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Divergent Communities of Marine Nematodes in Impacted Beaches of Bandar Abbas (Iran)

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ABSTRACT

Free-living marine nematodes play crucial roles in the benthic ecosystem and serve as valuable bioindicators for monitoring environmental stress. We explore the community structure of free-living marine nematodes in the beach ecosystem near Bandar Abbas port city of Iran. The research focused on assessing the impact of domestic and industrial influences during winter and summer seasons in 2018 and 2019. Three coastal locations, namely KhurGursuzan (KG), Power Plant (PP), and Resalat (RE), were sampled, with KG under domestic wastewater influence, PP characterized by industrial activities, and RE serving as the control site. A total of 41 nematode genera were identified during the study, and dominant genera varied across locations, namely, *Daptonema*, *Sabatieria*, *Promonhystra*, *Ptycholaimellus*, and *Eleutherolaimus* at KG; *Spirinia*, *Chromadorina*, *Terschellingia*, *Eleutherolaimus*, and *Promonhystra* at PP; and *Oncholaimus*, *Pomponema*, *Viscosia*, *Ptycholaimellus*, *Daptonema*, and *Eleutherolaimus* at RE. These dominant genera accounted for 80% of the total nematode community during the sampling periods. The study revealed significant differences in abundance and genus diversity among the sites, with pollution-affected sites exhibiting the lowest nematode diversity. Sediment granulometry showed a positive correlation with genus diversity across the sites, and the structure of the nematode assemblage was negatively influenced by polychlorinated biphenyls and total organic matter. Surprisingly, the spatial patterns in nematode assemblage structure and diversity remained consistent across both studied years. These findings contribute to our understanding of marine ecosystem health and the role of free-living nematodes as bioindicators in the Persian Gulf.

1 | Introduction

Free-living marine nematodes are a diverse and abundant group of meiofaunal organisms found in marine benthic ecosystems. They are the most common metazoan fauna in these ecosystems (Heip, Vincx, and Vranken 1985) and play vital roles in various ecological processes, such as organic matter decomposition, nutrient recycling, and biofilm formation (Chinnadurai and Fernando 2007; De

Mesel et al. 2003; Hubas et al. 2010) Additionally, they serve as an important food source for benthic and hyperbenthic macrofauna, and larval fishes (Coull 1990; Gee 1989; Schuckel et al. 2013). Numerous environmental impact studies have focused on nematode assemblages due to their unique characteristics. These include limited mobility, absence of larval dispersion, high abundance, short generation times, varying sensitivities to different disturbances at the species level, and a diverse range of feeding modes

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and trophic levels (Bongers and Ferris 1999; Moreno et al. 2011; Patricio et al. 2012; Sandulli and De Nicola 1991; Schratzberger et al. 2000). These traits make nematodes well-suited for assessing and studying the environmental effects of disturbances and changes in their habitats. The Persian Gulf is a significant marine ecosystem due to its strategic location, abundant oil and gas resources, and its role as a crucial economic, military, and political region (Potter 2009). Furthermore, it is a vital transportation route (Sale et al. 2011). Over time, the environment of the Persian Gulf has experienced rapid changes due to various pressures, including oil pollution, waste disposal (including sewage), coastal development, and recreational activities (Sheppard et al. 2010). These factors have the potential to significantly impact the benthic ecosystem (Dehghan Madiseh et al. 2012; Doustshenas et al. 2009; Ejlali Khanaghah et al. 2015; Farsi et al. 2015). Despite this, research focusing on the benthos in the northern part of the Gulf is limited, with most studies concentrating on macrofauna (Safahieh et al. 2012; Nourinezhad et al. 2013; Pourjomeh et al. 2014).

Only three studies have been carried out on meiofauna in the northern Persian Gulf, specifically focusing on the abundance, diversity, and genus composition of nematodes. These investigations were conducted on three sandy beaches near Bandar Abbas in Iran (Sahraean, Nara Bezerra, et al. 2017; Sahraean, Van Campenhout, et al. 2017; Sahraean et al. 2020). However, the limited scope of these studies highlights the need for more comprehensive research to understand the variability of marine nematodes in this region fully. In this current study, we aimed to explore the year-to-year variations in nematode assemblage structure and spatial patterns in the beach ecosystem of the northern Persian Gulf. Additionally, we investigated how these nematodes respond to environmental pollution, with the goal of identifying their potential and reliability as bioindicators.

2 | Materials and Methods

2.1 | Study Area

The sediment samples were collected from three distinct beaches in the Bandar Abbas area of the northern Persian Gulf, Iran. These beaches were selected based on their varying levels of contamination and pollution sources. They included KhurGursuzan (KG), which was impacted by sewage; power plant (PP), showing significant industrial contamination, including the presence of polychlorinated biphenyls (PCBs); and Resalat (RE), a relatively less disturbed beach without noticeable pollution sources. The sampling was conducted over two consecutive years (2018 and 2019), during both summer (August) and winter (January) seasons. This approach allowed for the assessment of potential seasonal variations in the nematode community and sediment characteristics.

2.2 | Sampling Procedures

Sediment cores were collected from the top 5 cm layer of sediment at each location for meiofaunal nematodes and sediment analysis. PVC hand corers with an inner diameter of 3.5 cm and a length of 30 cm were used for this purpose. Triplicate cores were collected from each location, spaced at regular intervals along a line perpendicular to the tidal water column. This ensured the collection

of representative sediment samples. In the laboratory, nematodes were extracted from the collected sediment samples using the centrifugation method (Vincx 1996). This method involves subjecting the sediment sample to centrifugation, where the nematodes are separated from the sediment particles using Ludox. The supernatant, containing the extracted nematodes, was collected over a 38- μ m mesh sieve. The use of this sieve allowed for the separation of nematodes from finer sediment particles, ensuring that only nematodes passed through. The nematodes retained on the sieve were transferred to a petri dish and counted. This step involved a systematic enumeration of nematode individuals. For taxonomic identification, ca. 100 randomly selected nematodes were processed through a series of ethanol-glycerol solutions. In cases where fewer than 100 specimens were observed, glass slides were prepared for those nematodes. This process is essential for preserving and preparing the nematodes for identification.

Nematodes were mounted on glass slides and identified up to the genus level using various resources, including pictorial keys and the Nemys database (Platt and Warwick 1983, 1988; Warwick and Clarke 1998; Bezerra et al. 2019). The identification process involved a careful examination of morphological characteristics, body shape, size, and other distinguishing features of the nematodes.

Additional triplicate samples were taken from the same locations for subsequent chemical and grain size analysis. In situ measurements of temperature, salinity, and pH were taken in the overlying bottom water at the sampling sites using an Ocean Seven 316 CTD Probe. The processing of sediment samples before sediment analysis involved drying, grinding, and homogenization to ensure uniform representation of the sediments' content. Grain size analysis was performed using a Malvern Hydro 2000G Particle Size Analyzer, and sediment fractions were categorized according to the Wentworth scale (Bale and Kenny 2005). Total organic matter (TOM) content was analyzed using a FLASH 2000 CHN elemental analyzer after removing inorganic carbon with a dilute HCl solution (Nieuwenhuize, Maas, and Middelburg 1994). PCBs were measured using the GCMS/MS method (Mohebbi Nozar et al. 2013), and the total concentration of three major PCB congeners, CB-138, CB-153, and CB-180, since they were the most active ones, was calculated as Σ PCB.

