon, a pattern that had already been evidenced by Pita et al. (2017) [49]. Proteins, which are the most abundant biopolymer in Rocha Lagoon, represent the main source of nitrogen for heterotrophic organisms and are consumed at a higher rate than carbohydrates [72], and their presence in sediments reflects the productivity of aquatic systems [73]. The PRT/CHO ratio is used as an indicator of the relative age of sedimentary organic matter [74], and when it is greater than 1, it is indicative of new and fresh organic matter, while if PRT/CHO < 1, it is indicative of old and degraded organic matter [71]. In spring in both sectors and in autumn in the inner sector, this ratio confirms the presence of new and fresh organic matter. In the outer sector, in autumn, values indicate the presence of old and degraded organic matter. Increases in organic matter recently produced are generally associated with peaks of benthic primary production [60] and recent phytoplankton inputs from water column deposition [75]. Therefore, the differences observed between sampling times must be related to seasonal patterns in productivity, with higher productivity in spring. This could also be related to the lagoon's morphodynamics, where the inner sector presents more stable conditions and the dominance of fine sediments, which retain more organic matter. This explains that even in a season of lower productivity, such as autumn, the inner sector presents new and fresh organic matter. In this sense, our results are consistent with the seasonal patterns found by Pita et al. (2017) regarding the relative age of sedimentary organic matter [49]. In addition, the lipid concentration has been related to the labile fraction of organic matter, and the CHO/LIP ratio is used as an indicator of the energy value of sedimentary organic matter as food for benthos [72]. In both samplings, the CHO/LIP ratio indicated a low energetic value of the organic matter. The results of this work differ in this aspect from those found by Pita et al. (2017), who reported a higher energetic value in sediments in spring with respect to those in autumn, attributing it to seasonal productivity differences [49]. This difference can be explained by the rainfall recorded in spring, which could have increased freshwater inflow into the lagoon and an influx of terrigenous particulate matter with low energy value. The concentrations of biopolymeric carbon (BPC) recorded were like previously reported in Rocha Lagoon, as was the record of its highest values in the inner sector of the lagoon [49], suggesting a better quality of organic matter in this sector [60].

The PCA performed in our study based on sediment characteristics (grain size and organic content and quality) showed a separation of the two sectors in both times. This pattern was reported by previous studies, which describes that the inner sector presents fine sediments with higher organic content than the outer sector [25,48].

4.2. Environmental Drivers of the Taxonomy Patterns

The observed assembly structure with a few dominant genera and a greater number with low abundance is typical of muddy substrates [5,18,76]. The presence of the genera *Enoplolaimus, Mesacanthion, Mesorhabditis, Monhystera, Pomponema,* and *Paracyatholaimus* exclusively in the outer sector would be explained by their preference for coarser sediments and would be consistent with previous research. In this sense, *Enoplolaimus* and *Monhystera* are typical genera of non-impacted sandy beaches [77–79]. *Mesacanthion* has been recorded on sandy and rocky beaches and oceanic islands, as has *Pomponema*, which has also been recorded in estuaries [77], with higher abundance in pristine, low-organic-load sites. [18,22,80]. *Mesorhabditis* is a terrestrial genus that feeds on bacteria, so its arrival in the outer sector of the lagoon would be the result of transport by runoff from land [81]. This also happens in marine coasts, and in the upper littorals of the sea, the genus *Rabditis*

also appears, which is terrestrial, always with low numbers. This is a casual phenomenon brought by rainfall currents, but terrestrial genera are short-lived in aquatic environments, so they would not have major implications on the sediment ecosystem dynamics in the outer sector. The genera *Halalaimus*, *Kosswigonema*, and *Meloidogyne* were recorded exclusively in the inner sector. *Halalaimus* is typical of environments with high content of mud [82], while *Kosswigonema* has been originally described in sandy beaches [79,83], with this being the second record in the inner sector of Rocha Lagoon, an environment with a predominance of fine sediment [11]. *Meloidogyne* is a parasitic nematode of terrestrial plants [84]. The multiple uses of coastal areas can mobilize terrigenous materials into water bodies in quantities similar or even greater than those introduced through natural meteorization processes [85]. So, the register of *Meloidogyne* in the inner sector of the lagoon would be the result of runoff transport.

