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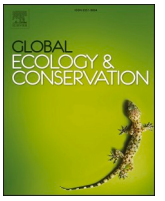

Original research article

How do the body size attributes of marine nematodes indicate the environmental changes in mangroves?

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ABSTRACT

Body size is a crucial functional trait of nematodes, which determines the biological and physiological processes and provides more comprehensive information concerning the ecological role of nematodes. To investigate how the body size attributes of marine nematodes indicate the environmental changes in mangroves, we studied the variations in body size and biomass size composition of marine nematodes in a subtropical mangrove ecosystem. The results revealed that median values of body length, width, length-to-width ratio, and individual dry weight were 956.88 μm, 40.98 μm, 22.51, and 0.24 μg, respectively. In summer, adults and juveniles exhibited a predominance of smaller-sized slender individuals, while in winter, large stout individuals were more common. Correspondingly, the biomass size spectra skewed towards smaller-size classes in summer, whereas in winter, they skewed towards larger-size classes. The body size attributes and biomass size composition of nematodes significantly correlated with environmental variables, effectively indicating the environmental changes, especially changes in interstitial water temperature and sediment pheophorbide. The reduction in body size was a prominent response of mangrove nematodes to temperature rise. The total biomass of nematodes and their carbon contribution have been calculated based on body length and width. This document will provide essential information to estimate the carbon stock of nematodes and their contribution to the blue carbon sink in mangrove ecosystems. Analysis based on body size is species-independent and more beneficial for promoting the application of nematodes in environmental implication and monitoring.

1. Introduction

Free-living marine nematodes are the most abundant metazoan in the ocean (Heip et al., 1985; Soetaert et al., 2002; Moens et al., 2014). They are the major consumers of benthic bacteria, microalgae, and benthic microorganisms, participating in the decomposition of organic matter and playing a crucial role in energy flow and material cycling in benthic ecosystems (Moens et al., 2014; Schratzberger and Ingels, 2018). Free-living nematodes are usually slender and cylindrical, with slightly pointed heads and tails, and easily identified by their typical morphological characteristics (Platt and Warwick, 1988; Tita et al., 1999). However, their numerous species

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exhibited a wide range of morphological adaptations, particularly in terms of body size and shape (Tita et al., 1999; Soetaert et al., 2002; Vanaverbeke et al., 2003; Schratzberger et al., 2007; Górska et al., 2020; Nguyen et al., 2023).

Body size and shape attributes, for example, body length, body width, and length-to-width (L/W) ratio, were recorded to be closely related to environmental factors (Tita et al., 1999; Soetaert et al., 2002; Materatski et al., 2018; Górska et al., 2020; Nguyen et al., 2023). Body size was considered a direct adaptation of nematodes to the sediment with a specific particle size they inhabit, and sediment grain size significantly influences their body length and width (Tita et al., 1999; Soetaert et al., 2009). Except for the physical constraints of interstitial space, oxygen level (Soetaert et al., 2002; Losi et al., 2013), sulfide system (Jensen, 1986, 1987), food supply (Soetaert et al., 2002; Losi et al., 2013), also directly or indirectly shape nematode morphology. Body size and shape are crucial functional traits of organisms that influence their behavior, life histories, metabolism, and energy requirements (Peters, 1983; Soetaert et al., 2002; Grzelak et al., 2020). Size-based analyses are believed to provide insights into the potential of nematodes as indicators of environmental changes and to evaluate ecosystem functioning (Ma et al., 2024).

Nematodes feed on detrital carbon and play a crucial role in absorbing and storing carbon in their bodies (Krishnapriya et al., 2021). When they die, the carbon in their body will be deposited into sediment and become part of the blue carbon sink (Wang and McSorley, 2005). Because nematodes are the most abundant meiofauna in sediments of various habitats, their contribution to blue carbon is negligible (Krishnapriya et al., 2021). Body width and length are commonly used to estimate the individual biomass of nematodes and have proven accurate (Warwick and Price, 1979; Feller and Warwick, 1988; Tita et al., 1999; Hua et al., 2013; Nguyen et al., 2023). Size-based analyses will help to estimate the total biomass of nematodes in the ecosystem accurately and contribute to understanding the carbon potential and blue carbon contribution of marine nematodes.

Examining nematode body size attributes offers an alternative approach to studying community function without reliance on taxonomic identification (Sroczyńska et al., 2021). The application of nematodes as a good indicator of environmental changes or external disturbances in environment monitoring studies was still limited (Hua et al., 2021; Sroczyńska et al., 2021). The main reason is that most descriptions of nematode communities, including the commonly used functional traits such as feeding type and life strategy, are based on taxonomic identification, which is generally time-consuming and requires researchers trained in taxonomic skills (Trigal-Domínguez et al., 2010; Sroczyńska et al., 2021). Body size attributes are non-taxonomic descriptors for studying community function (Hua et al., 2013; Nguyen et al., 2023). Previous studies have shown that body size attributes and biomass distribution were meaningful in evaluating functional changes in nematode communities as a result of a changing environment (Vanaverbeke et al., 2003; Losi et al., 2013; Materatski et al., 2018; Sroczyńska et al., 2021; Guo et al., 2022; Nguyen et al., 2023).