2.3 | Data Analysis

Ecological indices, including richness, Shannon–Weaver's diversity (H'), Simpson's dominance (S_i), and Pielou's evenness (J), were calculated using the DIVERSE routines in PRIMER v.6.0 (Clark and Gorley 2006). To examine differences in total nematode abundance, diversity indices, and environmental variables (such as temperature, pH, salinity, TOM, and PCB) across locations, months, and years, as well as their interactions, permutational multivariate analysis of variance (PERMANOVA) was performed on univariate data with 999 permutations. Euclidean distance was used as the similarity measure for univariate tests, and the homogeneity of multivariate dispersion was assessed using the PERMDISP routine. Location, month, and year were considered as independent fixed factors, and a pairwise test was applied to evaluate the significance of main and interaction effects under the full model.

Nematode assemblage structure for both years was visualized using non-metric Multidimensional Scaling (nMDS) based on the Bray–Curtis similarity of fourth-root transformed data. A distance-based redundancy analysis (db-RDA) was conducted to determine if variation in environmental variables contributed to the differences in nematode assemblages observed at different levels of anthropogenic pollution. Multivariate multiple regression using distance-based liner model (DISTLM) analysis was then employed to assess the significance of these relationships by fitting a linear model based on Bray–Curtis dissimilarities from square-rooted transformed abundance data.

Principal component analysis (PCA) was applied to normalized environmental data to investigate the importance of environmental variables in distinguishing the different sampling locations and years. These data were further analyzed using PERMANOVA with the same two-way design as for the abundance and diversity data. The genera that contributed the most to the dissimilarities between different locations, months, and years were identified through SIMPER analysis.

3 | Results

3.1 | Physico-Chemical Analysis

Temperature varied across the sampling locations and time periods, with KG recording the highest temperature in August 2018 ($35.72 \pm 0.67^\circ\text{C}$) and PP experiencing the lowest temperature in January 2019 ($22.56 \pm 1.2^\circ\text{C}$). Temperature did not show significant differences between locations, but it did vary significantly between seasons and years ($p=0.001$, Table 2). pH levels were highest at PP during August 2018 (8.49 ± 0.12) and lowest at

KG in August 2019 (7 ± 0.1). Salinity was highest at RE during August 2018 (39.50 ± 0.15 PSU) and lowest at PP in January 2018 (24.3 ± 0.11). The concentration of PCBs was highest at PP in August 2019 (11.09 ± 0.56 ppm) and lowest at RE in August 2019 (0.87 ± 0.14 ppm). TOM content was highest at KG in January 2018 (5.23 ± 0.51 mg/L/C) and lowest at RE in January 2018 (0.63 ± 0.21 mg/L/C) (Table 1). pH, salinity, and TOM showed significant differences between locations, seasons, and years ($p < 0.05$), and PCB concentrations differed significantly between locations ($p=0.001$, Table 2).

Sediment grain size analysis indicated that KG and PP had much finer grain size compared to RE, with approximately 55% of RE sediment characterized as coarse sand in both years (2018 and 2019), while KG and PP had only about 1.56% and 2.03% coarse sand during 2018 and 1.27% and 1.70% during 2019, respectively (Table 3).

The PCA analysis clearly separated the two impacted locations (PP, KG) and RE. RE was characterized by lower PCB and TOM% concentrations, contributing to its distinct position on the PCA plot (Figure 1).

3.2 | Nematode Abundance, Diversity, and Assemblage Structure

Nematode abundance showed significant variation among samples, ranging from 23 to 1320 individuals per 10cm^{-2} . The abundance differed significantly between locations and years but did not show any significant difference between seasons (Figure 2 and Table 4). RE exhibited the highest nematode abundance (1207 ± 64 ind.) in 2018 and the lowest (421 ± 199 ind.)

TABLE 1 | Environmental variables of the sediments at the sampled locations.

		Temperature (°C)	pH	Salinity (PSU)	PCB (ng/g dry weight)	TOM% (ng/g dry weight)
<i>2018</i>						
August	Khur Gursuzan	35.72 ± 0.67	7.9 ± 0.04	36.50 ± 0.25	6.16 ± 0.18	3.71 ± 0.06
	Power plant	35.30 ± 0.65	8.49 ± 0.12	33.97 ± 0.18	10.5 ± 0.21	2.22 ± 0.10
	Resalat	34.66 ± 0.08	8.08 ± 0.10	39.50 ± 0.15	0.98 ± 0.11	0.95 ± 0.04
January	Khur Gursuzan	24.8 ± 0.36	7.42 ± 0.04	28.2 ± 0.1	4.44 ± 0.04	5.23 ± 0.51
	Power plant	24.7 ± 0.28	7.64 ± 0.08	24.3 ± 0.11	2.84 ± 0.02	11.56 ± 0.34
	Resalat	25.25 ± 0.14	7.72 ± 0.05	32.4 ± 0.1	1.62 ± 0.04	0.63 ± 0.21
<i>2019</i>						
August	Khur Gursuzan	31.7 ± 0.35	7 ± 0.1	29.46 ± 0.34	5.12 ± 0.19	4.90 ± 0.19
	Power plant	30.33 ± 0.43	7.5 ± 0.30	27.6 ± 0.51	11.09 ± 0.56	2.43 ± 0.32
	Resalat	31.56 ± 0.5	7.5 ± 0.14	32.77 ± 0.28	0.87 ± 0.14	1.45 ± 0.26
January	Khur Gursuzan	22.83 ± 0.9	6.73 ± 0.2	27.5 ± 0.4	5.24 ± 0.24	4.8 ± 0.55
	Power plant	22.56 ± 1.2	7.26 ± 0.2	26.5 ± 1.4	2.7 ± 0.47	12.4 ± 0.51
	Resalat	24.83 ± 0.4	7.7 ± 0.15	30.4 ± 0.5	1.3 ± 0.15	0.64 ± 0.14

Values are in mean \pm SE.

Abbreviations: PCB = polychlorinated biphenyls, TOM = total organic matter.

