Russian Journal of Nematology, 2020, 28 (1), 53 – 70

Spatial and temporal changes in nematode assemblages inhabiting a seagrass biotope in the Tien Yen River estuary, Quang Ninh Province, Vietnam

Olga N. Pavlyuk[1], Yulia A. Trebukhova[1], Vladimir V. Mordukhovich[1, 2], Julia K. Zograf[1], Vladimir V. Yushin[1], Nguyen Dinh Tu[3], Nguyen Vu Thanh[3] and Cao Van Luong[4]

[1]A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 690041, Vladivostok, Russia
[2]Far Eastern Federal University, 690950, Vladivostok, Russia
[3]Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam
[4]Institute of Marine Environment Resources, Hai Phong, Vietnam
e-mail: mordukhovich.vv@dvfu.ru

Accepted for publication 21 June 2020

Summary. The seasonal changes in density, species biodiversity and trophic groups of free-living marine nematodes forming assemblages in tropical seagrass meadows have been studied in the Tien Yen River estuary (Gulf of Tonkin, South China Sea). Significant variations of the features of the nematode communities in the horizontal scale and in time were found. In the rainy season (October), the nematode density noticeably decreased, and the species composition and dominant species, as well as such parameters of assemblages as diversity and structure, changed as compared to April. A total of 71 nematode species were recorded from the studied area but only four species have been found at all stations in both seasons. The reasons for this are the high spatial heterogeneity of environmental conditions and their pronounced seasonal variations. Environmental conditions (granulometric composition of the bottom sediments, water temperature and salinity) were characterised by pronounced differences between stations as well as seasons. The precipitation (heavy rainfalls) in the intertidal zone of the estuary is the main factor responsible for seasonal changes of nematode assemblages.

Key words: environmental conditions, intertidal, meiofauna, rainfalls, seasonal changes.

Marine seagrasses are widely distributed in tropical and temperate coastal waters (Green & Short, 2003). Globally, seagrass systems occupy an area of 177000 km^2 and store about 20% of oceanic blue carbon (Spalding *et al.*, 2003; Short *et al.*, 2016). Due to the high production capacity they create important habitats for diverse fauna in coastal ecosystems (Duarte & Chiscano, 1999). Seagrasses play a considerable role in primary production, organic matter cycling, nutrients accumulation and bottom sediment stabilisation (Duarte & Chiscano, 1999; Green & Short, 2003; Fourqurean *et al.*, 2012). Despite their role, seagrass meadows are under increasing pressure of anthropogenic disturbances related to eutrophication, shading, siltation from deforestation, shoreline modification, trawling and anchoring (Duarte, 2002; Ralph *et al.*, 2006). These ecosystems are among the most threatened ecosystems and continue to decline at an estimated 7% per year globally (Waycott *et al.*, 2009). At the same time, seagrass meadows can be highly dynamic, changing as a result of natural influences.

Understanding and assessing the response of seagrass ecosystems to anthropogenic impact requires an understanding of the natural drivers of change and natural features of spatial and temporal variability in different spatiotemporal scales and for all groups of benthos distinguished by the body size. However, most studies dealing with seagrass beds

 doi: 10.24411/0869-6918-2020-10005

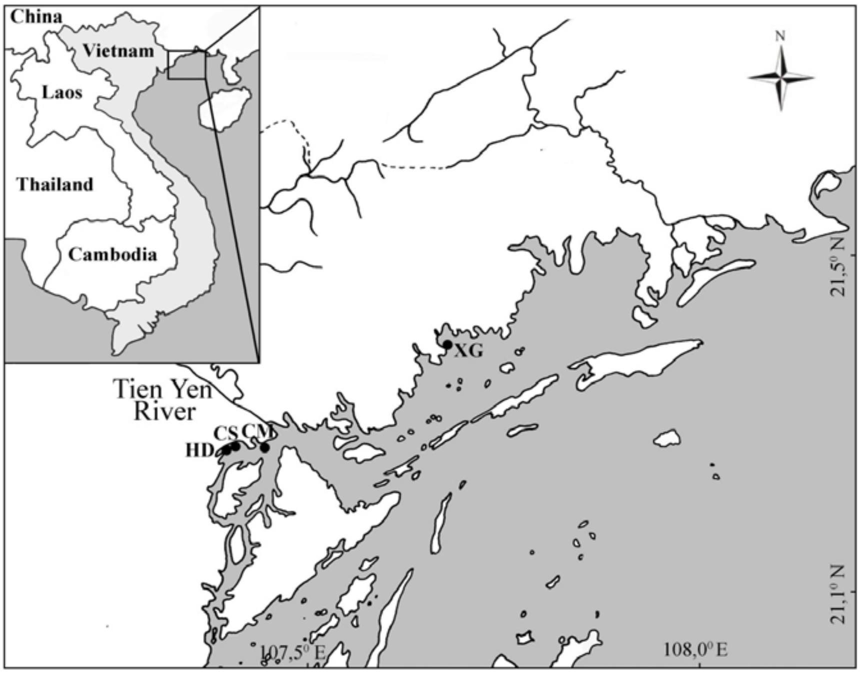

Fig. 1. Map of sampling stations in Tien Yen District, Quang Ninh Province, Vietnam. Station abbreviations: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Gia.

Table 1. Environmental variables of the studied stations.

Station	Latitude N	Longitude E	Temperature (C°)		Salinity (psu)		Sand content (%)		Mud content (%)		Median grain size (µm)	
			April	October	April	October	April	October	April	October	April	October
HD	21°16’46”	107°23’54”	20.5	23.4	18.6	17.0	25.6	48.9	72.9	48.6	26.2	65.5
CS	21°16’32”	107°16’45”	20.1	24.5	19.7	14.5	32.2	42.0	62.3	55.4	36.2	47.7
CM	21°16’11”	107°36’04”	20.3	24.3	24.2	18.2	76.8	65.4	22.5	34.2	147.4	126.8
XG	21°18’59”	107°25’52”	20.5	24.2	17.6	10.7	85.0	73.0	11.8	25.0	293.5	141.9

Note: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

merely focus on macrofauna and other groups, in particular, meiofauna are still poorly known. Although meiofauna comprises the most abundant metazoans in seagrass beds and can consume from 10% to more than 50% of the total primary production in a seagrass system (Danovaro & Gambi, 2002). Furthermore, it has been shown that meiofauna features are good indicators of environmental conditions and changes caused by anthropogenic activity (Balsamo *et al.*, 2012; Alves *et al.*, 2013).

Among meiofaunal communities associated with seagrass beds, free-living nematodes usually constitute the most abundant taxa (Fisher, 2003; Fonseca *et al.*, 2011; Liao *et al.*, 2015). The most comprehensive studies of intertidal nematode communities associated with different seagrass species, were carried out in tropical regions of Africa, Asia and Australia (Alongi, 1987a, 1990; Aryuthaka, 1991; Ndaro & Olafsson, 1999; De Troch *et al.*, 2001; Fisher, 2003; Fonseca *et al.*, 2011; Leduc & Probert, 2011; Liao *et al.*, 2015, 2016; Xu *et al.*, 2018). Both biotic (for example, food availability, the quality of the food, composition of seagrass species) and abiotic parameters (for example, salinity, temperature, sediment grain size) have been shown to affect nematode abundance and community composition and structure. Pronounced spatiotemporal variability has been demonstrated for community features. The relative contribution of different factors to the total variability of abundance or composition is not well understood.

In Vietnam, the first research on marine meiofauna, and, specifically, free-living nematodes, has been launched only recently (Nguyen *et al.*, 2002; Nguyen & Nguyen, 2003; Pavlyuk & Trebukhova, 2006; Pavlyuk *et al.*, 2008; Ngo *et al.*, 2007, 2010; Zograf *et al.*, 2017). To date, taxonomic and ecological studies have been conducted in different ecosystems, such as mangroves, shrimp farms and mud flats (Mokievsky *et al.*, 2011; Ngo *et al.*, 2010, 2013; Tran *et al.*, 2018a). However, the spatiotemporal variability of nematode communities inhabiting seagrass beds has not yet been investigated sufficiently. The total area of seagrass beds in Vietnam is estimated to be approximately 17000 ha and the distribution areas and densities of seagrass beds decreased by more than 50% in recent decades (Van Luong *et al.*, 2012). It is expected that in the coming years, human pressure on these communities will increase. As a baseline for assessing possible changes in the future, data on communities outside the anthropogenic pressure are needed. The goal of the present work is to study the density, species diversity, and structure of free-living nematode communities in tidal seagrass meadows of the Tien Yen estuary (Quang Ninh Province, Vietnam) in different seasons.