The genera *Anoplostoma*, *Daptonema*, *Leptolaimus*, *Paralinhomoeus*, and *Theristus* observed in both sectors showed no changes between sectors. They are also typical of marine and estuarine sediments; however, several species of these genera are found even in freshwater environments, indicating great plasticity and tolerance to different salinities [86,87]. The same occurred with *Terschellingia* and *Sabatieria*. These genera are tolerant to enrichment [11,88]. Species of the genus *Terschellingia* are tolerant to a diversity of stressors in soft bottoms [89]. *Sabatieria* is tolerant to aquaculture deposition and is even adapted to live in environments with high organic carbon loads and low-oxygen and high-sulfide concentrations, indicating great plasticity and tolerance to different conditions [90,91].

In addition, three types of responses were observed when evaluating the other genera: some genera showed spatial patterns (differences between sectors); others, temporal patterns (differences between times); and others showed different spatial performances depending on the time. The genus *Oxystomina* showed spatial patterns, and was more abundant in the inner than in the outer sector. *Oxystomina* appeared to be tolerant to enrichment [11,88]. *Neochromadora* was favored by medium and coarse sands in the outer sectors in spring.

The genus *Viscosia* showed temporal variations, and was more abundant in autumn than in spring. The increased abundance of these genera was reflected in the total abundance, which was higher in autumn than in spring. *Viscosia* was favored by medium and coarse sands in autumn and was more evident in both sectors. *Viscosia*'s ability to exploit a wide range of food resources may explain its high abundance [92]. The high abundances of *Viscosia* in both sectors in autumn could be explained considering that *Viscosia* is a scavenger and feeds on dead and decaying meiofauna.

The genus *Anonchus* showed different spatial patterns depending on time with higher abundance in the inner sites in autumn, while absent in spring. *Anonchus* is considered a euryhaline genus [87] and a facultative predator that occurs in great abundance in this sector, which may be benefiting from the mud sediment [93].

In previous studies on Uruguayan estuaries (including Rocha Lagoon), it was established that variables such as salinity and temperature have no direct effect on the assembly of meiofauna [25], and in the present study, no pattern related to aquatic variables could be observed in nematode assemblage. Small benthic organisms are subject to the same processes of erosion, suspension, and transport that act on sediment particles [94]. A lower pressure of these processes together with high food availability would explain the higher total abundance of nematodes in the more protected and less hydrodynamic inner sites.

The input of organic matter to the sediment is basically composed of a labile and a refractory fraction. The labile fraction is easily digestible and assimilated by heterotrophs; it is the bioavailable fraction, composed mainly of the biopolymer's carbohydrates, lipids, and proteins [74]. Organic matter is the main source of energy for benthic organisms [95,96]. The quantity, composition and quality of bioavailable organic matter influence the productivity of the benthic system [97]. In this sense, a higher concentration of biopolymers in the inner sector would be responsible for supporting a higher abundance of nematodes.

In addition, the nematode assemblage of the inner sector shows a variable behavior between times; in autumn, some inner sites (I+, those of the old sandbar) were grouped with those of the outer sites, while in spring, the inner sites located in the old sandbar (I+) of the lagoon remained together, forming a different group with a different nematode assemblage. This is probably related to the history of the old sandbar. In the past, the lagoon was connected to the Atlantic Ocean in this area, resulting in a sandier bottom environment than the remainder of the inner sector. Temporally, the strong winds of spring [98] probably have a higher effect on the main body of the lagoon, promoting more similar conditions in both sectors, except those of the old sandbar, which remain as a more sheltered environment.