TABLE 2 | The results of ANOVA for environmental variables.

	df	SS	MS	F	p
<i>Temperature</i>					
Lo	2.00	0.18	0.09	2.05	0.15
Mo	1.00	2.81	2.81	63.07	0.00
Ye	1.00	29.93	29.93	670.74	0.00
LoxMo	2.00	0.21	0.10	2.31	0.12
LoxYe	2.00	0.20	0.10	2.26	0.13
MoxYe	1.00	0.58	0.58	12.96	0.00
LoxMoxYe	2.00	0.01	0.01	0.13	0.88
Res	24.00	1.07	0.04		
Total	35.00	35.00			
<i>pH</i>					
Lo	2.00	7.15	3.57	12.51	0.00
Mo	1.00	12.17	12.17	42.57	0.00
Ye	1.00	3.94	3.94	13.77	0.00
LoxMo	2.00	1.68	0.84	2.94	0.07
LoxYe	2.00	1.19	0.60	2.09	0.14
MoxYe	1.00	1.74	1.74	6.10	0.02
LoxMoxYe	2.00	0.27	0.14	0.48	0.63
Res	24.00	6.86	0.29		
Total	35.00	35.00			
<i>Salinity</i>					
Lo	2.00	10.33	5.16	117.24	0.00
Mo	1.00	5.55	5.55	125.93	0.00
Ye	1.00	12.17	12.17	276.33	0.00
LoxMo	2.00	0.45	0.23	5.13	0.01
LoxYe	2.00	0.04	0.02	0.41	0.70
MoxYe	1.00	5.12	5.12	116.31	0.00
LoxMoxYe	2.00	0.29	0.14	3, 29	0.04
Res	24.00	1.06	0.04		
Total	35.00	35.00			
<i>TOM</i>					
Lo	2.00	30.87	15.43	239.45	0.00
Mo	1.00	0.61	0.61	9.40	0.01
Ye	1.00	0.73	0.73	11.33	0.00
LoxMo	2.00	0.84	0.42	6.54	0.00
LoxYe	2.00	0.06	0.03	0.44	0.68
MoxYe	1.00	0.30	0.30	4.69	0.05
LoxMoxYe	2.00	0.05	0.02	0.37	0.69

(Continues)

TABLE 2 | (Continued)

	df	SS	MS	F	p
Res	24.00	1.55	0.06		
Total	35.00	35.00			
<i>PCB</i>					
Lo	2.00	34.08	17.04	916.68	0.00
Mo	1.00	0.00	0.00	0.00	0.96
Ye	1.00	0.00	0.00	0.24	0.64
LoxMo	2.00	0.17	0.08	4.45	0.02
LoxYe	2.00	0.29	0.15	7.82	0.00
MoxYe	1.00	0.01	0.01	0.72	0.39
LoxMoxYe	2.00	0.00	0.00	0.12	0.89
Res	24.00	0.45	0.02		
Total	35.00	35.00			

Significant p (<0.05) are denoted in bold.Abbreviations: Df=degrees of freedom, SS=sums of squares, MS=means of squares, P(permutation)= p value obtained through permutations, Lo=location, Ye=year, Res=residual.

in January 2019. In 2019, KG showed the highest abundance (1107 ± 65.09 ind.) compared to the other locations in both seasons (Figure 2A).

A total of 41 genera (38 during 2018 and 39 during 2019) were identified during the study period (Table 5). The dominant genera varied among locations, with *Daptonema*, *Sabatieria*, *Promonhystera*, *Ptycholaimellus*, and *Eleutherolaimus* dominating at KG; *Spirinia*, *Chromadorina*, *Terschellingia*, *Eleutherolaimus*, and *Promonhystera* dominating at PP, and *Oncholaimus*, *Pomponema*, *Viscosia*, *Ptycholaimellus*, *Daptonema*, and *Eleutherolaimus* dominating at RE. These dominant genera accounted for over 80% of the total nematode abundance for KG and PP, and <60% for RE during the study period (Figure 3 and Table 5).

The abundances of several nematode genera showed significant differences between the studied locations (all $p < 0.05$). However, these differences were not found to be significant when comparing between different seasons or years, nor were there significant interactions observed between seasons and years (Figure 3). In contrast, genera richness exhibited significant variations not only between locations but also between seasons, years, and their interactions ($p < 0.05$). Specifically, the RE location consistently showed significantly higher richness compared to KG and PP in both seasons and years (Figure 2B). Additionally, when considering other diversity indices, such as Shannon–Weaver's diversity, Pielou's evenness, and Simpson's diversity, we found significant differences primarily between locations and years ($p < 0.001$, $p < 0.02$, and $p < 0.001$, respectively). Notably, only Shannon–Weaver's and Simpson's diversity showed no significant variations between months. Pair-wise tests indicated that RE exhibited significantly higher values for Shannon–Weaver's and Simpson's diversity compared to PP (Figure 4).

TABLE 3 | Sediment grain size at the three sampled locations (mean \pm SE).

		Khur Gursuzan	Power plant	Resalat
2018	Median grain size	129.95 \pm 5.07	113.74 \pm 6.77	166.26 \pm 4.19
	Silt	2.32 \pm 0.56	3.46 \pm 0.63	0.03 \pm 0.03
	%very fine sand	20.55 \pm 1.09	26.44 \pm 2.35	3.37 \pm 1.18
	%Fine sand	49.16 \pm 2.13	57.57 \pm 0.87	15.98 \pm 0.87
	%Medium sand	24.31 \pm 0.8	10.08 \pm 1.72	24.49 \pm 2.01
	%coarse sand	1.56 \pm 0.11	2.03 \pm 0.42	55.46 \pm 1.86
2019	Median grain size	133.49 \pm 5.81	116.74 \pm 7.23	169.00 \pm 5.80
	Silt	2.28 \pm 0.59	3.36 \pm 0.46	0.13 \pm 0.03
	%very fine sand	19.69 \pm 0.51	25.81 \pm 3.45	3.70 \pm 0.35
	%Fine sand	50.80 \pm 0.88	59.50 \pm 0.85	17.26 \pm 1.83
	%Medium sand	23.46 \pm 0.41	12.25 \pm 1.86	23.16 \pm 1.77
	%coarse sand	1.27 \pm 0.23	1.70 \pm 0.26	50.86 \pm 6.01

The non-metric multidimensional scaling (nMDS) analysis showed significant differences in nematode assemblages between locations, years, and their interactions, but not between seasons, with three main groups being clustered (Figure 5). SIMPER analysis revealed dissimilarity between months (August and January) (28.67%), mainly due to shifts in the abundances of *Viscosia*, *Eleutherolaimus*, *Promonhystera*, *Oncholaimus*, *Sabatieria*, *Daptonema*, *Ptycholaimellus*, and *Terschellingia* at different locations and years (30%). Spatial variability among the sampled locations was mainly due to shifts in relative abundances of *Sabatieria*, *Viscosia*, *Eleutherolaimus*, *Promonhystera*, *Oncholaimus*, and *Daptonema*. A strong dissimilarity was observed between PP and RE (82%) due to the differences in abundances of the genera *Spirinia*, *Chromadorina*, *Oncholaimus*, and *Pomponema*. PERMANOVA also revealed significant differences in the composition of nematode assemblages between locations ($p = 0.001$). Pair-wise tests for the interaction effect of Location \times Year highlighted significant differences in nematode assemblages between all pairs of locations during 2018 and 2019, but the interaction effect of Location \times Month did not show any significant differences between all pairs of locations (Figure 5). Furthermore, the relation between the distribution of nematode assemblages and environmental variables, analyzed by DISTLM and dbRDA, indicated that PCB, TOM%, salinity, and grain size were the variables that explained most of the assemblage structure during the study period, with clear correlations between PCB and nematode assemblages from the PP location, and TOM with nematode assemblages of the KG location (Figure 6 and Table 6).