MATERIAL AND METHODS

Study area. The study was conducted in April and October 2015, in the Tien Yen River estuary, located in the Tien Yen Bay, northeastern Vietnam, which connects the river with the South China Sea (Fig. 1). A distinguishing feature of the estuary is the regular diurnal tidal cycles with a maximum tide range from 4.0 to 4.5 m. Therefore, the main oceanographic factors having an effect on the waters of the estuary are tide waves and near-shore currents. The most important ecosystems in the estuary include mangroves, seagrasses and intertidal mud flats. Samples were collected on two sampling occasions (April 2015 and October 2015) from a total of four intertidal sites where seagrasses are usually abundantly distributed (Table 1): Ha Dong (station HD), Con Mat (station CM), Cua Song (station CS) and Xom Giao (station XG).

Sample collection and laboratory processing. At each station, three meiofauna samples (upper 5 cm layer) were taken randomly during a low tide using hand cores (3.6 cm in diameter and 30 cm in height) from the same sampling site (1 m^2) in April and in October. Seagrass cover for each station was estimated visually in each quadrant. All samples were fixed in 5% neutralised formaldehyde. In addition, one sample for sediment granulometry was taken at each sampling plot.

Animals were extracted from the sediments by Ludox flotation (Heip *et al.*, 1985). From each sample, about 200 nematodes (or all individuals if fewer) were picked out, transferred to pure glycerol, mounted onto permanent slides, and identified to genus/putative morphospecies using the pictorial keys (Platt & Warwick, 1988; Warwick *et al.*, 1998), dedicated articles, and the NeMys Database (Bezerra *et al.*, 2019). The trophic types of nematodes were classified by the morphology of buccal cavities: 1A – selective deposit feeders; 1B – non-selective deposit feeders; 2A – epigrowth feeders; 2B – omnivorous/predators (Wieser, 1953).

Salinity and temperature of the near-bottom water layer were measured *in situ* with a Water Quality Checker WQC-22A. Sediment grain size analysis was undertaken by dry sieving through a series of mesh sizes (2000, 1000, 500, 250, 125 and 63 µm). The sand fraction and the clay-silt fraction, referred to as mud, were categorised according to the traditional nomenclature (Table 1).

Data analysis. For each sample, diversity was evaluated for nematode species using the following indices: species richness (the total number of different species), Pielou's evenness (J'), Shannon-Wiener diversity (H', using log-base *e*), expected species richness for a sample of 50 individuals (ES(50)). Moreover, species-accumulation curves, plotting the cumulative number of species observed (Sobs) as a function of the number of stations studied, were produced by randomly adding stations and repeating this procedure 9999 times. Additionally, the non-parametric Chao1 and Jacknife1 (Jack1) estimators were used to estimate the total number of species present for the whole data set and for each season (Gotelli *&* Colwell, 2011). All indices were calculated in the PRIMER 7 software (Clarke *&* Gorley, 2015). In addition, k-dominance (Lambshead *et al.*, 1983) curves were plotted to assess differences in community structure.

The environmental variables (salinity, temperature, and sediment characteristics) were compared between seasons (spring *vs* autumn) by the non-parametric Wilcoxon tests using the Past v.3.11 software (Hammer *et al.*, 2001).

The PERMANOVA routine in PRIMER was used to assess the relative influences of station and season on community parameters (Anderson *et al.*, 2008; Clarke & Gorley, 2015). The untransformed data on nematode community (abundance, species richness, Shannon diversity index, Pielou's evenness) were tested for significant differences based on resemblance matrices derived from Euclidean distances (Anderson *et al.*, 2008). PERMANOVA was conducted using a two fixed-factor crossed design comprising 'station' and 'season' as factors. Values were considered significant when $P < 0.05$. After the PERMANOVA routines, pairwise pseudo *t* tests were performed between all pairs of levels to determine significant differences between each combination. Subsequently, PERMDISP routines were performed to test homogeneity of multivariate dispersions, indicating location differences through equally dispersed distance to centroids. The square-root value of estimates of components of variation (√ECV) was used to compare the relative strengths of significant factor effects (Anderson *et al.*, 2008).

Similarity matrices for multivariate data (nematode community structure) were built using the Bray-Curtis similarity measure of square root-transformed species abundance data (Anderson *et al.*, 2008). The same two-factor design was used as described for univariate community data followed by the PERMDISP analysis. Following the PERMANOVA analysis, SIMPER analysis was performed based on Bray-Curtis, with a cut-off of 70% for low contributions (Clarke & Warwick, 2001). A non-metric multi-dimensional scaling plot (MDS) was used to visualise patterns in a multivariate community structure (Clarke & Warwick, 2001).

RESULTS

Environmental conditions. In the Tien Yen estuary dense seagrass beds occur in HD, CS and CM sites (about 60-70% cover). A total of six species of seagrasses were identified: *Halophila ovalis* (R. Brown) Hooker, 1858; *Halophila beccarii* Ascherson, 1871; *Halodule pinifolia* (Miki) den Hartog, 1964; *Halodule uninervis* (Forsskål) Ascherson, 1882; *Zostera japonica* Ascherson & Graebn, 1907; *Ruppia maritima* Linnaeus, 1753. At HD station the dominant seagrass species were *Halophila ovalis* (approximately 35-40%) and *Z. japonica*, patches of *H. beccarii* (less than 10%), *H. pinifolia* (5%) and *H. uninervis* (5%) were occasionally encountered and interspersed with *R. maritima*. At the CS station, three seagrass species *Z. japonica* (approximately 55%), *H. ovalis* (35%), predominated with *H. pinifolia* (less than 10%). At CM station only *H. ovalis* was identified. No seagrasses were found at XG in April; however, a seagrass meadow consisting of *Z. japonica* began to recover in October.

Water temperature and salinity were characterised by pronounced shifts of values between seasons (Table 1). In April, the water temperature at the sampling sites was about 20°C, which is significantly ($P < 0.05$) different from that in October, reaching an average value of 24.1°C. Salinity values decreased at all stations in October compared to April (average values of 15.1 and 20.0 psu, respectively) but these changes were not significant ($P = 0.07$).

The stations are distinctly distinguished by the granulometric composition of the bottom sediments and their seasonal changes (Table 1). In April, sediments were represented by sandy mud at the HD and CS stations, and muddy sand at XG and CM; in October, the percentage of silty particles decreased at HD and CS, and increased at XG and CM.

Abundance and structure of nematode communities. PERMANOVA results, based on the total nematode abundance (Table 2), showed significant differences ($P < 0.05$) between stations and seasons. The estimates of components of variation (√ECV) showed that station and season accounted for approximately the same proportions of variability in nematode community abundance (Table 3). Higher values were recorded in April, with the average nematode density being 545.8 ± 200.7 ind. 10 cm^{-2}. The highest density (753.3 ± 287.5 ind. 10 cm^{-2}) was recorded from the HD site; the lowest average density (386.7 ± 130.5 ind. 10 cm^{-2}) was registered at station CS (Table 3). The average nematode density in October decreased to 346.7 ± 244.8 ind. 10 cm^{-2} and the highest density (590.0 ± 278.7 ind. 10 cm^{-2}) was recorded from the station HD, the lowest one (153.3 ± 40.4 ind. 10 cm^{-2}) was registered at the station CM (the density decreased by one and a half compared to the value in April).

A total of 71 nematode species were recorded from the studied area (Table 4). In April, we identified 61 species, belonging to 39 genera and 16 families; in October 50 species belonging to 15 families and 32 genera were identified. The number of observed nematode species for both seasons and the whole data set were less than predicted by species richness estimators Chao1 and Jack1 (Fig. 2). At the same time, species-accumulation curves did not approach an asymptote. Obviously, we did not determine the complete set of species of the surveyed area and the true number of nematode species could be significantly higher than currently known for the Tien Yen River estuary.

Table 2. Results of PERMANOVA analysis test for the effects of station, season, and their interaction on parameters of nematodes community. Negative components of variation were set to 0 (Graham & Edwards, 2001). The results of pairwise comparisons are given only for significant differences at $P < 0.05$. (d.f. = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistics, P = probability, Perms = number of unique permutations, √ECV = square root of estimates of components of variation, * – significant differences at $P < 0.05$).