4.3. Environmental Drivers of Functional Patterns

The functional role of nematodes according to feeding type was first described by Wieser (1953) and can be exploited to better understand the dynamics of a particular ecosystem, as this approach, despite its known limitations, provides valuable information about the ecosystem [20]. The relative proportion of each of the four nematode feeding groups in a community generally depends on the nature of the available food, which in turn depends on the composition of the sediment [24,92]. The quantity and quality of organic matter have a fundamental influence on the biomass distribution and trophic structure of benthic communities in general [93]. Meiofaunal organisms, particularly nematodes, are agile and rapidly exploit fresh organic material [99]. This is reflected in the present study in the different spatial performances depending on the time of some trophic groups and MI. The sediment in spring in both sectors showed new and fresh organic matter, explaining the non-differences between the inner and outer sectors in the groups 1A and 1B, which benefited from the greater availability of new and fresh organic matter.

During the autumn sampling, old and degraded organic matter and a higher presence of predatory organisms (2B) and epigrowth feeder (2A) characterized the outer sector. This also highlights the low percentages of deposit feeders in this sector. On the other hand, new and fresh organic matter and the dominance of deposit feeders 1A and 1B characterized the inner sector. This agrees with other research that determined that fine sediments with high concentrations of organic matter promote the dominance of nematodes' selective deposit feeders, 1B and 2A, as they can utilize excess organic matter in the sediments and diatom primary production [100,101].

The high abundance of predators, according to Semprucci et al. (2015), would show a more heterogeneous and well-structured trophic assemblage, indicating greater habitat complexity [102]. The present results do not agree with this assessment, as the lowest trophic diversity was found in the outer areas in autumn, with a predominance of predators.

The assemblage of trophic groups observed in the nMDS diagrams shows that in spring, there is a separation between the outer and inner sectors, and in turn, the inner sectors of the old bar are separated from those of the lagoon body. These patterns cannot be attributed to the quality of the organic matter as it was fresh at all sites. While in autumn, the separation is between the inner and outer sites, in this case, it seems to be responding to the differences between sectors of the organic matter quality.

The MI, according to Semprucci et al. (2010, 2013), responds to the river discharge and is more efficient than diversity indices in detecting disturbance effects; however, it is also sensitive to sediment grain size [103,104]. The MI and c-p categories can sometimes fail to identify the dominant stressor when multiple stressors act together [103]. Estuaries are environments where multiple stressors act in combination (e.g., variation in salinity, organic inputs); however, the MI showed a good performance. It was able to detect changes in the quality of organic matter (freshness), both spatially and temporally. In this sense, the MI would be appropriate for the monitoring of Laguna de Rocha.

5. Conclusions

From the above, we conclude that trophic groups respond differentially to the quality of organic matter, specifically to its palatability, and that this response is reflected in the trophic diversity index. This index has generally been used to relate trophic diversity to pollution levels. The present study suggests its use in evaluating other aspects of the communities, while a greater amount of organic matter is responsible for sustaining a more abundant community, which was evidenced by a higher abundance in the inner sector of all genera. The functional (trophic) structure of the community is determined by the quality of that matter, which was reflected in the different proportion of the trophic groups in response to the organic matter freshness.

Our study shows that the content and composition of organic matter is the modeling factor of the taxonomic and trophic structure of the nematode community. In addition, we show a more robust analysis of the community through the joint analysis of both attributes. The functional traits introduce a new dimensionality that could not be detected otherwise using solely taxonomical information, making information available for the detection of changes in the trophic status of sediments in coastal ecosystems. This type of information could be useful as a baseline for the long-term monitoring of estuarine ecosystems, even more so under the current scenario of intensifying the eutrophication and land use of these ecosystems.

Supplementary Materials: The following supporting information can be downloaded at https: //www.mdpi.com/article/10.3390/d16110688/s1: Table S1. PCA Results of abiotic variables. Correlation coefficients of the variables for axes PC1 and PC2 are marked in bold. Table S2. List of genera identified in both samplings. Total abundance and relative abundance (%) for sector and time, type of mouth, and cp value. * Genera selected for analysis of data. Highlighted in bold are the most abundant genera by sector.

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