4 | Discussion

The findings of this investigation reveal that TOM, PCBs, and grain size significantly influence the community of free-living marine nematodes on the Iranian coast. Notably, nematode abundance demonstrates an increase in sediments with a very

fine grain size, aligning with previous research (e.g., Heip, Vincx, and Vranken 1985). Two out of the three beaches studied, KG and PP, experienced an upsurge in nematode abundance during 2019 compared to previous years. However, at RS, a significant decrease of 51% in August 2019 and 64% in January 2019 was observed compared to 2018. The decline in nematode abundance at RS during the second year suggests potential significant disturbances, that is, overfishing, pollution, eutrophication, in the coastal environment. These disturbances have emerged as significant threats in recent years (Wynberg and Branch 1994; Dronkers and de Vries 1999; Riera, Núñez, and Brito 2012). This decline in nematode abundance indicates the need for careful monitoring and management of coastal areas to mitigate adverse impacts on the benthic community. However, these results need to be taken with caution since they capture a limited spatial (three locations) and temporal (four field surveys) variability of the meiofaunal nematodes in the study area. Meiofaunal nematode populations can indeed exhibit natural fluctuations in response to various environmental factors. Hence, the observed declines in nematode abundance at RS may be influenced by a range of factors, including both anthropogenic disturbances and natural variability in nematode species.

We conducted a multivariate PCA that integrated meiofauna data with sedimentary environmental parameters to investigate the relationship between nematodes and different stressors, such as chemical, organic, and physical properties. Grain size is one of the most critical environmental factors influencing the distribution and abundance of the meiobenthic community, which includes nematodes (Heip, Vincx, and Vranken 1985; Vanaverbeke et al. 2011; Vanaverbeke, Gheskiere, and Vincx 2000; Riera et al. 2011). In our study, we observed significant environmental variability among locations, potentially impacting the diversity and abundance of meiofauna. Surprisingly, we found no correlation between nematode abundance/diversity, and sediment granulometry, though there are differences between beaches since sediments

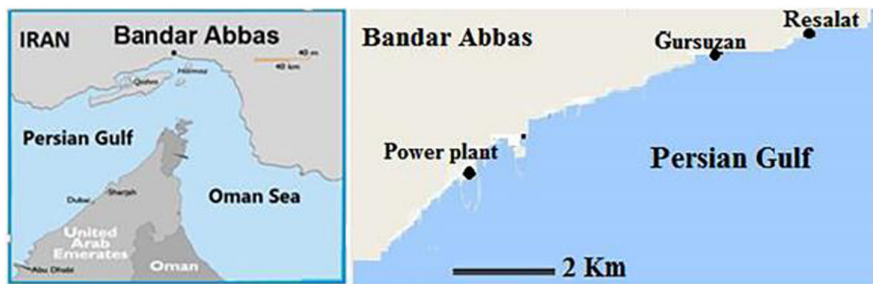


FIGURE 1 | Map of the study area showing the three sampled locations on the coastline of Bandar Abbas (Iran).

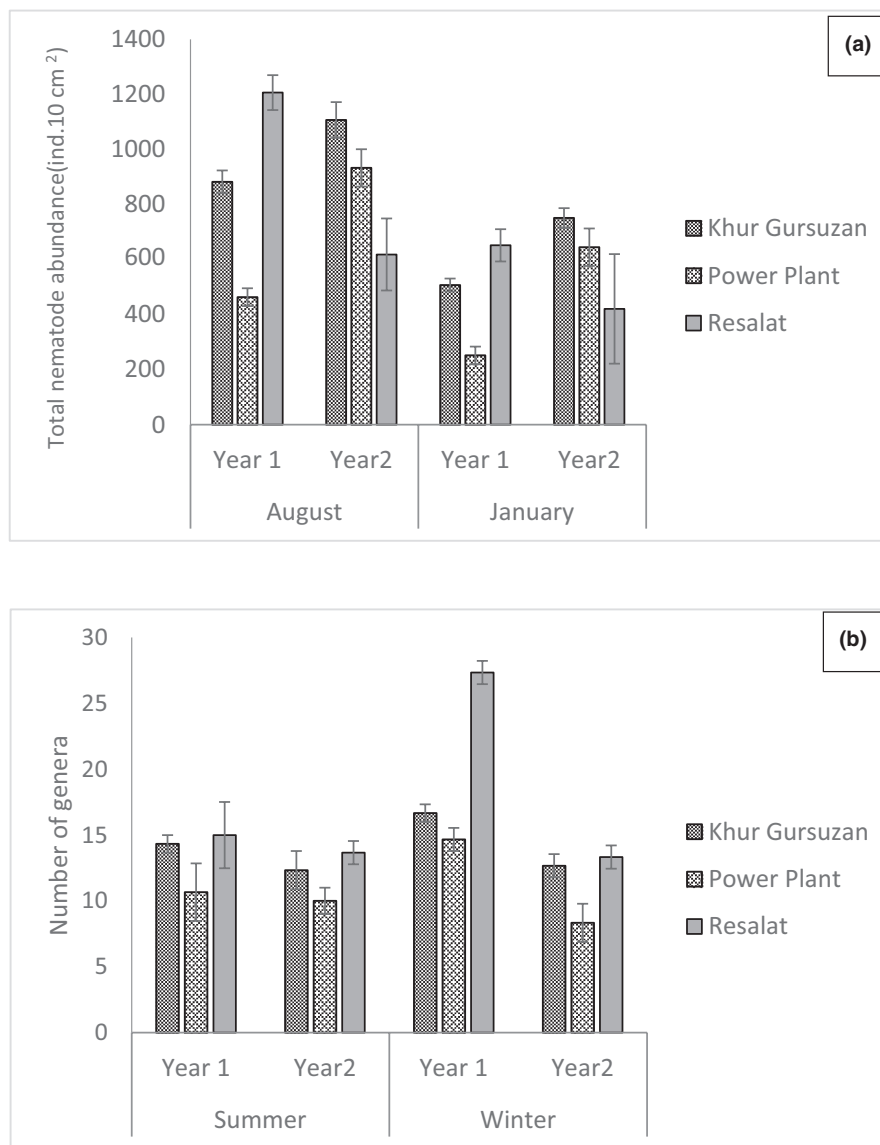


FIGURE 2 | A. Total nematode abundance per location. B. Nematode diversity showing the abundance of different genera during the study period. Data are means \pm SE.