Source	d.f.	SS	MS	Pseudo-F	*P*	Perms	√ECV
Abundance [ind. 10cm^{-2}]							
Station (St)	3	4340.1	1446.7	4.1428	0.026*	9959	13.52
Season (Se)	1	2380	2380	6.8155	0.020*	9829	13.01
Interaction (St × Se)	3	1094.1	364.71	1.0444	0.406	9945	2.27
Residuals	16	5587.3	349.21				18.69
Total	23	13402					
Pairwise test, term 'Station': HD × CM (*P* = 0.030); XG × CM (*P* = 0.047)							
Species richness							
Station (St)	3	165	55	6.1682	0.007*	9955	2.77
Season (Se)	1	368.17	368.17	41.29	0.0001*	9737	5.47
Interaction (St × Se)	3	79.5	26.5	2.972	0.067	9944	2.42
Residuals	16	142.67	8.9167				32.99
Total	23	755.33					
Pairwise test, term 'Station': HD × XG (*P* = 0.009); CS × XG (*P* = 0.014); XG × CM (*P* = 0.038)							
ES(50)							
Station (St)	3	75.3	25.1	6.9	0.003*	9955	1.89
Season (Se)	1	145.8	145.8	40.2	0.0001*	9815	3.44
Interaction (St × Se)	3	59.4	19.8	5.5	0.012*	9963	2.32
Residuals	16	58.1	3.6				1.91
Total	23	338.7					
Pairwise test, term 'Station': HD × XG (*P* = 0.014); CS × XG (*P* = 0.002); XG × CM (*P* = 0.02) Pairwise test, term 'St × Se' for pairs of levels of factor 'Location', within level 'Spring' of factor 'Season': CS × XG (*P* = 0.002); XG × CM (*P* = 0.012); within level 'Autumn' of factor 'Season': HD × CM (*P* = 0.03) Pairwise test, term 'St × Se' for pairs of levels of factor 'Season' within level 'CS' of factor 'Station' (*P* = 0.004) and level 'CM' of factor 'Station' (*P* = 0.002)							
Shannon's index (H')							
Station (St)	3	0.72	0.24	3.61	0.036*	9959	0.17
Season (Se)	1	1.69	1.69	25.59	0.0003*	9814	0.37
Interaction (St × Se)	3	0.82	0.27	4.12	0.024*	9952	0.26
Residuals	16	1.06	0.07				0.26
Total	23	4.27					
Pairwise test, term 'St × Se' for pairs of levels of factor 'Location', within level 'Spring' of factor 'Season': CS × XG (*P* = 0.006); XG × CM (*P* = 0.012) Pairwise test, term 'St × Se' for pairs of levels of factor 'Season' within level 'CS' of factor 'Station' (*P* = 0.006) and level 'CM' of factor 'Station' (*P* = 0.001)							
Pielou's evenness (J')							
Station (St)	3	0.02	0.00670	1.4144	0.2747	9953	0.018
Season (Se)	1	0.002	0.00150	0.31737	0.5784	9845	0.000
Interaction (St × Se)	3	0.04	0.01258	2.6539	0.082	9950	0.051
Residuals	16	0.08	0.00474				0.069
Total	23	0.14					

Note: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

Table 3. Nematode abundance and diversity indices. Results are mean (SE). N, nematode abundance (ind. 10 cm^{-2}); S, species richness; ES(50), expected number of species number for 50 individuals; H' Shannon's index; J, Pielou's evenness.

	Station	N	S	ES(50)	H'	J'
April	HD	753.3 (166.0)	24.2 (3.2)	15.8 (1.6)	2.30 (0.22)	0.88 (0.03)
	CS	386.7 (75.4)	22.0 (2.5)	16.5 (0.8)	2.32 (0.07)	0.91 (0.02)
	XG	563.3 (57.0)	17.4 (2.1)	12.0 (0.7)	1.96 (0.13)	0.83 (0.03)
	CM	480.0 (28.9)	24.2 (2.9)	16.0 (1.3)	2.26 (0.12)	0.86 (0.01)
October	HD	590.0 (160.9)	19.7 (1.9)	14.0 (1.2)	2.07 (0.19)	0.84 (0.06)
	CS	393.3 (169.5)	15.9 (2.0)	10.5 (0.9)	1.66 (0.13)	0.72 (0.07)
	XG	250.0 (25.2)	18.2 (3.0)	13.1 (1.4)	2.09 (0.20)	0.87 (0.03)
	CM	153.3 (23.3)	16.7 (0.7)	12.3 (0.3)	2.03 (0.06)	0.87 (0.01)

Note: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

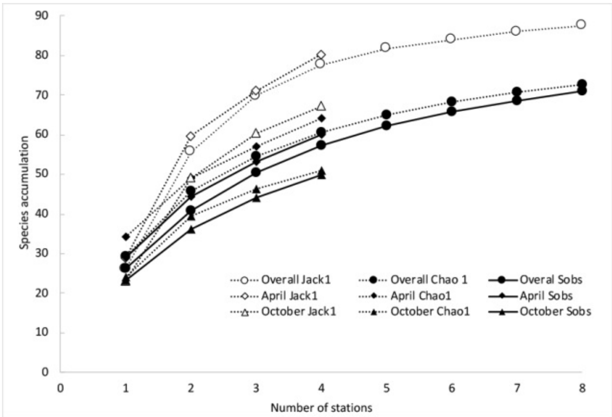

Fig. 2. Species accumulation curves for nematode species (S_{obs} – observed community richness, Chao1 and Jack1 – richness estimators).

In general, the present study has shown that eight families of nematode species dominated the Tien Yen estuary in the study period: Comesomatidae − accounted for 27%; Linhomoeidae = 16%, Axonolaimidae = 16%; Oncholaimidae = 12%; Sphaerolaimidae = 9.7%; Xyalidae = 8.6%; Chromadoridae = 7.5% and Desmodoridae = 7.5%. As regards the nematode assemblages, the percentage of dominant nematode genera and species significantly varied between stations and different seasons (Tables 2 & 5). Only four species – *Sphaerolaimus callisto*, *Paralinhomoeus* sp. 1, *Sabatieria doancanhi* and *S. parvula* – were commonly found at all sites in April and October. The MDS plot has shown that the characteristics of nematode assemblages differed between all stations and seasons (Fig. 3). The two-way PERMANOVA, based on the nematode species composition, showed significant differences ($P < 0.001$) between stations and seasons (Table 6). According to the √ECV analysis, station and the factors interaction gave relatively large proportions of variability in community structure, whereas seasonal changes gave smaller proportions (Table 6). The pairwise comparisons has shown significant ($P < 0.05$) differences for all stations. The dissimilarity in nematode community structure between stations (found using SIMPER) was more than 61%, between seasons for all stations – 66%, and between seasons at each station more than 50% (Table 7).

Diversity and trophic structure of nematode communities. The diversity parameters were characterised by a substantial temporal and spatial variability (Table 3), with the lowest values recorded from the XG station in spring and the CS station in autumn.

The species richness and Shannon index showed significant differences between seasons (PERMANOVA, $P < 0.001$) and stations (PERMANOVA, $P < 0.01$ and $P < 0.05$, respectively; Table 2). According to the √ECV analysis, season has played a crucial role in variability of diversity. No significant difference in Pielou's index between stations, seasons, and their relationship was found (Table 2). In general, a significant decrease in biodiversity was observed at stations HD, CS, and CM in autumn. It can be explained by the significant reduction of species richness in that period (Table 2). These changes were not found only at the XG station. These tendencies are pronounced on the chart of curves of accumulated abundance (Fig. 4).

During the period of observations (April-October), the proportions of trophic groups of nematodes have also changed (Fig. 5). The proportion of selective deposit feeders (1A) at all

Table 4. Species composition, trophic groups, and percentage of nematodes at the stations in the Tien Yen estuary, Vietnam.