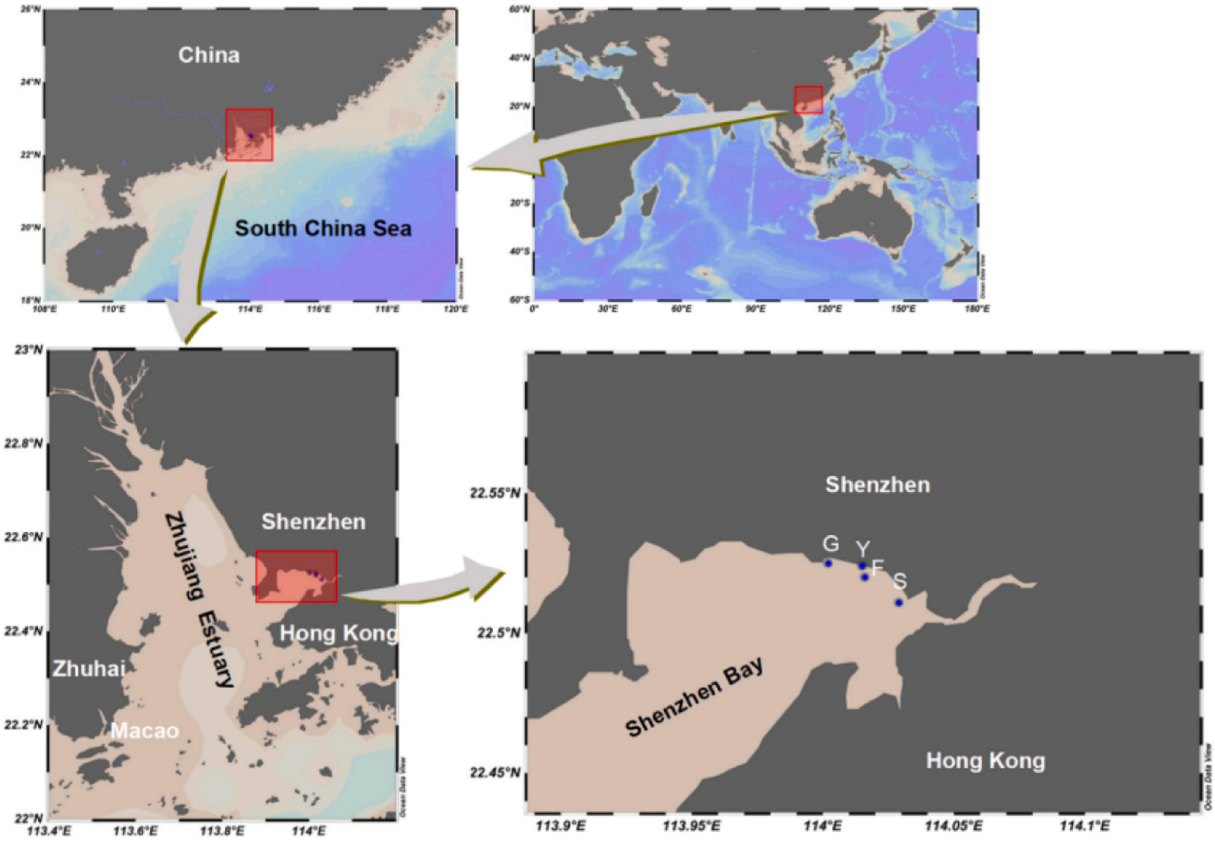

Fig. 1. Map of the study mangrove reserve. Blue circles indicate the sampling area. G, Guanniao Pavilion; F, Fengtang Estuary; S, Shazui Wharf; Y, Fishpond.

However, our knowledge of nematodes, especially the body size attributes and their responses to habitat heterogeneity, is still limited. Further study is necessary on the body size attributes of nematodes as indicators of functional changes influenced by human and natural impact.

Mangroves are among the most valuable marine habitats globally and one of the most productive ecosystems on Earth (Kaiser et al., 2011; Pinto et al., 2013). The total area of mangroves in the world is estimated to be 147,256 km^2 (Leal and Spalding, 2024), playing a crucial role in maintaining the local and global ecological balance (Ghosh and Mandal, 2019). Free-living marine nematodes are ecologically valuable as they enhance nutrient cycling, promote microbial production, and decompose mineralized organic debris in their environment (Somerfield et al., 1998). Studies on marine nematodes in mangrove habitats have been conducted worldwide, with reports in mangroves of Australia (Abdullah and Lee, 2016), Africa (Olafsson et al., 2000), Brazil (Netto and Gallucci, 2003), China (Tan et al., 2017; Hua et al., 2020; Fu et al., 2021), India (Chinnadurai and Fernando, 2007; Ghosh and Mandal, 2019), France (Rzeznik-Orignac et al., 2003), Malaysia (Somerfield et al., 1998), Vietnam (Xuan et al., 2007; Mokievsky et al., 2011), etc. These studies have promoted our understanding of the structure and influencing factors of mangrove nematode community structure. However, studies on the body size attributes of nematode communities in mangrove ecosystems are still rare.

This study focused on body length, body width, individual dry weight, and biomass size composition of marine nematodes in a subtropical mangrove. It aims to discover the variation patterns of body size attributes and size composition, understand the crucial factors determining body size and shape, and explore how the body size attributes of marine nematodes indicate environmental changes. Additionally, the total biomass of nematodes and their carbon contributions were estimated using their length and width. This document will provide essential data for estimations of the total carbon contribution of nematodes for a profound understanding of carbon cycling in mangroves.

2. Materials and methods

2.1. Study area

Futian Mangrove Nature Reserve in Shenzhen (Guangdong Province, China) is a subtropical mangrove forest (113°45' E, 22°32' N). It is situated on the east coast of the Zhujiang Estuary and covers an area of approximately 3.38 km^2 (Li et al., 2012) (Fig. 1). Native vegetation is mainly made up of *Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina*, *Excoecaria agallocha*, *Acanthus ilicifolius*, and *Bruguiera gymnorhiza* (Lu et al., 2014). The tides in this area are irregular semi-diurnal, with a mean tidal range of 1.9 m (Zan et al., 2002). Its climate belongs to the subtropical monsoon climate, with a characteristic of long summer and short winter (Climate Overview and Seasonal Characteristics of Shenzhen City, 2024). According to climatological classification standards, there are four seasons: winter (from late January to early February), spring (from early February to late April), summer (from late April to early November), and autumn (from early November to late January in the next year). The average annual temperature is 22℃, and the average annual precipitation is 1927 mm (Li et al., 2012). Approximately 80 % of the rainfall occurs from April to September, with monthly totals of 100–400 mm (Climate Overview and Seasonal Characteristics of Shenzhen City, 2024).

2.2. Field sampling

Sampling was carried out in July 2013 (rainy summer), October 2013 (dry summer), and January 2014 (winter) during low tide. This study determined four sampling areas: Guanniao Pavilion (G), Fengtang Estuary (F), Shazui Wharf (S), and Fishpond (Y) (Fig. 1). Three equal-distance sampling sites were established perpendicular to the waterline, extending from the high-water line to the low-water line at area G, F, and S. In area Y, only one site has been established. All sampling sites were on the intertidal mudflats, excluding the upper intertidal zone, which was the distribution area of the mangrove vegetation. Due to the limitations of sampling conditions in July 2013, no samples were collected in area F. At each sampling site, three replicated core samples were collected with a sawn-off syringe (2.9 cm inner diameter) to a depth of 11 cm for nematode analyses and fixed with 5 % buffered formaldehyde. Additional surface sediment samples were collected at each site for analyses of granulometric composition, Chlorophyll a (Chl-a) and pheophorbide a (Pheo-a) content, and total organic matter content (OM). Interstitial water temperature and salinity were measured using YSI600XLM-M Multi-Parameter Water Quality Sonde (YSI Inc., USA) at each sampling site *in situ*.

2.3. Sample processing

In the laboratory, environment variables of sediments were determined according to the methods of specifications for the oceanographic survey (State Quality and Technical Supervision Administration of China, 2007). Briefly, sedimentological analysis was conducted using the Malvern Mastersizer 3000 particle size analyzer. The medium particle diameter (Md, μm) indicated the particle diameter corresponding to the 50 %-point of the cumulative scale. The total organic matter content in sediment was measured using the $K_2Cr_2O_7$-H_2SO_4 oxidation method. The contents of Chl-a and Pheo-a in the sediment were determined using the spectrophotofluorometry method.