at KG and PP were much finer than at RE (coarse sand). Notably, the highest nematode abundance was associated with locations having finer sediment fractions, in agreement with previous works (Tietjen 1984; Gheskiere et al. 2004, 2005; Giere 2009; Riera, Sanchez-Jerez, et al. 2012; Moens et al. 2013). However, it is interesting to note that the RE site, dominated by coarser sands, exhibited instances of the highest nematode abundances during certain months. Our study

underscores the vital role of grain size as a crucial factor influencing the community structure of meiofauna, since the presence of finer sediments favors higher nematode abundances. It is evident that grain size variations play a pivotal role in shaping the nematode community, and this is consistent with previous research (Heip, Vincx, and Vranken 1985; Vanaverbeke et al. 2011; Vanaverbeke, Gheskiere, and Vincx 2000; Riera et al. 2011). The complexity of interactions

TABLE 4 | The results of ANOVA for nematode abundance and genera richness.

	df	SS	MS	F	p
<i>Total abundance</i>					
Lo	2	3.50E+05	1.75E+05	8.3904	0.004
Mo	1	65,536	65,536	3.1436	0.093
Ye	1	9.84E+05	9.84E+05	47.203	0.001
LoxMo	2	1.16E+06	5.81E+05	27.846	0.001
LoxYe	2	29,337	14,669	0.70362	0.514
MoxYe	1	22,400	22,400	1.0745	0.329
LoxMoxYe	2	78,083	39,041	1.8727	0.165
Res	24	5.00E+05	20,847		
Total	35	3.19E+06			
<i>Genus richness</i>					
Lo	2	247.17	123.58	23.416	0.001
Mo	1	103.36	103.36	19.584	0.001
Ye	1	72.25	72.25	13.689	0.003
LoxMo	2	44.056	22.028	4.1737	0.03
LoxYe	2	45.167	22.583	4.2789	0.027
MoxYe	1	200.69	200.69	38.026	0.001
LoxMoxYe	2	39.389	19.694	3.7316	0.048
Res	24	126.67	5.2778		
Total	35	878.75			
<i>Pielou's evenness</i>					
Lo	2	1.16E-02	5.81E-03	4.184	0.022
Mo	1	2.83E-03	2.83E-03	2.04	0.18
Ye	1	9.88E-03	9.88E-03	7.1148	0.008
LoxMo	2	1.28E-03	6.38E-04	0.45947	0.66
LoxYe	2	1.65E-03	8.24E-04	0.59363	0.565
MoxYe	1	1.47E-02	1.47E-02	10.555	0.006
LoxMoxYe	2	5.73E-03	2.86E-03	2.0636	0.144
Res	24	3.33E-02	1.39E-03		
Total	35	8.10E-02			
<i>Shannon–Wiener's</i>					
Lo	2	0.61167	0.30584	16.97	0.001
Mo	1	0.14351	0.14351	7.9634	0.014
Ye	1	0.38958	0.38958	21.617	0.001
LoxMo	2	4.59E-02	2.29E-02	1.2733	0.304
LoxYe	2	5.14E-02	2.57E-02	1.4254	0.249
MoxYe	1	0.16281	0.16281	9.0342	0.005
LoxMoxYe	2	0.13286	6.64E-02	3.686	0.048

(Continues)

TABLE 4 | (Continued)

	df	SS	MS	F	p
Res	24	0.43252	1.80E-02		
Total	35	1.9702			
<i>Simpson diversity</i>					
Lo	2	1.46E-02	7.31E-03	9.7654	0.001
Mo	1	2.36E-03	2.36E-03	3.157	0.089
Ye	1	6.38E-03	6.38E-03	8.5164	0.009
LoxMo	2	1.97E-03	9.86E-04	1.3167	0.286
LoxYe	2	2.76E-04	1.38E-04	0.18424	0.837
MoxYe	1	4.35E-04	4.35E-04	0.58065	0.475
LoxMoxYe	2	3.40E-03	1.70E-03	2.2677	0.12
Res	24	1.80E-02	7.49E-04		
Total	35	4.74E-02			

Significant differences were highlight in bold ($p < 0.05$).

Abbreviations: Df= degrees of freedom, SS/SM = sums and means of squares, Lo= location, Ye= year, Res= residual.

among environmental parameters, including grain size, needs to be further explored to fully understand the mechanisms governing nematode responses within the meiofaunal community.

RE obtained the maximum abundance during 2018 and lowest during 2019 in both seasons, whereas during 2019, KG showed the maximum abundance than the remaining locations. This indicates that pollution and sediment properties significantly affect the nematode community, where nematode abundance increases in fine and polluted sediments (McIntyre and Murison 1973; Bally 1983; Sandulli and Nicola 1991). Coull and Chandler (1992) showed that shifts in meiobenthic community structure and lower diversity are affected by sewage pollution and that nematodes can tolerate osmotic stress, regulating their water content by changes in their cuticle (Forster 1998). According to Danovaro (1996), a substantial portion (around 56–84%) of sedimentary organic carbon remains unused by benthic organisms, with only a small fraction being available in the form of labile biopolymers, such as carbohydrates, proteins, and lipids, which serve as highly nutritious food sources. However, in areas near sewage discharge, the positive effect of organic matter on meiofauna abundance may not be observed (Oliveira and Soares-Gomes 2003). Aside from sewage-related organic matter input, natural variations in organic matter content within the sediment column also occur. If the input of organic matter, either from natural or anthropogenic sources, exceeds the degradation rate within the system, it can lead to organic matter accumulation and create an anoxic environment (Pinto and Bemvenuti 2006). This results in a restricted zone where meiofauna can thrive, limited to a thin superficial layer, where meiobenthic nematodes tend to dominate (Schratzberger and Warwick 1998). The genus *Terschellingia*, identified in our study and one of the most abundant genera in the PP station, has demonstrated a remarkable capacity to withstand low oxygen conditions. This resilience is pivotal for their sustenance in habitats characterized by hypoxia or anoxia, where oxygen

TABLE 5 | Composition of nematode genera and their relative abundance (%) at the three sampling locations and average over all sampling locations over two different season and 2years.