Species	Trophic groups	April				October			
		HD	CS	XG	CM	HD	CS	XG	CM
Anticoma sp.	1A	–	–	–	–	–	–	–	1.30
Paranticoma sp.	1A	–	–	–	0.34	–	–	–	1.30
Adoncholaimus sp.	2B	–	1.08	4.12	0.34	–	0.79	–	–
Oncholaimus qingdaoensis	2B	–	–	–	–	–	–	–	2.60
O. multisetosus	2B	1.41	–	–	–	–	–	–	–
Oncholaimus sp.	2B	–	–	3.53	–	2.09	0.79	–	–
Prooncholaimus tani	2B	–	–	–	–	2.09	3.17	–	–
Viscosia glabra	2B	–	–	3.53	1.08	–	–	–	–
V. longicaudatoides	2B	–	–	–	–	–	7.94	3.23	–
V. pygmaea	2B	–	–	–	–	–	3.17	4.30	1.30
V. timmi	2B	–	1.08	21.18	3.21	0.70	2.38	5.38	6.50
Belbolla sp.	2B	–	3.23	–	2.04	–	–	–	5.20
Halalaimus durus	1A	–	–	–	0.34	0.52	–	–	–
H. luticolus	1A	–	–	–	1.36	–	–	–	–
Oxystomina elegans	1A	–	–	–	0.68	–	–	1.08	–
Bathylaimus setosicaudatus	1B	9.89	3.23	–	7.82	–	–	–	–
Dichromadora sp.	2A	4.24	–	–	1.36	–	–	1.08	–
Graphonema sp.	2A	–	7.52	0.59	0.34	–	–	–	–
Neochromadora sp.	2A	–	1.08	0.59	5.78	–	–	–	–
Panduripharynx ornatum	2A	1.41	–	–	–	–	2.38	4.30	–
Ptycholaimellus macrodentatus	2A	10.84	–	1.76	20.07	–	–	4.30	–
Paracanthonchus multisupplementatus	2A	–	2.15	5.88	–	1.57	6.35	1.08	–
Acanthonchus singaporensis	2A	1.88	–	–	1.36	3.14	–	–	–
Halichoanolaimus sp.	2B	2.83	4.30	–	3.22	0.52	0.79	–	0.52
Desmodora vietnamica	2A	–	–	–	–	–	–	1.08	–
Metachromadora minor	2A	–	2.15	–	–	1.05	42.86	2.15	–
Onyx mangrovi	2A	–	1.08	–	4.08	–	–	–	1.30
O. orientalis	2A	–	1.08	–	–	–	–	–	1.30
Spirina sp.	2A	–	2.15	–	–	–	–	–	–
Microlaimus orientalis	2A	–	1.08	–	–	–	–	–	–
Thalassomonhystera leptosoma	1B	–	3.23	–	–	–	–	–	–
Diplolaimelloides elegans	1B	0.71	–	–	–	–	3.17	–	–
Elzalia gerlachi	1B	0.47	–	–	–	–	–	–	–
Daptonema brevisetosum	1B	7.30	10.75	–	1.7	–	7.94	1.08	3.90
D. dihystera	1B	5.89	–	0.59	1.36	–	–	–	–
D. dolichurus	1B	2.83	–	–	0.68	–	–	–	–
D. hirtum	1B	–	–	–	–	–	–	–	7.79
D. iners	1B	1.41	2.15	–	0.34	0.52	–	–	–
D. pumilus	1B	0.94	–	–	–	–	–	–	–
D. orientale	1B	5.65	–	–	–	–	–	–	–

Table 4. (continued) Species composition, trophic groups, and percentage of nematodes at the stations in the Tien Yen estuary, Vietnam.

Species	Trophic groups	April				October			
		HD	CS	XG	CM	HD	CS	XG	CM
Pseudosteineria inaequispiculata	1B	–	–	–	1.30	–	–	–	1.30
Sphaerolaimus maeoticus	2B	0.47	–	0.59	–	–	0.79	2.15	–
Sphaerolaimus callisto	2B	9.89	4.30	1.18	2.72	4.43	7.14	2.15	1.30
Sphaerolaimus io	2B	2.83	2.15	–	–	0.52	–	–	1.30
Sphaerolaimus ganymede	2B	3.14	–	–	–	4.18	0.79	–	–
Sphaerolaimus sp. 4	2B	1.10	–	–	–	0.8	–	–	–
Parasphaerolaimus pilosus	2B	–	–	–	1.36	–	0.79	–	2.60
Subsphaerolaimus major	2B	–	1.08	9.41	–	–	–	8.60	–
Metalinhomoeus sp.	1B	–	10.75	–	4.76	–	–	–	–
Paralinhomoeus sp. 1	1B	1.41	1.08	1.76	4.14	1.05	3.17	1.08	2.60
Paralinhomoeus sp. 2	1B	0.71	1.08	1.18	0.68	1.57	–	2.15	–
Terschellingia communis	1B	4.00	5.38	5.29	–	16.20	–	4.30	2.60
T. longicaudata	1B	0.71	4.30	0.59	8.16	7.84	–	3.23	14.69
T. obese	1B	0.47	–	–	–	2.61	–	–	–
Terschellingia sp. 1	1B	–	–	0.59	–	–	–	–	–
Terschellingia sp. 2	1B	0.94	–	–	–	3.14	–	–	–
Siphonolaimus sp.	2B	–	–	–	1.7	–	–	–	1.30
Axonolaimus sp.	1B	0.47	–	–	–	–	–	–	–
Parodontophora fluviatilis	1B	–	–	–	–	–	0.79	–	–
P. leptosoma	1B	2.36	–	8.82	2.04	–	–	–	–
P. obesa	1B	–	2.15	–	–	–	–	–	–
Dorylaimopsis halongensis	2A	–	12.90	–	7.48	1.05	–	2.08	6.50
D. tumida	2A	0.71	–	–	1.7	3.14	–	–	–
Hopperia communis	2A	0.94	–2.15	–	–	–	–	1.18	6.02
H. dorichurus	2A	–	–	–	2.04	–	–	3.23	16.86
H. mira	2A	–	–	1.18	–	–	–	–	–
Paracomesoma elegans	2A	–	–	–	–	6.79	–	4.30	1.30
P. lissum	2A	–	–	1.18	2.04	3.66	–	–	–
P. paralongispiculum	2A	–	–	–	–	1.57	0.79	–	–
Sabatieria doancanhi	1B	2.36	2.15	17.65	2.04	19.34	0.79	15.05	6.50
S. parvula	1B	9.78	3.23	8.82	0.34	9.93	3.17	21.51	2.20

Note: '–' species not found.

Trophic groups: 1A – selective deposit feeders; 1B – non-selective deposit feeders; 2A – epistrate feeders; 2B – omnivores/predators.

Station abbreviations: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

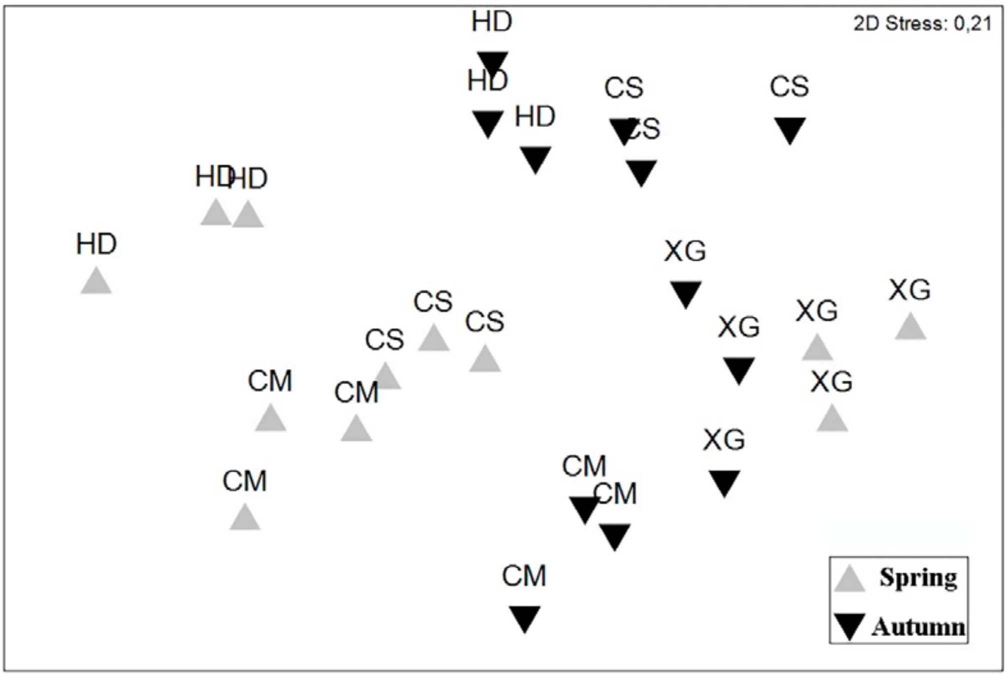

Fig. 3. Two dimensional nMDS ordination based on abundance of nematode species at different stations.

Table 5. Abundances (ind. 10 cm^{-2}) of the five dominant nematode species.