Samples for meiofauna extraction were stained with Rose Bengal for more than 24 h, then washed through sieves with mesh widths of 500 μm and 31 μm. Meiofauna extractions were used the Ludox TM-50 (Aldrich Chemical Company, gravity of 1.13 g/cm^3) centrifugation technique (Giere, 2009). All meiofauna specimens retained in the 31 μm mesh sieve were sorted and counted manually. Two hundred nematodes were randomly collected from each sample and mounted on permanent slides after a transparent treatment to prevent dehydration. Nematodes were identified to genus level using an Olympus BX51 compound microscope (Olympus, Tokyo,

Japan), following the pictorial keys of Platt and Warwick (1983, 1988), Warwick et al. (1998), and NeMys online identification keys (Nemys, 2024). The life stage, namely juvenile or adult, was identified for each specimen. Since fully formed gonads and copulatory apparatus are only found in adults (Warwick and Platt, 1988), individuals without fully formed gonads and copulatory apparatus were considered juveniles. Nematodes were assigned to different trophic groups based on buccal cavity morphology as selective deposit feeders 1A, non-selective deposit feeders 1B, epistratum feeders 2A, or omnivores/predators 2B (Wieser, 1953).

2.4. Body size attributes and biomass size of nematodes

All identified nematode individuals were measured for length (L, excluding filiform tail portions) and maximum body width (W) under an Olympus BX51 compound microscope with AJ-VERT software. Calculate the length-to-width (L/W) ratio of nematode specimens and classify them into three shape categories based on the L/W ratio: stout (L/W ratio < 18), slender (L/W ratio between 18 and 72), and long/thin (L/W ratio >72) (Schratzberger et al., 2007). Individual volume was estimated using a formula given by Feller and Warwick (1988): $V = 530 \times L \times W^2$, where V is in nl and W and L in mm. The volumes were converted to wet weights using a density of 1.13 g cm^{-3} (Wieser, 1960). Nematodes wet weights were converted to dry weights (μg) using a dry-to-wet-weight ratio of 0.25 (Wieser, 1960; Feller and Warwick, 1988). Nematode carbon content (μg) was estimated to be 12.4 % of the wet weight (Jensen, 1984). Each nematode individual was assigned a size class, a $\log_2$-transformed individual dry weight. The size class represents the nematodes' dry weights within the class; for example, the body size class of 0 encompasses organisms with weights $\geq 2^0$ and $< 2^1$ μg or dry weight ≥ 1 and < 2 μg (Vanaverbeke et al., 2003; Hua et al., 2013).

2.5. Statistical analysis

Ocean Data View (ODV v5.3.0; Schlitzer, 2020) was used to create the map of the area studied. The differences in the nematode data were analyzed using One-way analysis of variance (ANOVA) or Kruskal-Wallis tests. Before performing these tests, the normality of the data was validated using the Kolmogorov-Smirnov test. ANOVA test was applied when the data met normality assumptions; otherwise, the Kruskal-Wallis test was utilized. If significant differences were found ($p < 0.05$), pairwise comparisons were conducted, with *p*-values corrected by Bonferroni corrections. All the above statistical analyses were performed using SPSS 20.0 software.

PRIMER v7 and the PERMANOVA add-on package were used to perform analyses of environmental datasets and nematode size composition (Anderson et al., 2008; Clarke and Gorley, 2015). The differences in environmental variables were analyzed using principal coordinates analysis (PCoA) on normalized data and the Euclidean resemblance matrix. Biological data were standardized and fourth-root transformed before calculating Bray–Curtis resemblance. RELATE tests were conducted to assess how closely related two sets of multivariate data were. Permutational multivariate analysis of variance (PERMANOVA) was used to evaluate the differences in nematode size composition among different sampling months. The tests of homogeneity of dispersion (PERMDISP) were performed to determine whether a significant PERMANOVA result is caused by the homogeneity of the sample dispersion within the group. A pairwise comparison of the observed significant differences was conducted further, and the *p*-levels of the pairwise tests were corrected by Bonferroni corrections. A distance-based linear model (DistLM) using a step-wise selection procedure was applied to test the relationships between environmental variables and the nematode data. The fitted models from DistLM were visualized in multi-dimensional space, using distance-based redundancy analysis (dbRDA).

Table 1
Environmental variables of the study mangrove. Abbreviations: G, Guanniao Pavilion; F, Fengtang Estuary; S, Shazui Wharf; Y, Fishpond; Temp, interstitial water temperature; Sal, interstitial water salinity; Silt & clay, proportion of sediment silt and clay; Md, medium particle diameter; Chl-a, chlorophyll a; Pheo-a, pheophorbide a; OM, total organic matter. In July 2013, no samples were collected in Area F due to restrictions.

Month	Area	Temp ℃	Sal ‰	Silt & clay %	Md μm	Chl-a μg/g	Pheo-a μg/g	OM %
July	F	-	-	-	-	-	-	-
	G	27.6 ± 0.4	2.5 ± 0.9	97.8 ± 0.8	6.12 ± 0.57	0.52 ± 0.09	7.57 ± 1.77	8.89 ± 1.91
	S	30.1 ± 0.7	3.8 ± 0.7	99.6 ± 0.1	6.02 ± 0.12	0.49 ± 0.12	5.99 ± 0.31	9.40 ± 0.52
	Y	35.0	1.9	100.0	4.98	0.72	8.22	10.31
	Mean	30.9 ± 3.8	2.7 ± 1.0	98.2 ± 2.2	5.93 ± 0.68	0.58 ± 0.12	7.26 ± 1.15	9.54 ± 0.72
October	F	27.8 ± 0.1	12.3 ± 0.3	85.5 ± 9.2	7.85 ± 1.23	1.27 ± 0.27	8.72 ± 1.86	6.46 ± 2.56
	G	27.6 ± 0.3	10.6 ± 0.1	98.8 ± 0.6	6.17 ± 0.31	1.35 ± 0.41	7.08 ± 0.53	9.26 ± 2.26
	S	27.0 ± 1.5	11.1 ± 0.3	97.5 ± 0.8	6.80 ± 0.15	1.51 ± 0.60	7.11 ± 0.77	10.25 ± 1.19
	Y	27.1	6.8	91.0	6.52	1.48	8.56	13.19
	Mean	27.4 ± 0.4	10.2 ± 2.4	93.2 ± 6.2	6.83 ± 0.72	1.40 ± 0.11	7.87 ± 0.89	9.79 ± 2.78
January	F	17.7 ± 2.1	19.3 ± 1.2	90.9 ± 3.2	7.26 ± 0.36	1.36 ± 0.41	6.39 ± 0.47	9.57 ± 1.15
	G	21.7 ± 1.2	20.0 ± 1.7	95.9 ± 3.9	6.32 ± 0.89	1.15 ± 0.35	6.64 ± 0.57	8.98 ± 0.71
	S	21.0 ± 1.0	19.7 ± 0.6	98.8 ± 0.7	6.46 ± 0.47	2.65 ± 0.94	6.07 ± 1.72	9.52 ± 1.16
	Y	13.0	19.0	94.6	6.22	2.09	8.94	16.27
	Mean	18.3 ± 4.0	19.5 ± 0.4	95.0 ± 3.3	6.56 ± 0.47	1.81 ± 0.69	7.01 ± 1.31	11.08 ± 3.47

3. Results

3.1. Environmental changes in mangrove

The sediments were composed of extraordinarily high proportions of silt and clay (>90 %) at the vast majority of sampling sites, resulting in a small Md (5.0 μm - 8.6 μm). The total organic matter content was high (9.51 ± 2.25 %) and varied little among sampling months (Table 1). The highest temperature was observed in July (30.9 ± 3.8 ℃), while the lowest value was found in January (18.3 ± 4.0 ℃). A steady decline in temperature was observed from July to January. On the contrary, a successive increase in salinity and Chl-a concentration from July to January was prominent (Table 1).