Nematode genera	Khur gursuzan	Power plant	Resalat	Average
<i>Daptonema</i>	27.51	2.08	9.06	12.88
<i>Oncholaimus</i>	6.03	3.68	23.61	11.10
<i>Spirinia</i>	0.15	30.05	0.42	10.20
<i>Ptycholaimellus</i>	12.36	0.23	12.06	8.22
<i>Promonhystera</i>	16.77	6.33	1.37	8.16
<i>Chromadorina</i>	0.21	22.51	0.39	7.71
<i>Eleutherolaimus</i>	6.46	8.76	7.48	7.57
<i>Pomponema</i>	0.22	1.41	19.04	6.89
<i>Sabatieria</i>	17.12	0.44	0.62	6.06
<i>Terschellingia</i>	1.47	14.64	1.08	5.73
<i>Viscosia</i>	2.62	0.07	10.78	4.49
<i>Paramonhysrera</i>	0.36	5.78	1.53	2.56
<i>Eumorpholaimus</i>	0.80	0.07	2.48	1.12
<i>Theristus</i>	1.35	0.65	1.03	1.01
<i>Metalinhomous</i>	0.30	0.38	1.71	0.80
<i>Metoncholaimus</i>	0.65	0.21	0.32	0.39
<i>Paraethmolaimus</i>	0.71	0.22	0.23	0.39
<i>Desmodora</i>	0.67	0.29	0.17	0.38
<i>Chromadora</i>	0.66	0.00	0.40	0.36
<i>Dichromadora</i>	0.31	0.51	0.08	0.30
<i>Onyx</i>	0.43	0.00	0.47	0.30
<i>Enoplolaimus</i>	0.00	0.29	0.57	0.29
<i>Rhynchonema</i>	0.44	0.08	0.34	0.29
<i>Paracanthonchus</i>	0.66	0.00	0.17	0.28
<i>Camacolaimus</i>	0.22	0.43	0.17	0.27
<i>Prochromadora</i>	0.29	0.00	0.41	0.23
<i>Nygmatonchus</i>	0.14	0.14	0.40	0.23
<i>Tripyloides</i>	0.00	0.08	0.51	0.19
<i>Actinonema</i>	0.09	0.00	0.47	0.19
<i>Enoploides</i>	0.00	0.15	0.40	0.18
<i>Graphonema</i>	0.00	0.22	0.32	0.18
<i>Thalassomonhystera</i>	0.00	0.08	0.41	0.16
<i>Spilophorella</i>	0.25	0.00	0.23	0.16
<i>Hypodontolaimys</i>	0.17	0.00	0.25	0.14
<i>Metachromadora</i>	0.14	0.00	0.23	0.12
<i>Xenolaimus</i>	0.08	0.00	0.23	0.10
<i>Haliplectus</i>	0.08	0.23	0.00	0.10

(Continues)

TABLE 5 | (Continued)

Nematode genera	Khur gursuzan	Power plant	Resalat	Average
<i>Cyatholaimus</i>	0.15	0.00	0.16	0.10
<i>Phanoderma</i>	0.00	0.00	0.23	0.08
<i>Odontophora</i>	0.07	0.00	0.15	0.07
<i>Polysigma</i>	0.08	0.00	0.00	0.03

Note: Data are means of three replicates per location, for each season and year.

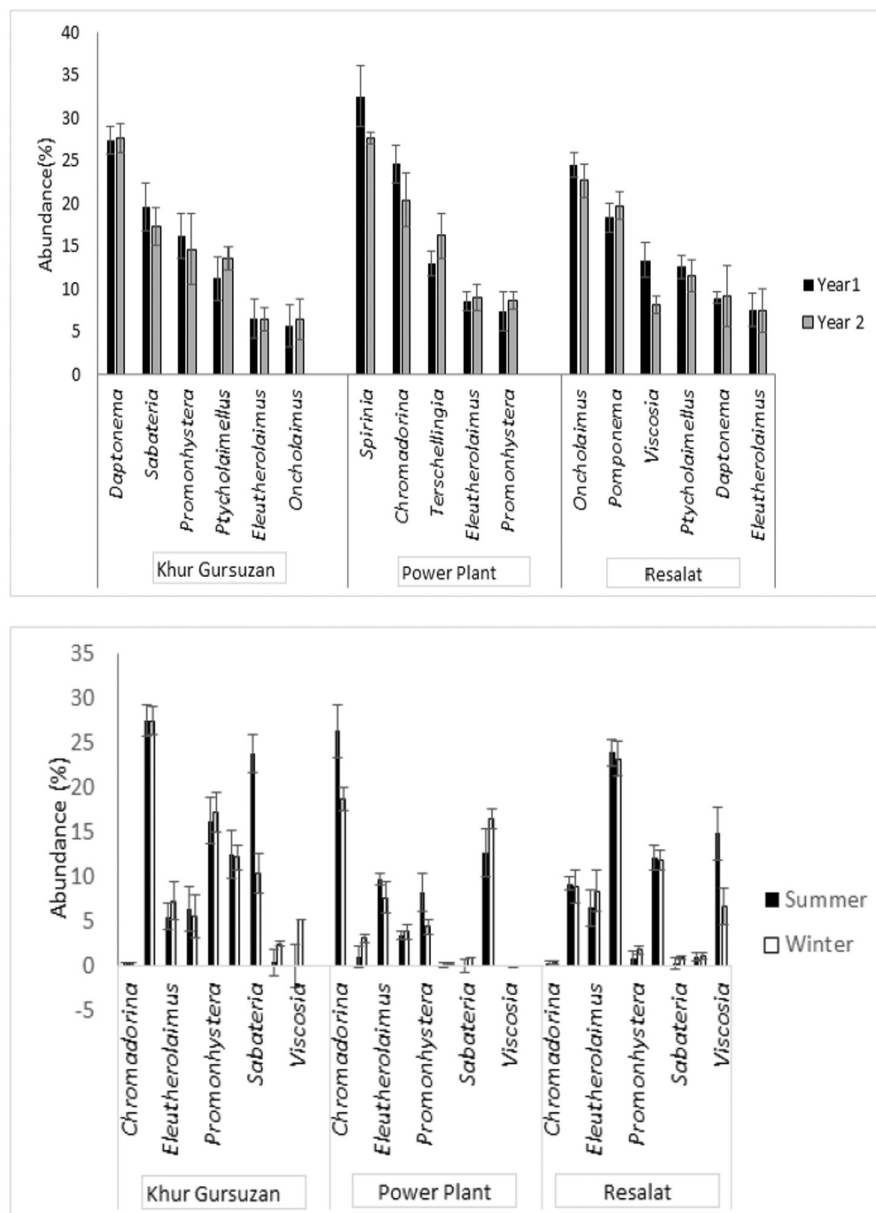


FIGURE 3 | Abundance of the most dominant genera during the study period. Data are means \pm SE.

availability is limited. *Terschellingia*, among other genera, exemplifies the adaptability of meiofauna to diverse environmental stressors, emphasizing the importance of considering these adaptations in the broader context of ecosystem dynamics. In comparing our findings with Vincx and Vanreusel (1989), Boyd, Rees, and Richardson (2000), and Schratzberger et al. (2000),

notable congruence emerges. These studies collectively support the prevalence of deposit-feeding nematodes, including *Daptonema*, in organically enriched and oxygen depleted marine sediments. Further strengthens our conclusions by highlighting the dominance of *Daptonema* in anoxic, degraded, and polluted habitats. Nevertheless, it is crucial to acknowledge