Station	Spring			Autumn		
	Species	**Mean**	**SE**	**Species**	**Mean**	**SE**
HD	*Ptycholaimellus macrodentatus*	76.7	16.1	*Sabatieria doancanhi*	92.5	53.4
	Bathylaimus setosicaudatus	70.0	17.3	*Terschellingia communis*	77.5	61.3
	Sphaerolaimus callisto	70.0	21.2	*Sabatieria parvula*	47.5	29.6
	Sabatieria parvula	69.2	38.0	*Terschellingia pontica*	37.5	32.5
	Daptonema brevisetosum	51.7	29.8	*Paracomesoma elegans*	32.5	18.8
CS	*Dorylaimopsis halongensis*	40.0	15.4	*Metachromadora minor*	135.0	79.4
	Daptonema brevisetosum	33.3	10.8	*Viscosia longicaudatoides*	25.0	8.7
	Metalinhomoeus sp.	33.3	10.8	*Daptonema brevisetosum*	25.0	13.0
	Graphonema sp.	26.7	20.5	*Sphaerolaimus callisto*	22.5	10.1
	Terschellingia communis	16.7	12.8	*Paracanthonchus multisupplemetatus*	20.0	11.6
XG	*Viscosia timmi*	120.0	21.2	*Sabatieria parvula*	66.7	6.4
	Sabatieria doancanhi	100.0	38.5	*Sabatieria doancanhi*	46.7	18.0
	Subsphaerolaimus major	53.3	20.5	*Subsphaerolaimus major*	26.7	10.3
	Parodontophora leptosoma	50.0	38.5	*Viscosia timmi*	16.7	2.6
	Sabatieria parvula	50.0	38.5	*Terschellingia communis*	16.7	6.4
CM	*Ptycholaimellus macrodentatus*	105.0	49.1	*Hopperia dorichurus*	53.3	20.5
	Terschellingia longicaudata	40.0	11.5	*Terschellingia longicaudata*	43.3	12.8
	Bathylaimus setosicaudatus	38.3	1.0	*Daptonema hirtum*	20.0	11.6
	Dorylaimopsis halongensis	36.7	19.3	*Viscosia timmi*	16.7	9.0
	Neochromadora sp.	28.3	16.4	*Dorylaimopsis halongensis*	16.7	12.8

Note: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

Table 6. Results of PERMANOVA analysis test for the effects of locality, season and their interaction on nematodes community structure (d.f. = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistics, *P* = probability, Perms = number of unique permutations, √ECV = square root of estimates of components of variation, * – significant factors at the 5% level).

Source	d.f.	SS	MS	Pseudo-F	*P*	Perms	√ECV
Station (St)	3	24229	8076.4	8.7229	0.0001*	9918	34.5
Season (Se)	1	8921.1	8921.1	9.6353	0.0002*	9944	25.8
Interaction (St × Se)	3	14389	4796.3	5.1803	0.0001*	9881	35.9
Residuals	16	14814	925.88				30.4
Total	23	62353					

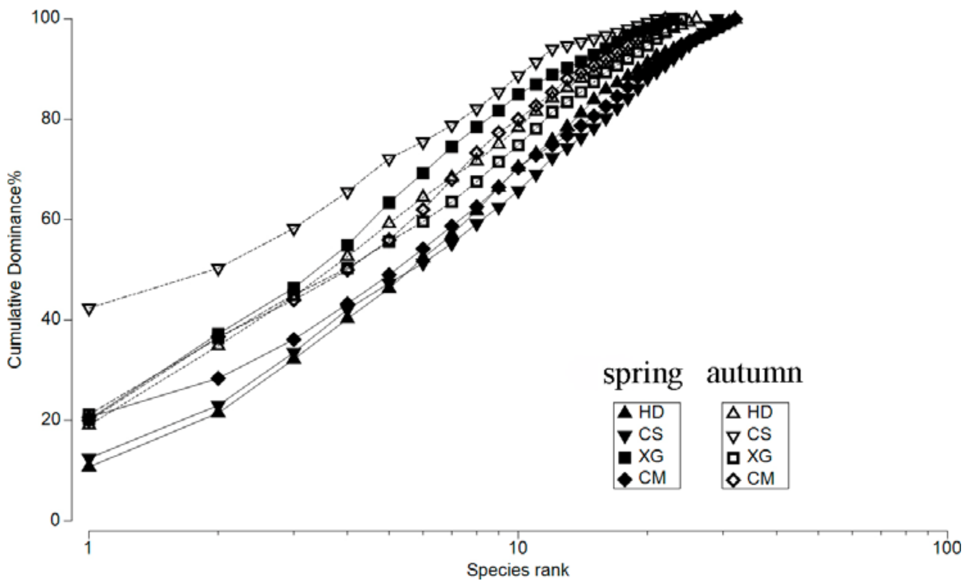

Fig. 4. *k-dominance* curves for nematode assemblages at the sampling stations. Station abbreviations: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

stations was very low (0.5-2.7%) or they were completely absent in both seasons. In April, non-selective deposit feeders dominated at HD, CS and XG and the epistratum feeders dominated at CM. In October, the percentage of deposit feeders increased slightly at the HD, XG and CM and decreased drastically at CS where epistratum feeders became the dominant group. A pronounced increase in the proportion of epistratum feeders was also noted for XG, with a simultaneous decrease in the proportion of predators/omnivores. In general, the smallest changes in the trophic structure were noted for HD, at the remaining stations the changes were significant and had different patterns.

DISCUSSION

High variability of environmental conditions has been shown in the studied area. It should be noted that while temporal changes in the parameters of water column had general trends, the characteristics of bottom sediments varied unevenly. In Vietnam's monsoon climate, characterised by well-defined wet and dry seasons, heavy rainfalls cause significant surface runoff that leads to changes in the habitat of coastal ecosystems. In Quang Ninh Province of Vietnam, the monsoon season lasts from late April to early October. During heavy rainfalls, fresh water penetrates and intermix the upper layers of sea bottom sediments (Foster, 1998). In this case, small sediment particles are washed out at some places and accumulate at others, causing the sediment structure to change. The formation and functioning of benthic communities in the estuarine areas is largely determined by the high spatiotemporal heterogeneity of environmental conditions (Remane, 1934; McLusky, 1981). These patterns were also well demonstrated for meiofauna (Smol *et al.*, 1994; Coull, 1999; Udalov *et al.*, 2005), particularly for nematode communities (Nicholas *et al.*, 1992; Riemann, 1966;

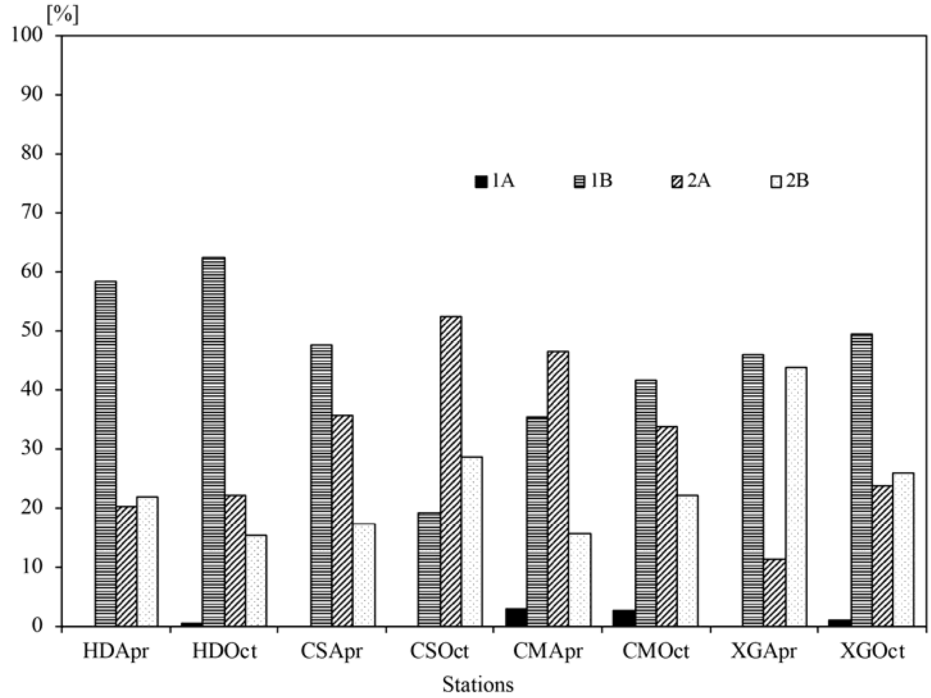

Fig. 5. Trophic composition (relative abundance) of nematode communities at the sampling stations. (1A – selective deposit feeders; 1B – non-selective deposit feeders; 2A – epistrate feeders; 2B – predator/omnivores). Station abbreviations: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

Soetaert *et al.*, 1995). At the same time, the development of plant communities is of great significance for fauna (Castel *et al.*, 1989; Boström *et al.*, 2006; Liao *et al.*, 2015). During our study, a significant spatial and temporal variability was observed in the abundance, composition and structure of nematode communities simultaneously with the variability of environmental conditions. However, it is impossible to estimate the contribution of individual environmental factors (for example, temperature, salinity, granulometric composition of bottom sediments) to changes in communities because of the limitation of the experimental design.