The principal coordinates analysis (PCoA) was performed to assess the overall differences in environmental variables concerning sampling months (Fig. 2). The first two axes of the PCoA plot accounted for 70.2 % of the total environment variability. Along the PCo1 axis, high absolute scores (>0.6) were because of salinity (-0.828), Md (-0.750), the proportion of silt and clay (0.691), temperature (0.634), and Chl-a (-0.608). Along the PCo2 axis, high absolute values (>0.6) related to sediment Pheo-a (-0.661), OM (0.652), and proportion of silt and clay (0.640). The sampling sites were aggregated into three groups, indicating the differences in environmental variables among sampling months, particularly a continuous variation of temperature, salinity, and Chl-a content from July to January (Fig. 2).

3.2. Body size attributes of nematodes

A total of 3692 nematode individuals were measured. Histograms (Figs. S1-S3) and the Kolmogorov-Smirnov tests ($p < 0.05$, Table S1) proved that the distributions of body length, maximum body width, and L/W ratio did not follow a normal distribution.

The body length of nematodes ranged from 320.62 μm to 3488.62 μm. The lowest median value was noted in October (799.91 μm) and the highest value in January (1226.64 μm) (Table 2; Fig. 3A). Maximum body width of nematodes ranged from 11.76 μm to 173.44 μm, and the highest median value also appeared in January (78.21 μm), followed by July and October with median width of 39.67 μm and 29.21 μm, respectively (Table 2; Fig. 3B). The L/W ratio varied between 7 and 75. The lowest median value of the L/W ratio was noted in January (median L/W ratio of 16.09), and the highest value appeared in October (median L/W ratio of 26.74). The median L/W ratio in July was 22.83 (Table 2; Fig. 3C).

The Kruskal-Wallis tests showed significant differences in body length, body width, and L/W ratio among the sampling months (Table S2, all $p < 0.001$). The pairwise comparisons showed significant differences in these attributes between the two sampling months after a Bonferroni correction (Table S3, all $p < 0.001$).

In this study, adult individuals accounted for 86.2 % of the total nematodes, while juveniles accounted for 13.8 %. The proportion of juveniles in July, October, and January was 15.4 %, 14.8 %, and 9.5 %, respectively, without fluctuations between sampling months (Kruskal-Wallis test, H=1.438, $p > 0.05$). The median body length of adults was 988.24 μm, the median body width was 43.38 μm, and the median L/W ratio was 22.19 (Table 2). The median L, W, and L/W ratio of juveniles was 791.37 μm, 31.73 μm, and 24.39, respectively (Table 2). The temporal variation patterns of these attributes for adults and juveniles were similar. The highest length and width values were all observed in January, while the lowest L/W ratio was noted in January (Fig. 3D-F). The Kruskal-Wallis tests showed significant differences in body length, body width, and L/W ratio for adults across the sampling months (Table S2, all

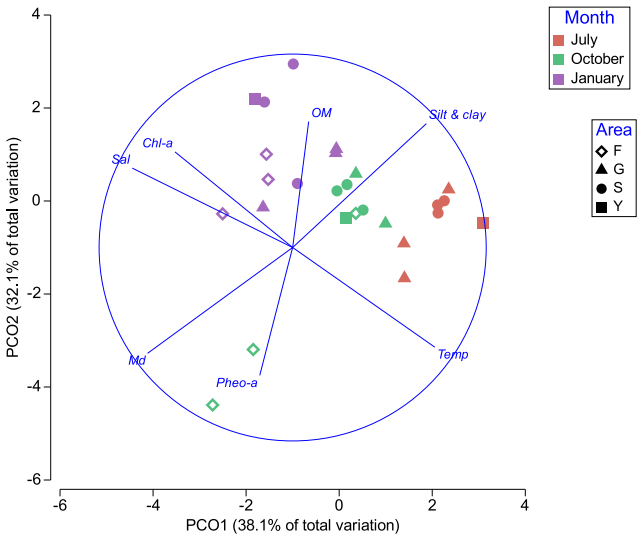

Fig. 2. Principal coordinates analysis (PCoA) results of environmental factors in the study area. Blue circles and lines are superimposed vectors. Vectors are the raw Pearson correlations of variables with the PCO axes. Abbreviations: G, Guanniao Pavilion; F, Fengtang Estuary; S, Shazui Wharf; Y, Fishpond. Abbreviations for environmental variables are the same as in Table 1.

Table 2
Body size data of the study nematodes. Abbreviations: L, body length; W, maximum body width; L/W ratio, length-to-width ratio; DW, individual dry weight; C_{carbon}, individual carbon content; N, individual number.

	Month	Adult + Juvenile			Adult			Juvenile		
		N	Mean	Median	N	Mean	Median	N	Mean	Median
L (μm)	July	1509	1028.77	946.21	1276	1069.11	990.57	233	807.83	792.45
	October	1291	887.11	799.91	1100	905.93	826.93	191	778.76	695.45
	January	892	1241.57	1226.64	807	1252.30	1234.73	85	1139.70	976.97
	All	3692	1030.65	956.88	3183	1059.16	988.24	509	852.34	791.37
W (μm)	July	1509	47.13	39.67	1276	49.77	42.71	233	32.71	30.58
	October	1291	33.91	29.21	1100	34.22	29.35	191	32.11	28.64
	January	892	76.18	78.21	807	76.93	79.03	85	69.10	61.97
	All	3692	49.53	40.98	3183	51.28	43.38	509	38.56	31.73
L/W ratio	July	1509	24.21	22.83	1276	23.86	22.17	233	26.14	25.52
	October	1291	28.49	26.74	1100	28.83	27.05	191	26.53	25.36
	January	892	17.58	16.09	807	17.57	16.06	85	17.66	16.28
	All	3692	24.11	22.51	3183	23.98	22.19	509	24.87	24.39
DW (μg)	July	1509	0.503	0.220	1276	0.480	0.270	233	0.191	0.110
	October	1291	0.236	0.110	1100	0.225	0.110	191	0.201	0.090
	January	892	1.341	1.130	807	1.039	1.180	85	0.753	0.610
	All	3692	0.612	0.240	3183	0.656	0.280	509	0.341	0.120
C_{carbon} (μg C)	July	1509	0.222	0.110	1276	0.238	0.132	233	0.095	0.054
	October	1291	0.108	0.053	1100	0.112	0.055	191	0.100	0.044
	January	892	0.502	0.559	807	0.515	0.586	85	0.373	0.301
	All	3692	0.304	0.117	3183	0.325	0.139	509	0.169	0.059

$p < 0.001$). The pairwise comparisons showed significant differences in these attributes between the two sampling months after a Bonferroni correction (Table S3, all $p < 0.001$). For juveniles, Kruskal-Wallis tests indicated significant differences in body length, body width, and L/W ratio across the sampling months (Table S2, all $p < 0.001$). The pairwise comparisons indicated that there were no significant differences in body width and L/W ratio between July and October (Table S3, all $p > 0.05$), while there were significant differences between other sampling months (Table S3, all $p < 0.01$).