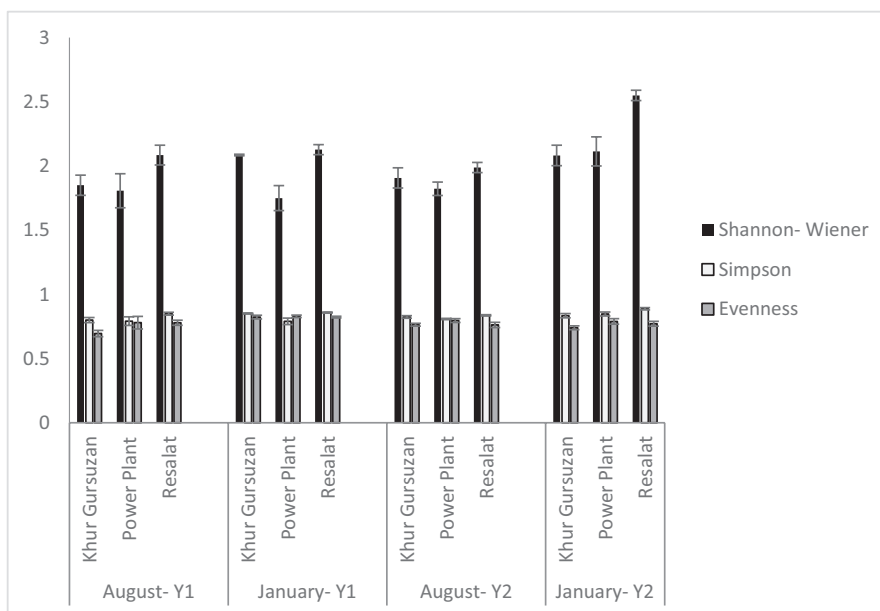


FIGURE 4 | Nematode indices for each location, each month, and different year (Y1 = 2018, Y2 = 2019). Shannon–Wiener’s diversity index, Simpson’s dominance index, and Pielou’s evenness index.

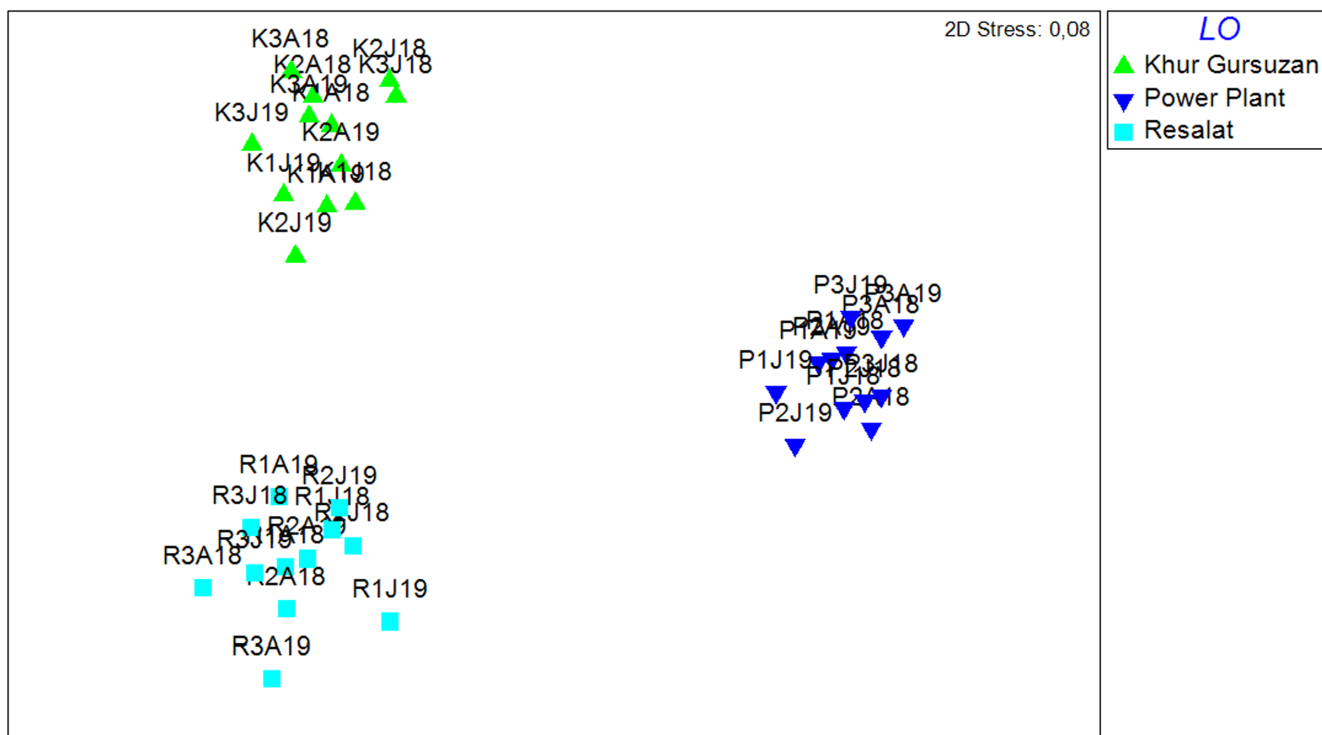


FIGURE 5 | Non-metric multidimensional scaling (nMDS) of nematode assemblages observed during the study period. A = August, J = January, 18 = year 2018, and 19 = year 2019.

potential species-specific variations within genera and the influence of behavioral strategies on nematode responses to anoxia. Steyaert et al. (2007) underscore the importance of considering factors such as vertical migrations in sediments, which may impact the duration of exposure to anoxic conditions under field circumstances.

Moreover, sewage contamination can introduce particulate and dissolved organic carbon into the sediment (Austen and

Warwick 1995), a phenomenon supported by POC (particulate organic carbon) data in our study. Elevated carbon levels can affect various sediment environmental factors. For instance, organic material accumulation in interstitial spaces can reduce sediment porosity, negatively impacting space-limited meiofaunal populations (Moens et al. 2013). On the other hand, organic matter serves as an important direct or indirect food source for benthic organisms, and in eutrophic conditions, its increase can enhance benthic metabolism (Gray 1981). Namely,