It has been shown that the mean values of nematodes abundance can have a wide range on the tidal seagrass beds – from 38 to 5231 ind. 10 cm^{-2} (Ndaro & Olafsson, 1999; Leduc & Probert, 2011; Mokievsky *et al.*, 2011; Liao *et al.*, 2015; Tran *et al.*, 2018b). In nearby tidal areas of Vietnam, the values of nematodes density varied from 184 to 4580 ind. 10 cm^{-2} (Ngo *et al.*, 2007, 2010; Mokievsky *et al.*, 2011; Tran *et al.*, 2018a). Our results (518.6 ind. 10 cm^{-2} in April and 339.9 ind. 10 cm^{-2} in October), fell into this range, but are close to its lower limit. We have also observed that seasonal changes in abundance (decrease in autumn) are consistent with previous data (Tietjen, 1969; Aryuthaka & Kikuchi, 1996). According to Cai and co-authors (2012) the similar seasonal changes in nematode abundance were observed outside the Tien Yen Estuary in the Gulf of Tonkin at depths of about 30 m with the average abundance of nematodes about 935.5 ind. 10 cm^{-2}. Such results may indicate that the monsoons play significant role in the formation of the nematode communities of coastal ecosystems.

In Vietnam, since the first research on free-living marine nematodes commenced, extensive studies have been made on taxonomic and ecological aspects in different ecosystems (Lai Phu Hoang, 2007; Nguyen Vu Thanh, 2007; Mokievsky *et al.*, 2011; Nguyen Dinh Tu *et al.*, 2011; Ngo Xuan Quang *et al.*, 2013). These scientists provided a significant contribution to the knowledge on nematodes from the South China Sea, and 208 species of free-living nematodes have been reported from mangrove forests along four Vietnamese rivers (the Mekong, Be, Red and Yen Rivers) (Gagarin, 2018). However, our work is the first description of nematode communities inhabiting seagrass beds in Vietnam. In general, the number of nematode species

Table 7. SIMPER results indicating (dis)similarity between station and season and distinguishing the species that contributed to the (dis)similarity. Individual species cut-off level for similarity was 5% and 3.5% for dissimilarity.

SIMPER similarity (%, contribution > 5%)					
Station: HD	44.2%	Station: CS	30.7%	Station: XG	49.3%
Sabatieria parvulus	15.0	*Daptonema brevisetosum*	21.1	*Sabatieria doancanhi*	18.4
Sphaerolaimus callisto	11.0	*Sphaerolaimus callisto*	14.9	*Subsphaerolaimus major*	13.8
Sphaerolaimus ganymede	9.5	*Sabatieria parvula*	13.6	*Sabatieria parvula*	13.8
Terschellingia communis	9.5	*Paracanthonchus multisupplemetatus*	10.5	*Viscosia timmi*	10.9
Paracomesoma lissum	7.8	*Metachromadora minor*	10.5	*Terschellingia communis*	10.9
Acanthonchus singaporensis	6.7			*P. macrodentatus macrodentatus*	6.7
Paralinhomoeus sp. 1	5.5				
Station: CM	41.1%	Season: Spring	37.5%	Season: Autumn	34.8%
Terschellingia longicaudata	14.7	*Sphaerolaimus callisto*	8.0	*Sabatieria doancanhi*	12.5
Dorylaimopsis halongensis	12.8	*Paralinhomoeus* sp.1	6.6	*Sphaerolaimus callisto*	9.8
Viscosia timmi	10.4	*Sabatieria parvula*	6.2	*Viscosia timmi*	9.2
Paralinhomoeus sp. 1	8.5	*Terschellingia communis*	5.9	*Sabatieria parvula*	7.7
Belbolla sp.	7.4	*Bathylaimus setosicaudatus*	5.7	*Terschellingia communis*	6.1
Daptonema brevisetosum	7.4			*Terschellingia longicaudata*	6.0
Hopperia communis	7.4			*Daptonema brevisetosum*	5.0
Sabatieria doancanhi	7.4				
SIMPER dissimilarity (%, contribution > 3.5%)					
Stations: HD *vs* CS	65.0%	Stations: HD *vs* XG	61.3%	Stations: CS *vs* XG	66.0%
Metachromadora minor	6.0	*Viscosia timmi*	5.4	*Sabatieria doancanhi*	6.3
Sabatieria doancanhi	3.8	*Subsphaerolaimus major*	5.4	*Metachromadora minor*	6.1
Terschellingia communis	3.6	*Sabatieria doancanhi*	3.9	*Subsphaerolaimus major*	4.3
		Sphaerolaimus ganymede	3.7	*Daptonema brevisetosum*	4.3
				Viscosia timmi	3.6
Stations: XG *vs* CM	68.8%	Stations: HD *vs* CM	69.5%	Stations: CS *vs* CM	66.1%
Sabatieria parvula	6.1	*Sabatieria parvula*	4.9	*Metachromadora minor*	7.0
Subsphaerolaimus major	4.9	*Hopperia dorichurus*	3.6	*Terschellingia longicaudata*	4.3
Terschellingia longicaudata	4.2			*Hopperia dorichurus*	4.0
Hopperia dorichurus	3.7			*P. macrodentatus*	3.7
P. macrodentatus macrodentatus	3.7				
Station: HDspr. *vs* HDaut.	55.8%	Station: XGspr. *vs* XGaut.	60.7%	Station: CMspr. *vs* CMaut.	58.9%
Sabatieria doancanhi	8.3	*Parodontophora leptosoma*	6.7	*P. macrodentatus macrodentatus*	8.4
Bathylaimus setosicaudatus	6.1	*Viscosia timmi*	5.1	*Hopperia dorichurus*	8.1
Daptonema brevisetosum	5.3	*Adoncholaimus* sp.	4.6	*Bathylaimus setosicaudatus*	5.1
Paracomesoma elegans	4.9	*Viscosia pygmaea*	4.6	*Daptonema hirtum*	4.9
Daptonema dihystera	4.6	*Panduripharynx ornatum*	4.6	*Neochromadora* sp.	4.5
Daptonema orientale	4.6	*Oncholaimus sp.*	4.2	*Metalinhomoeus* sp.	3.9
Dichromadora sp.	4.1	*Viscosia glabra*	4.2	*Halichoanolaimus* sp.	3.6
P. macrodentatus macrodentatus	4.1	*Viscosia longicaudatoides*	4.2		
Terschellingia pontica	3.8	*Terschellingia longicaudata*	4.2		
Terschellingia communis	3.8	*Hopperia dorichurus*	4.2		
		Sabatieria parvula	3.8		
Stations: CSspr. *vs* CSaut.	69.3%	Seasons: Spring *vs* Autumn	66.0%		
Metachromadora minor	8.4	*Metachromadora minor*	3.8		
Dorylaimopsis halongensis	5.9	*Sabatieria doancanhi*	3.7		
Metalinhomoeus sp.	5.4				
Graphonema sp.	4.9				
Viscosia longicaudatoides	4.7				
Terschellingia communis	3.8				

Note: HD – Ha Dong, CM – Con Mat, CS – Cua Song and XG – Xom Giao.

that were found in Tien Yen is relatively high. Some taxa have been registered for the first time for Vietnam and a high number of putative species of nematodes were recognised in our study. Apparently, some of the latter are new to science. For example, four new species of the family Sphaerolaimidae from Tien Yen estuary have recently been described: *Parasphaerolaimus pilosus* (Zograf *et al.*, 2017), *Sphaerolaimus callisto*, *S. ganymede*, *S. io* (Zograf *et al.*, 2020).

The analysis of the nematode community through the study period showed distinct separation between each season's communities. In general, the taxonomic diversity of nematodes at the family level was similar to that of communities inhabiting of the seagrass meadows in tropical estuaries of Asia, Australia and Africa (Alongi, 1987a, b, 1990; Ndaro & Olafsson, 1999; Fischer, 2003; Fischer & Sheaves, 2003; Ngo *et al.*, 2010). The exception was 'meadows' of *Zostera capricornis* (New South Wales, Australia), where two families dominated Linhomoeidae and Ironidae (Fonseca *et al.*, 2011).

At low taxonomic levels, nematode assemblages differed greatly between all stations and seasons in the Tien Yen River estuary. Significant changes in the number of species (in the autumn the species richness significantly decreased (Fig. 2) with practically unchanged evenness at all stations) were observed together with the changes in the composition of species and genera.