According to the shape category, the dominant shape of nematodes in the study area was slender (L/W ratio between 18 and 72), accounting for 71.3 % of the total individuals. The abundance of stout nematodes accounted for 28.6 % of the total abundance, while long/thin nematodes were rarely present in the study area (0.1 %). The nematode assemblages showed variations in terms of body shape concerning the investigated months (Fig. 4). Slender nematodes constituted 77.5 %, 89.2 %, and 35.0 % of the total number of nematodes in July, October, and January, respectively. Compared to July and October, the percentage of stout nematodes increased in January (64.9 %). The slender shape was still the main body shape for adults and juveniles, accounting for 69.7 % and 81.5 % of the total number of nematodes, respectively. As far as sampling month was concerned, adults and juveniles with slender shapes dominated in July and October, while stout adults and juveniles were dominant in January (Fig. 4).

3.3. Individual dry weight of nematodes and total biomass of nematode community

The distributions of individual dry weight in different sampling months did not follow a normal distribution (Fig. S4), confirmed by the Kolmogorov-Smirnov tests ($p < 0.05$, Table S1). The individual dry weight of nematodes varied in a wide range between 0.011 μg and 7.004 μg, and the median value was 0.24 μg. The median individual dry weight was the highest in January (1.13 μg) and the lowest in October (0.11 μg). The median individual dry weight in July (0.22 μg) fell between the other two months (Table 2). Kruskal-Wallis tests showed significant differences in nematodes' dry weight across the sampling months (H=1197.850, $p < 0.001$; Table S2) and between the two sampling months after a Bonferroni correction (all $p < 0.001$; Table S3). The median individual dry weight for adults was 0.28 μg, while the median value for juveniles was 0.12 μg (Table 2). Similarly, the median individual dry weights of adults and juveniles were highest in January (Table 2).

A total of 46 genera belonging to 17 families of free-living marine nematodes were identified in the study area. Axonolaimidae and Linhomoeidae were the most abundant families. *Pseudolella*, *Terschellingia*, *Daptonema*, *Parodontophora*, *Subsphaerolaimus*, *Thalassironus*, *Chromadorina*, *Trissonchulus*, *Omicronema*, *Metalinhomoeus*, and *Ptycholaimellus* were dominant genera with > 5 % of the total individuals in any sampling month. *Pseudolella*, *Terschellingia*, and *Daptonema* were commonly observed at investigated sites in all three months, accounting for 20.7 %, 14.8 %, and 14.1 % of the total individuals, respectively. Genus-specific individual dry weights for these dominant genera were analyzed (Table S4). In general, the median genus-specific individual dry weights (both adults and juveniles) of genera *Pseudolella*, *Terschellingia*, *Daptonema*, *Parodontophora*, *Subsphaerolaimus*, and *Metalinhomoeus* fluctuated among sampling months (Kruskal-Wallis test, $p < 0.05$; Table S4), with values in January significantly higher than those in July and October (pairwise comparisons, $p < 0.05$).

The total biomass or carbon contribution of the nematode community in each site was estimated by multiplying the abundance with the mean individual dry weight or individual carbon content at that site. The results showed that the mean biomass of the nematode community was 886.4 ± 207.8 μg/10 cm^2, and the annual mean total carbon contribution of nematodes was 407.1 ± 95.5 μg C/10 cm^2 (Table S5). Total biomass was 2442.7 ± 2267.8 μg/10 cm^2 in July, 122.9 ± 124.9 μg/10 cm^2 in October, and 796.4 ± 1415.5 μg/

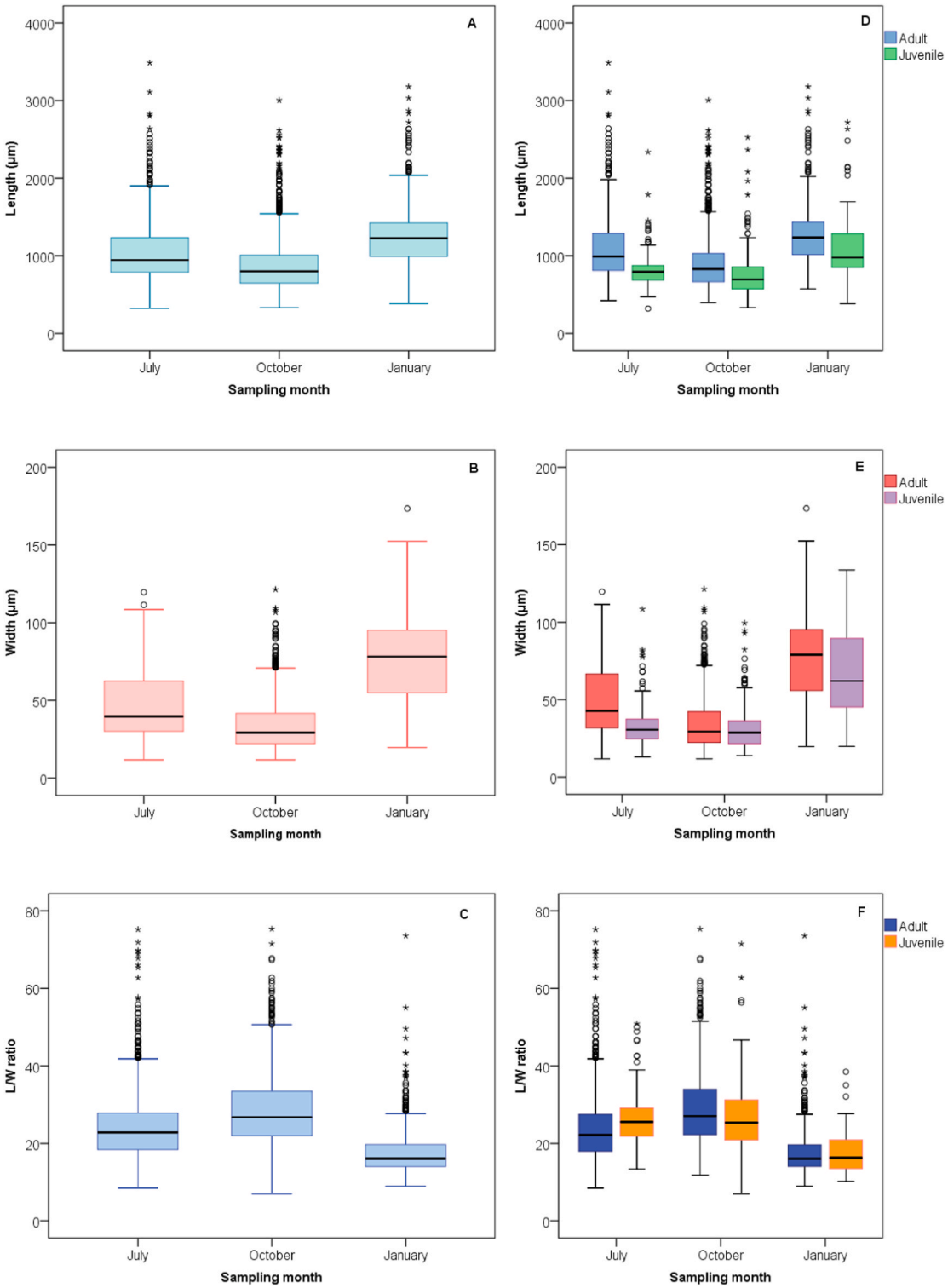

Fig. 3. Body length, maximum body width, and length-to-width (L/W) ratio of nematodes across different sampling months. Horizontal lines = median, boxes = interquartile range, vertical lines = nonoutlier range, dot = outlier values.