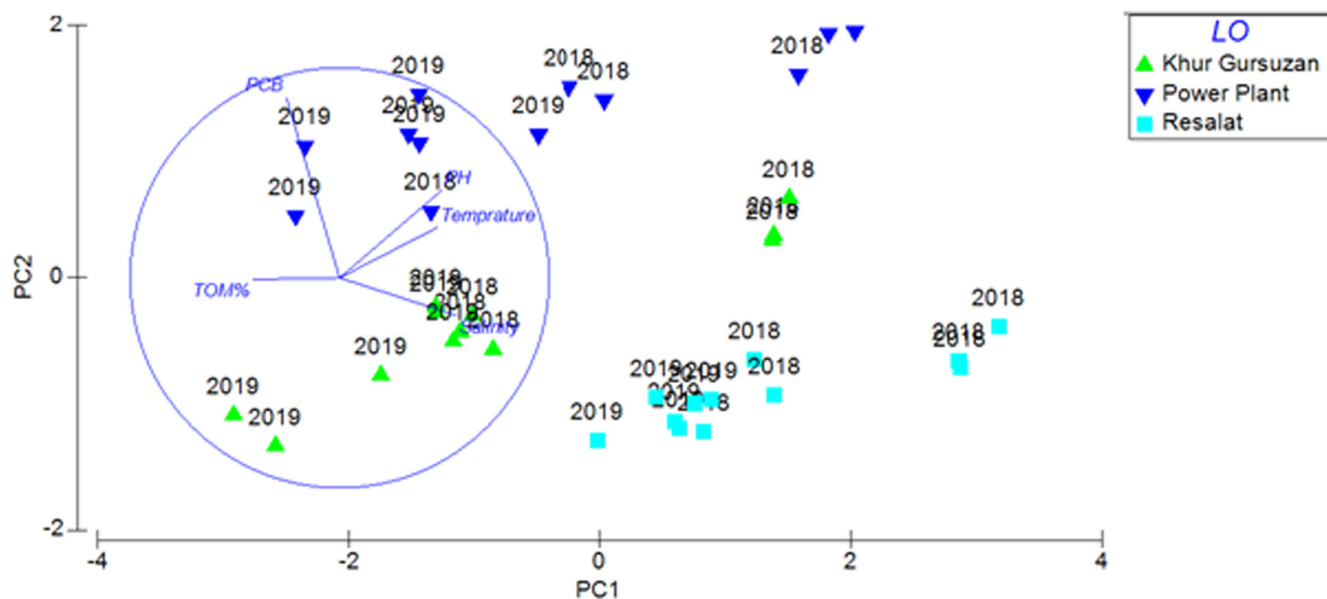


FIGURE 6 | Principal component analysis (PCA) based on the environmental variables: Salinity, temperature, pH, polychlorinated biphenyls (PCBs), and total organic matter (TOM %). Number indicates different sampling years.

TABLE 6 | Results of the distance-based liner model (DISTLM) analysis determining the suite of environmental variables that describe significant and independent proportions of the variation in nematode composition.

Variable	Sequential tests			
	SS (trace)	Pseudo-F	p	Prop.
Temperature	836.17	0.52459	0.728	1.5195E-2
pH	2480.6	1.605	0.174	4.5078E-2
Salinity	6567.5	4.6076	0.005	0.11934
TOM%	9244.3	6.8648	0.002	0.16799
PCB	23,295	24.957	0.001	0.42331
Very fine sand	17,277	15.56	0.001	0.31396

Note: Values in bold indicate significance ($p < 0.05$).

Abbreviations: PCB = polychlorinated biphenyls, TOM = total organic matter.

some nematode genera, such as *Sabatieria* and *Pontonema*, are particularly abundant in organically enriched locations (Warwick and Robinson 2000; Armenteros et al. 2010; Riera et al. 2013). The previous studies are in agreement with our findings, which highlight significant variations in the former nematode abundance, diversity, and assemblage structure among the sampling stations exposed to diverse environmental conditions, ranging from polluted (KG and PP) to unpolluted (RE). Our results further underscore the impact of pollution and other environmental factors, including sediment grain size, in shaping the nematode communities within the study area. The trophic groups of the three most abundant nematode species in KG are non-selective deposit feeders (*Daptonema* and *Promonhystra*) and epistrate feeders (*Sabatieria*). These trophic groups were also found in the PP, that is, non-selective deposit feeders (*Spirinia*) and epistrate (*Chromadorina*) feeders, together with selective deposit feeders (*Terschellingia*). The unpolluted station (Resalat) was dominated by epistrate feeders, namely *Oncholaimus*, *Pomponema*, and *Viscosia*.

The contamination of marine ecosystems with PCBs has raised concerns about its potential impact on various organisms, including meiofauna (Cook et al. 2000; Schratzberger et al. 2003; Hale et al. 2011). Therefore, PCBs pollution in our study has may originated from different industrial sources, though the use of PCBs is regulated and restricted in Iran. One of our surveyed sites, PP, is located near the PP unit, which have been already known as the primary source of PCBs in the region (Mohebbi Nozar et al. 2013). This study reveals that PCB pollution can significantly impact meiofauna communities, with potential implications for ecosystem functioning and biodiversity. Moreover, we highlight the role of ecological conditions, such as warming and hypoxia, in shaping meiofaunal responses to PCB contamination (Kingston 2002; Beyrem et al. 2010; Mahmoudi et al. 2005; Ernst et al. 2006). Guerrini, Colangelo, and Ceccherelli (1998) showed through a field experiment that nematodes were particularly resistant to the induced hypoxic/anoxic disturbance, wherein similar environmental conditions were observed at KG in our study. For example, the genus *Daptonema* that was the most abundant in KG samples

has been observed to survive in anoxic and partially sulfidic conditions (Steyaert et al. 2007). Other abundant genera in this location, for example, *Sabatieria*, have been reported as tolerant to hypoxic conditions in microcosm experiments (Modig and Ólafsson 1998). *Pomponema*'s sensitivity to pollutants, coupled with its epistrate feeding strategy, positions it as a potential bioindicator species. This sensitivity reflects the impact of environmental stressors on nematode communities, emphasizing the ecological relevance of this genus in assessing environmental health. *Daptonema* and *Promonhystera*, identified as non-selective deposit feeders, not only contribute to nutrient cycling but also exhibit notable tolerance to various types of pollution, showcasing their resilience in organically enriched marine sediments. The response of *Ptycholaimellus*, an epigrowth feeder, to microphytobenthos blooms suggests its sensitivity to changes in biofilm composition, making it relevant in assessing the impact of organic matter fluctuations (Sommerfeld et al. 2003; Moens et al. 2013; Schratzberger et al. 2003). These nematode genera are adapted to extreme environments through detoxification strategies and high anaerobic capacity (Veit-Köhler et al. 2009; Vopel et al. 1998).

Nematodes have been previously used as tools to assess the sources of disturbance and detect the effects of various ecosystem perturbations (e.g., Sutherland et al. 2007; Riera, Núñez, and Brito 2012). Coastal eutrophication, anthropogenic disturbances, and organic enrichment have wide-ranging impacts and represent significant challenges on disturbed beaches. However, there is a lack of research on the effects of pollutants and factors influencing soft-bottom communities, particularly meiofauna, in tropical and subtropical ecosystems compared to temperate regions (e.g., Longhurst and Pauly 1987; Schratzberger et al. 2000; Oliveira and Soares-Gomes 2003; Riera, Nunez, and Brito 2014). Therefore, there is an urgent need to direct impact research towards understanding the taxonomy and function of nematodes. Such efforts would enhance our comprehension of ecosystem functioning in poorly explored regions, such as the Persian Gulf. By focusing on nematodes, we can gain valuable insights into the ecological dynamics and responses of these relatively understudied areas to environmental disturbances and anthropogenic influences. To enhance the robustness of future research in this area, we recommend selecting reference sites with sediment characteristics more similar to the impacted areas. This approach will reduce the potential bias introduced by grain-size differences and enable a more precise assessment of the impact of contaminants and other stressors on different sediment types and their associated meiofaunal communities.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available upon request to the first author (N.S.).

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