The five dominant species contributed approximately 50-60% of all nematode abundance (Table 5). Each station had its own set of dominant species in April and in October, and their quantitative ratio and density often differed. Representatives of the dominant genera (*Bathylaimus*, *Daptonema*, *Dorylaimopsis*, *Hopperia*, *Metachromadora*, *Metalinhomoeus*, *Neochromadora*, *Paracanthonchus*, *Parodontophora*, *Ptycholaimellus*, *Sabatieria*, *Sphaerolaimus*, *Subsphaerolaimus*, *Terschellingia*, *Viscosia*) are often found in brackish-water habitats (Heip *et al.*, 1985), especially in Vietnam (Gagarin & Nguyen Vu Thanh, 2006, 2012; Ngo *et al.*, 2007, 2010). In particular, Liao with co-authors discussed the dominance of specific nematode taxa in habitats comprising distinct seagrass species (Liao *et al.*, 2016), namely *Daptonema*, which usually dominates wide seagrass habitats, especially in sandy sediments (Ndaro & Ólafsson 1999; Fonseca *et al.*, 2011). Previous studies in other shallow-water seagrass habitats have revealed a high dominance also of *Metalinhomoeus* species (Fisher, 2003; Fisher & Sheaves, 2003; Monthum & Aryuthaka, 2006). The nematode communities in the seagrass were similarly preoccupied by *Terschellingia* species, namely *T. longicaudata* (Fisher & Sheaves 2003); it has been also found to dominate subtropical and tropical seagrass sediments and with high densities in intertidal and silty sediments (Alongi, 1987a; Ndaro & Olafsson, 1999). *Terschellingia* species are usually evident in subtropical seagrass sediments (Hopper & Meyers, 1967). All of these nematode species are usually characteristic also for estuarine muddy sediments (Heip *et al.*, 1985). Some species of the genus *Ptycholaimellus* were found earlier in mangrove habitats of both tropical (Decraemer & Coomans, 1978) and temperate (Hodda & Nicholas, 1985, 1986) Australia. *Ptycholaimellus macrodentatus* was found and described from the Bay of Bengal (Timm, 1961) and off the Kenyan coast (Muthumbi & Vincx, 1998), and was recorded also from some water bodies of Northern Vietnam, mostly from estuaries (Gagarin, 2018). *Metachromadora minor* was found and described from the mangrove of Mekong River Delta (Gagarin & Nguyen Vu Thanh, 2010). Several species that were abundant, belonging to Comesomatidae: *Dorylaimopsis halongensis*, *Sabatieria doancanhi* and *Hopperia dolichurus*, are commonly found in coastal estuarine sediments in Vietnam (Gagarin, 2018).

It is known that regional differences between the nematode fauna in tidal ecosystems can be very high at the generic and species levels (Mokievsky *et al.*, 2011). Therefore, the comparison of faunas often shows the absence of common species or genera. Moreover, differences in the composition and structure of nematode communities between stations within particular areas are also strongly pronounced (Tita *et al.*, 2002; Fischer, 2003; Leduc & Probert, 2011; Liao *et al.*, 2016; Du *et al.*, 2018). Obviously, this could be due to the high spatial-temporal heterogeneity of the environmental conditions of the tidal ecosystems of estuaries in the macro- and mesoscales. Such diversity of fauna determines the complexity of the use of nematodes in monitoring of the environment. Adequate results of the assessment of anthropogenically induced changes will only be possible after careful studies to obtain preliminary data on the natural nematode communities and their dynamics.

Considerable spatial and temporal variability was observed not only for the diversity and composition of nematode communities, but also for trophic structure. Seagrass meadows significantly affect the structure and activity of meiobenthic communities on a small spatial scale by changing the properties of bottom sediments and transporting the organic matter into them (Leduc & Probert, 2011). This organic matter provides nearly unlimited resources making the microbe-consisting food supply available, which results in the high proportion of non-selective deposit feeders. By contrast, overabundance of benthic and epiphytic microalgae causes increasing of the proportion of species belonging to epistrate feeders (Hopper & Meyers, 1967; Ndaro & Olafsson, 1999; Danovaro & Gambi, 2002; Fisher, 2003; Fonseca *et al.*, 2011; Liao *et al.*, 2016). In the Tien Yen estuary, non-selective deposit feeders (particularly, such genera as *Daptonema*, *Terschillingia*, *Metalinhomoeus* and *Sabatieria*) dominated both in spring and autumn; however, the proportion of 1B in the trophic structure varied greatly between stations (Fig. 5). Dominance of epistrate feeders (2A) was recorded only at two stations: CM in April and CS in October. Increases in the densities of the genera *Dorylaimopsis*, *Hopperia*, *Metachromadora*, *Paracanthonchus* and *Ptycholaimellus* across seasons contributed to the pool of epistratum feeders and their dominance in the study area.

It is also necessary to mention that a high percentage of predator/omnivore species of the genera *Sphaerolaimus*, *Viscosia* and *Halichoanolaimus* were observed at all stations; they constituted from 15 to 43% of the total nematode density in April, and from 15 to 28.5% in October (Fig. 5). Research carried out in grassy meadows in southern part of New Zealand revealed that predator/omnivore species were almost non-existent in the surface sediment layer of seagrass zones. In the authors' opinion, this fact shows that interaction between seagrasses and nematode communities depends on environment characteristics, *i.e.* hydrodynamic conditions and sediment granulometric composition (Leduc & Probert, 2011). Contrary to this, other studies point out the high density of predator species in grassy meadows such as those on the Bay of Biscay coast where *Metoncholaimus scissus* dominated in *Thalassia* beds (Hopper & Meyers, 1967). In mangrove estuaries of Australian coast the unusual predominance of predators (such as *Sphaerolaimus*, *Enoplus* and *Viscosia*) was recorded along with the low average density of nematodes (< 400.10 ind. cm^{-2}) (Alongi, 1987b). It is supposed that tannins contained in mangrove leaves may negatively affect the nematode abundance (Alongi, 1987b). At XG station most exposed to mangroves pressure, in April predator species amounted to 43%. In October the density of predators decreased and was 25.8%, probably caused by changes in sediment composition (amount of silty-clay particles increased up to 22.5%). Earlier it was established that even a small increase of silt content in sand caused a rapid decrease of predators number (Gallucci *et al*., 2005).

As a whole, all four stations were characterised by spatial and temporal variability within and between stations and can be characterised as brackish-water intertidal nematode assemblage with salinity-tolerant nematodes, including *Daptonema*, *Metachromadora* and *Metalinhomoeus* (Heip *et al*., 1985), being dominant. Although the composition of seagrass species was the same in April and October, the set of common species of nematodes did not remain constant and nematode communities at each station revealed a range of changes in their density and composition. This could be explained by the high spatial heterogeneity of environmental conditions and their pronounced seasonal variations. The precipitation (heavy rainfalls) in the intertidal zone of the Tien Yen estuary is the main factor responsible for seasonal changes of density, diversity and composition of nematode assemblages.

ACKNOWLEDGEMENTS

The field work and sample collection by the bilateral research team were supported by Vietnam Academy of Science and Technology (funding code VAST.HTQT.NGA.09/15-16); and the joint project of Far-Eastern Branch of the Russian Academy of Sciences (FEB RAS) and Vietnam Academy of Science and Technology (VAST), chapter BAHT, project no. BAHT 17-010; data analysis was supported by the Russian Science Foundation (project no. 17-04-00719). Article preparation and processing was supported by the Russian Science Foundation (project no. 14-50-00034) and were partly done in the Laboratory of Ecology and Evolutionary Biology of Aquatic Organisms of the Far Eastern Federal University.

REFERENCES

ALONGI, D.M. 1987A. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. *Marine Ecology Progress Series* 40: 103-114.

ALONGI, D.M. 1987B. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Marine Biology* 95: 447-458.

ALONGI, D.M. 1990. Community dynamics of free-living nematodes in some tropical mangrove and sandflats habitats. *Bulletin of Marine. Science* 46: 358-373.

ALVES, A.S., ADÃO, H., FERRERO, T.J., MARQUES, J.C., COSTA, M.J. & PATRÍCIO, J. 2013. Benthic meiofauna as indicator of ecological changes in estuarine ecosystems: the use of nematodes in ecological quality assessment. *Ecological Indicators* 24: 462-475. DOI: 10.1016/j.ecolind.2012.07.013

ANDERSON, M.J., GORLEY, R.N. & CLARKE, K.R. 2008. *PERMANOVA + for PRIMER: Guide to Software and Statistical Methods*. UK, PRIMER-E Ltd. 214 pp.

ARYUTHAKA, C. 1991. Meiofauna community in Khung Kraben Bay, Chanthaburi, East Thailand. *Thai Marine Fishery Research Bulletin* 2: 47-57.

ARYUTHAKA, C. & KIKUCHI, T. 1996. Sediment meiobenthos community in the seagrass (*Zostera marina* L.) bed and its vicinity in Amakusa, south Japan. I. Spatial and seasonal variation of nematode communities. *Publications from the Amakusa Marine Biological Laboratory* 12: 79-107.