10 cm^2 in January (Table S5). The total carbon contribution of nematodes was 927.6 ± 789.4 μg C/10 cm^2, 61.0 ± 62.0 μg C/10 cm^2, and 395.0 ± 702.1 μg C/10 cm^2 in July, October, and January, respectively (Table S5). The ANOVA test showed significant differences in total biomass and total carbon contribution of nematodes among three sampling months (F=8.326 and 7.638, $p < 0.001$). The result

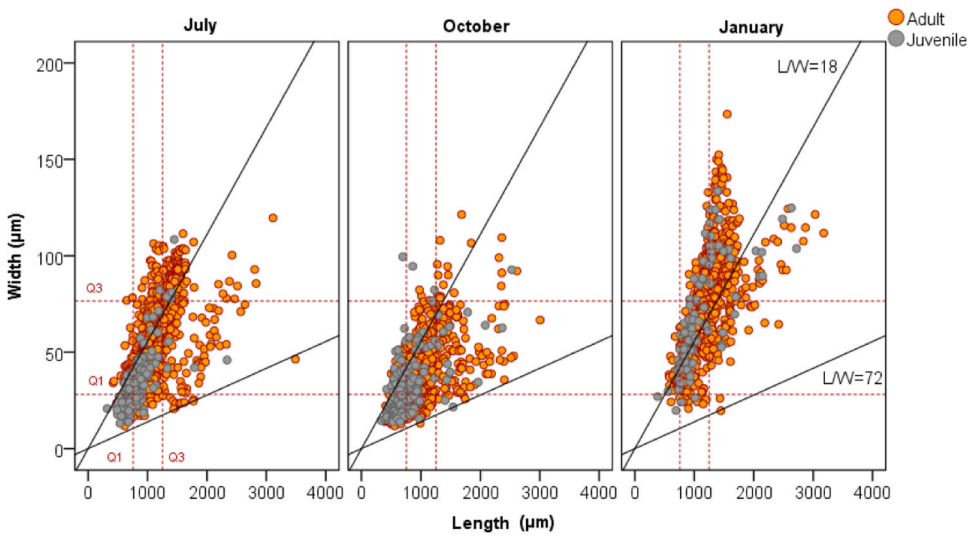

Fig. 4. Length-width relationship plots. Each measurement displays a single data point. Length-to-width (L/W) ratio < 18, stout; L/W ratio between 18 and 72, slender; L/W ratio > 72, long/thin. Q1 indicates the first quartile, and Q3 indicates the third quartile calculated for all data. $Q1_{Length}$ = 757.32 μm, $Q3_{Length}$ = 1250.49 μm; $Q1_{Width}$ = 28.06 μm, $Q1_{Width}$ = 67.58 μm.

of pairwise comparison showed significant differences between July and any of the other two months (after a Bonferroni correction, $p < 0.05$).

3.4. Biomass size composition of nematode community

The total individual numbers of each biomass size class were calculated (Fig. 5). In July, the distribution of nematode size classes showed the initial peak at body size class −3 (0.125 μg) and the second peak at size class 0 (Fig. 5). In October, the spectrum skewed towards the smaller size classes and peaked in body size class −4 (Fig. 5). The spectrum for January skewed towards the larger size classes and peaked in body size class 0, which reflected the commonly observed stout nematodes (Fig. 5). The distribution patterns of adults were the same as that of all individuals (Fig. 5). The peak of juveniles appeared at one size class earlier or almost the same size class as adult individuals. The results of the RELATE test showed that there was a remarkable match in nematode size class composition

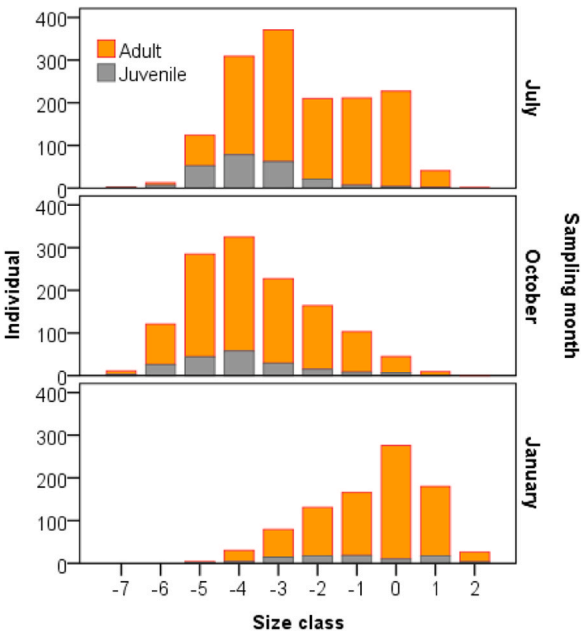

Fig. 5. Total individual number of each biomass size class.

for juveniles and adults (ρ=0.65, $p = 0.001$), and there was a significant match in size class composition with and without juveniles (ρ=0.964, $p = 0.001$).

The results of the PERMANOVA test showed that nematode composition based on biomass size class differed significantly among sampling months (Pseudo-F= 12.342, $p = 0.001$). No significant p-value (F = 1.7226, $p = 0.199$) was reported by PERMDISP analysis, confirming the significant temporal differences. The results of the PERMANOVA pairwise test confirmed that nematode composition based on biomass size class in January differed significantly from July and October after a Bonferroni correction ($p = 0.004$ and 0.001). The PERMDISP analysis confirmed the significant difference between January and October (t = 0.84829, $p = 0.399$).

3.5. The correlation between body size attributes and environmental variables

The DistLM results of the sequential test demonstrated that Pheo-a, interstitial water temperature, and salinity were the significant variables influencing the nematode size composition and body size attributes, including body length, maximum body width, L/W ratio, and individual dry weight (Table 3). Pheo-a and temperature were almost present in every DistLM model and were the most prominent variables (Table 3).

The dbRDA routine was used for ordinations of fitted values from the given DistLM model (Fig. 6). The first two dbRDA axes captured 56.5 % of the total variation in the biomass size composition, the dbRDA1 axis contributed the vast majority of the total variation (51.5 %). Along the dbRDA1 axis, sampling sites differentiated across sampling months (Fig. 6).

4. Discussion

4.1. Ability of nematode body size attributes to indicate environmental changes

The temperature indicated a gradient change from July (rainy summer) to October (dry summer) and then to January (winter) in the present study. A phenotypically plastic response known as the “temperature-size rule” is found in organisms including bacteria, protists, invertebrates, plants, and ectothermic vertebrates (Atkinson, 1994; Atkinson and Sibly, 1997; Forster et al., 2012). According to this rule, organisms mature at smaller body sizes when reared in warmer conditions. This rule also applies to free-living nematodes (Heip et al., 1985; Majdi et al., 2019). The high temperatures would shorten the generation time of nematodes (Heip et al., 1985), and nematodes tend to hatch and mature at smaller body sizes with increasing temperatures (Majdi et al., 2019). In the present study, the nematode community was composed of smaller individuals (both adults and juveniles), and the proportion of juveniles was higher in warmer seasons (July and October). The genus-specific individual dry weights also proved that the individual dry weights of the commonly dominant genera were smaller at higher temperatures and larger at lower temperatures. Furthermore, there was a significant negative relationship (r = - 0.514, $p = 0.007$) when regressing the proportion of juveniles against mean body length. These results followed the temperature-size rule, indicating that an increase in temperature led to a decrease in body size and led to maturity at smaller body sizes.

Oxygen plays a central role in explaining the temperature-size responses of larger aquatic organisms (Forster et al., 2012). Dissolved oxygen contents are usually low in high-temperature water. Larger aquatic organisms increasingly adopted mechanisms to either increase oxygen supply or reduce demand in the warmth (Atkinson et al., 2006; Forster et al., 2012). It was well known that larger organisms have higher respiration rates and corresponding lower metabolic rates (Gerlach et al., 1985). In other words, an increase in the nematode’s body size will reduce its ability to absorb oxygen because the ratio of respiratory absorption surface area to body mass will decrease. Jensen (1986), (1987) found that thiobiotic species were slender and had a higher proportion of body surface

Table 3
Results of the DistLM sequential test for nematode body size attributes and biomass size class composition. SS, mean square; F, F statistic; Prop, the proportion of the variability explained; Cumul, the cumulative proportion of the variability. **, $p < 0.01$; *, $p < 0.05$. Abbreviations for environmental variables are the same as in Table 1.

	Variables	Adjusted R^2	SS (trace)	Pseudo-F	*P*	Prop	Cumul.
Length	Pheo-a	0.18487	65.679	6.6699	0.024*	0.2175	0.2175
	Silt & clay	0.19888	13.74	1.4198	0.249	0.0455	0.2630
	Sal	0.25693	25.106	2.7969	0.120	0.0831	0.3461
Width	Pheo-a	0.39231	328.78	17.1390	0.001**	0.4166	0.4166
	Temp	0.57198	149.63	11.0740	0.004**	0.1896	0.6062
Length to Width ratio	Temp	0.39473	131.68	17.3040	0.001**	0.4189	0.4189
	Pheo-a	0.55485	53.912	9.6330	0.009**	0.1715	0.5905
	Md	0.57575	11.378	2.1332	0.164	0.0362	0.6267
	Silt & clay	0.58884	8.7888	1.7002	0.212	0.0280	0.6546
	Chl-a	0.59199	5.961	1.1621	0.309	0.0190	0.6736
Individual dry weight	Pheo-a	0.34778	1773.8	14.3300	0.001**	0.3739	0.3739
	Sal	0.47196	665.83	6.6444	0.011*	0.1403	0.5142
	Silt & clay	0.49546	198.3	2.0710	0.151	0.0418	0.5560
Body size composition	Pheo-a	0.25109	4441.8	9.3818	0.001**	0.2810	0.2810
	Temp	0.41082	2796	7.5068	0.010*	0.1769	0.4580
	Silt & clay	0.44326	823.57	2.3400	0.101	0.0521	0.5101
	Sal	0.44778	411.95	1.1800	0.294	0.0261	0.5361

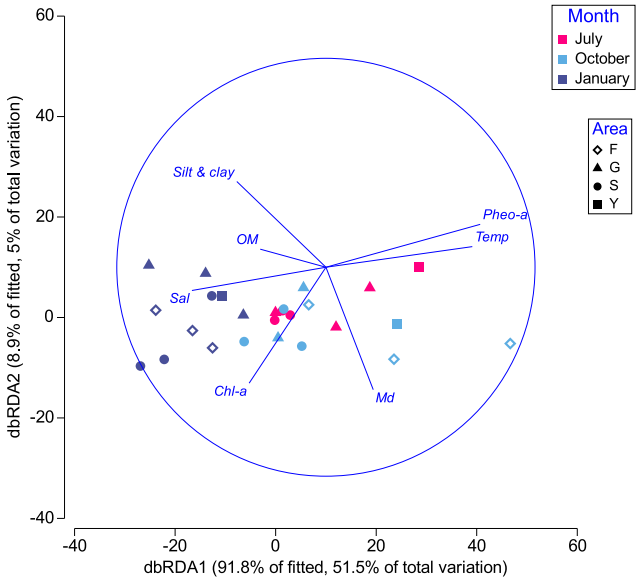

Fig. 6. dbRDA ordination for the fitted model of nematode data, Bray-Curtis after fourth-root transformation of an individual number of biomass size class (log_2-transformed individual dry weight), versus environmental variables. Variables in the DistLM analyses are displayed as vectors, and the length of each categorical vector is a measure of the strength of the relationship between that category and the dbRDA axes. Abbreviations: G, Guanniao Pavilion; F, Fengtang Estuary; S, Shazui Wharf; Y, Fishpond. Abbreviations for environmental variables are the same as in Table 1.

area per body volume than the oxibiotic species to support a higher cuticular uptake of dissolved oxygen and organic matter. Soetaert et al. (2002) also demonstrated that the thinner nematodes have a higher tolerance to low oxygen levels, as the thinner the body, the less oxygen diffusion limitation. Slender nematodes could represent an adaption to poor-oxygenated sediments (Nguyen et al., 2023), while short and thick nematodes were an indicator of well-oxygenated sediments with high food quality (Grzelak et al., 2016). Therefore, as observed in the present study, nematodes tended to be thinner at warm temperatures and short and thick at cool temperatures. Combining these previous findings in nematodes, we believe that decreasing body size is a crucial morphological response of nematodes to increasing temperature in mangrove sediments.

Food type and quality also significantly affect nematode body size (Soetaert et al., 2002; dos Santos et al., 2008). Long nematodes often have a longer intestine, whereas the length of the intestine is related to the function of digestion and absorption efficiency, and the longer, the higher the efficiency (Soetaert et al., 2002; Zhang et al., 2024). Thicker animals allocated a large amount of food to storage products rather than structural growth to increase the maintenance time in food shortage (Soetaert et al., 2002). Female nematodes mature at smaller sizes under food stress (dos Santos et al., 2008). Pheo-a and Chl-a contents indicate microalgal food resources for nematodes, which became abundant and diverse with increasing Chl-a and Pheo-a content (Hua et al., 2021). Their contents were relatively high in this study, indicating sufficient food to satisfy the demands of nematodes. The results of the nematodes' feeding structure have precisely proved that epigrowth feeders (2 A), predominantly feed on microalgae, were the most dominant feeding type in the mangrove studied (Hua et al., 2020). Besides microalgae, nematodes feed on bacteria, protozoans, fungi, and detrital materials (Moens et al., 2014; Schratzberger and Ingels, 2018). Coull (1999) concluded that food quantity does not appear to limit meiofaunal abundance in estuarine soft-bottom habitats. Therefore, Pheo-a content might indirectly shape the body size attributes and size composition of mangrove nematodes in this study. It is worth noting that an increasing number of microalgae or detritus in surface sediments can lead to rapid consumption of oxygen during deterioration, resulting in a low-oxygen environment, which may have more significant impacts on the body size attributes of nematodes.

The variations in body size attributes might be a response to the deterioration of environmental quality status. From the early 1990s, with the increase of pollution load in Shenzhen Bay, the concentration of heavy metals and nutrients in sediments changed significantly, leading to a decline in the ecosystem quality of the mangrove studied (Lei et al., 2020). From the indicative role of marine nematodes, a high proportion (>10 %) of genera, such as *Terschellingia*, *Daptonema*, and *Parodontophora*, are often used to indicate bad or poor environmental quality status (Moreno et al., 2011; Hua et al., 2021). Referring to the study on the taxonomic structure of nematodes in the study area, the annual mean proportion of *Terschellingia* was high (>10 %), especially in summer (Hua et al., 2020), suggesting a bad environmental quality. In the present study, slender nematodes were the most dominant group during all sampling months, and long/thin nematodes were rare. According to Nguyen et al. (2023), the proportion of long/thin nematodes negatively correlated with concentrations of Fe and Pb. Based on the above discussion, we would like to infer that reducing body size might be a morphological response of nematodes to a deteriorated environmental status in mangrove sediments. Unfortunately, the concentrations of heavy metals or pollutants in sediments were not analyzed simultaneously by the present study. Although the present study cannot confirm the inference, the relationship between the contaminants and nematode body size attributes deserves further attention.

The results of the present study indicated that nematode body size attributes and size composition were highly correlated with

environment variables and have an indicative role in environmental changes. The community size composition was determined by the processes, which were essentially species-independent, indicating that ecological roles seem to be more influential than taxonomic distinctions (Kerr, 1974; Tita et al., 1999; Zhao et al., 2015). Recent studies conducted in estuaries also showed that body size attributes were highly dependent on the surrounding environment, and these attributes contributed to a better understanding of nematode responses to environmental conditions (Sroczyńska et al., 2021; Nguyen et al., 2023). Our findings supported the effectiveness of nematode body size attributes and biomass size composition as good indicators of environmental changes or external disturbances. In particular, analyses based on body size did not rely on taxonomic identification, which is more meaningful for promoting the application of nematodes in environmental monitoring.

There was undeniably a concern about whether the life stage affects the variation patterns in body size attributes. Nematode juveniles have sizes and body proportions significantly different from adults, which suggests food partitioning and lifestyle differences between juveniles and adults (Warwick, 1984; Tita et al., 1999). Adults represent the achievement of the morphological adaption of the species to a given ecological rule, and they are more suitable to describe this same rule (Tita et al., 1999). In the present study, there were no significant differences in the temporal variation patterns of biomass size composition of nematode communities with or without juveniles. A previous survey obtained a similar conclusion that the age structure of nematode communities did not affect the patterns in body size changes (Grzelak et al., 2020). The percentage of juveniles was low (<50 % of the total community), and their impact was limited. On the other hand, juveniles' body size and biomass responded similarly to environmental changes as adults in the present study. Life stage did not affect the variation patterns in biomass size composition of nematode, which would further simplify the application of size-based analyses in environmental monitoring.

4.2. Application of body size data in estimating the total carbon contribution of marine nematodes

Nematodes are crucial in absorbing and storing carbon in their bodies and contribute to the blue carbon sink (Wang and McSorley, 2005; Krishnapriya et al., 2021). An estimate of the total biomass of nematodes and their carbon contribution based on body size data deserves attention. The biomass of nematodes was usually estimated using the biovolume method, extrapolating from volume calculation (Warwick and Price, 1979; Feller and Warwick, 1988; Tita et al., 1999; Hua et al., 2013; Nguyen et al., 2023). Some ecological studies estimated the total biomass of nematodes by multiplying their total abundance by 0.4 μg, an individual dry weight value provided by Juario (1975). Body size was related to environmental factors and varied among habitats (Jensen, 1986, 1987; Tita et al., 1999; Soetaert et al., 2002; Losi et al., 2013). According to the studies conducted in mangroves in China, individual biomass of marine nematodes varied spatially, ranging from 0.06 μg to 2.08 μg (Liu et al., 2013, 2018). At the same time, the present findings also indicated that the individual biomass varied with the temporal variations of environmental variables. Although nematode biomass was considered a crucial property, accurate estimation of the individual biomass of nematodes or the total biomass of the whole community has not received much attention from researchers, and studies on the carbon contribution of nematodes were scarce.

A recent study reported that blue carbon deposition by nematodes was relevant in mitigating the climatic change in the Arctic system (Krishnapriya et al., 2021). Mangroves are known for their enormous carbon storage capacity. Mangroves store an average of 394 tons of carbon per hectare, and approximately 78 % of that carbon is related to the top 1 m of the soil, 15 % with the aboveground biomass of the mangrove forests, and 7 % from the belowground biomass (Leal and Spalding, 2024). The present study calculated the carbon content in the individual nematodes and their total carbon sequestered. According to the estimation of this study, the annual average carbon contribution of mangrove nematodes reached 0.004 tons of carbon per hectare. As such a small-sized organism, this is a remarkable value, indicating its non-ignorable role in the mangrove ecosystem. We should pay close attention to the spatial and temporal differences in abundance and individual biomass, which may lead to overestimation or underestimation in the prediction. Therefore, well-documented body size data application will help estimate the total biomass of nematodes in the ecosystem and contribute to understanding the carbon potential and blue carbon contribution of marine nematodes. The total biomass of nematodes and their total carbon contribution revealed by the present study provided effective attempts to estimate nematodes' carbon stock and contribution to the blue carbon sink in mangroves. This blue carbon stock and burial of carbon in the sediment of mangroves may play a role in eliminating CO_2 from the atmosphere and mitigating global warming.

5. Conclusions

Generally, nematodes' body size attributes and biomass size composition exhibited effective and quick responses to environmental changes. Among them, interstitial water temperature and sediment Pheo-a content might play a more crucial role in explaining nematodes' morphological responses since the results of the present study indicated that nematodes' body size attributes and biomass size composition were correlated significantly with these environmental factors. Of course, other related factors, such as oxygen limitation and pollution, cannot be ignored in their impact on nematodes' morphological characteristics. In addition, the total biomass and total carbon contribution of nematodes estimated based on the body size attributes have constructive significance for studying the roles of nematode carbon stock and contribution to the blue carbon sink in mangroves.

Ethics

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03545.

Data availability

Data will be made available on request.

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