BALSAMO, M., SEMPRUCCI F., FRONTALINI, F. & COCCIONI, R. 2012. Meiofauna as a tool for marine ecosystem biomonitoring. In: *Marine Ecosystems* (A. Cruzado Ed.). pp. 77-104. Rijeka, Croatia, IntechOpen. DOI: 10.5772/34423

BEZERRA, T.N., DECRAEMER, W., EISENDLE-FLÖCKNER, U., HODDA, M., HOLOVACHOV, O., LEDUC, D.,MILJUTIN, D., MOKIEVSKY, V., PEÑA SANTIAGO, R., SHARMA, J., SMOL, N., TCHESUNOV, A., VENEKEY, V., ZENG, Z. & VANREUSEL, A. 2019. *Nemys: World Database of Nematodes*. URL: http://nemys.ugent.be/ (accessed: March 29, 2019).

BOSTRÖM, C., JACKSON, E.L. & SIMENSTAD, C.A. 2006. Seagrass landscapes and their effects on associated fauna: a review. *Estuarine Coastal Shelf Sciences* 68: 383-403. DOI: 10.1016/j.ecss.2006.01.026

CAI, L., FU, S., YANG, J. & ZHOU, X. 2012. Distribution of meiofaunal abundance in relation to environmental factors in Beibu Gulf, South China Sea. *Acta Oceanologica Sinica* 31: 92-103. DOI: 10.1007/s13131-012-0256-2

CASTEL, J., LABOURG, P.J., ESCARAVAGE, V., AUBY, I. & GARCIA, M. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meiobenthos and macrobenthos in tidal flats. *Estuarine Coastal Shelf Science* 28: 71-85.

CLARKE, K.R. & GORLEY, R.N. 2015. *PRIMER v7: User Manual/Tutorial*. UK, PRIMER-E Ltd. 296 pp.

CLARKE, K.R. & WARWICK, R.M. 2001. *Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation*. UK, PRIMER-E Ltd. 176 pp.

COULL, B.C. 1999. Role of meiofauna in estuarine soft□bottom habitats. *Australian Journal of Ecology* 24: 327-343. DOI: 10.1046/j.1442-9993.1999.00979.x

DANOVARO, R. & GAMBI, C. 2002. Biodiversity and trophic structure of nematode assemblages in seagrass systems: evidence for a coupling with changes in food availability. *Marine Biology* 141: 667-677. DOI: 10.1007/s00227-002-0857-y

DECRAMER, W. & COOMANS, A. 1978. Scientific report on the Belgian expedition to the Great Barrier Reef in 1967. Nematodes XII. Ecological notes on the nematode fauna in and around mangroves on Lizard Island. *Australian Journal of Marine and Freshwater Research* 29: 497-508.

DE TROCH, M., GURDEBEKE, S., FIERS, F. & VINCX, M. 2001. Zonation and structuring factors of meiofauna communities in a tropical seagrass bed (Gazi Bay, Kenya). *Journal of Sea Research* 45: 45-61. DOI: 10.1016/S1385-1101(00)00055-1

DU, Y., GAO, S., LIU, X., ZHANG, L. & INGELS, J. 2018. Meiofauna and nematode community characteristics indicate ecological changes induced by geomorphic evolution: a case study on tidal creek systems. *Ecological Indicators* 87: 97-106. DOI: 10.1016/j.ecolind.2017.12.037

DUARTE, C.M. 2002. The future of seagrass meadows. *Environmental Conservation* 29: 192-206. DOI: 10.1017/S0376892902000127

DUARTE, C.M. & CHISCANO, C.L. 1999. Seagrass biomass and production: a reassessment. *Aquatic Botany* 65: 159-174. DOI: 10.1016/S0304-3770(99)00038-8

FISHER, R. 2003. Spatial and temporal variations in nematode assemblages in tropical seagrass sediments. *Hydrobiologia* 493: 49-63. DOI: 10.1023/A:1025481732236

FISHER, R. & SHEAVES, M. 2003. Community structure and spatial variability of marine nematodes in tropical Australian pioneer seagrass meadows. *Hydrobiologia* 495: 143-158. DOI: 10.1023/A:1025406624390

FONSECA, G., HUTCHINGS, P. & GALLUCCI, F. 2011. Meiobenthic communities of seagrass beds (*Zostera capricorni*) and unvegetated sediments along the coast of New South Wales, Australia. *Estuarine Coastal Shelf Science* 91: 69-77. DOI: 10.1016/j.ecss.2010.10.003

FOSTER, S.J. 1998. Osmotic stress tolerance and osmoregulation of intertidal and subtidal nematodes. *Journal of Experimental Marine Biology and Ecology* 224: 109-125. DOI: 10.1016/S0022-0981(97)00192-5

FOURQUREAN, J.W., DUARTE, C.M., KENNEDY, H., MARBA, N., HOLMER, M., MATEO, M.A., APOSTOLAKI, E.T., KENDRICK, G.A., KRAUSE-JENSEN, D., MCGLATHERY, K.J. & SERRANO, O. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5: 505-509. DOI: 10.1038/ngeo1477

GAGARIN, V.G. 2018. An annotated checklist of the free-living nematodes from mangrove thickets of Vietnam. *Zootaxa* 4403: 261-288. DOI: 10.11646/zootaxa.4403.2.3

GAGARIN, V.G. & NGUYEN VU THANH. 2006. [Three new species of free-living nematodes (Nematoda) of the family Axonolaimidae from the Mekong River Delta

(Vietnam)]. *Zoologicheskii Zhurnal* 85: 675-681 (in Russian).

GAGARIN, V.G. & NGUYEN VU THANH. 2010. [Three new species of free-living marine nematodes of the order Desmodorida (Nematoda) from Vietnam]. *Zoologicheskii Zhurnal* 89: 398-406 (in Russian).

GAGARIN, V.G. & NGUYEN VU THANH. 2012. Free-living nematodes of the Tra Ly River in the Red River mouth, Vietnam. *Inland Water Biology* 5: 11-18. DOI: 10.1134/S1995082912010038

GALLUCCI, F., STEYAERT, M. & MOENS, T. 2005. Can field distributions of marine predacious nematodes be explained by sediment constraints on their foraging success? *Marine Ecology Progress Series* 304: 167-178. DOI: 10.3354/meps304167

GRAHAM, M.H. & EDWARDS, M.S. 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. *Oikos* 93: 505-513. DOI: 10.1034/j.1600-0706.2001.930317.x

GOTELLI, N.J. & COLWELL, R.K. 2011. Estimating species richness. In: *Biological Diversity. Frontiers in Measurement and Assessment* (A.E. Magurran & B.J. McGill Eds). pp. 39-54. New York, USA, Oxford University Press Inc.

GREEN, E.P. & SHORT, F.T. 2003. *World Atlas of Seagrasses*. USA, University of California Press. 324 pp.

HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1-9.

HEIP, C., VINCX, M. & VRANKEN, G. 1985. The ecology of free-living nematodes. *Oceanography and Marine Biology: An Annual Review* 23: 399-489.

HODDA, M. & NICHOLAS, W.L. 1985. Meiofauna associated with mangroves in the Hunter River Estuary and Fullerton Cove, Southeastern Australia. *Australian Journal of Marine and Freshwater Research* 36: 41-50.

HODDA, M. & NICHOLAS, W.L. 1986. Temporal changes in littoral meiofauna from the Hunter River Estuary. *Australian Journal of Marine and Freshwater Research* 37: 729-741.

HOPPER, B.E. & MEYERS, S.P. 1967. Population studies on benthic nematodes within a subtropical seagrass community. *Marine Biology* 1: 85-96.

LAI PHU HOANG. 2007. *Meiobenthos with special reference to free-living marine nematodes as bioindicators for different mangrove types in Can Gio Biosphere Reserve, Vietnam*. D.Sc. Dissertation, University of Bremen, Bremen, Germany, 105 pp.

LAMBSHEAD, P.J.D., PIATT, H.M. & SHAW, K.M. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* 17: 859-974.

LEDUC, D. & PROBERT, P.K. 2011. Small-scale effect of intertidal seagrass (*Zostera muelleri*) on meiofaunal abundance, biomass, and nematode community structure. *Journal of the Marine Biological Association of the United Kingdom* 91: 579-591. DOI: 10.1017/S0025315410001645

LIAO, J.X., YEH, H.M. & MOK, H.K. 2015. Meiofaunal communities in a tropical seagrass bed and adjacent unvegetated sediments with note on sufficient sample size for determining local diversity indices. *Zoological Studies* 54: 14. DOI: 10.1186/s40555-014-0101-8

LIAO, J.-X., YEH, H.M. & MOK, H.K. 2016. Do the abundance, diversity, and community structure of sediment meiofauna differ among seagrass species? *Journal of the Marine Biological Association of the United Kingdom* 96: 725-735. DOI: 10.1017/S0025315415000879

MCLUSKY, D.S. 1981. *The Estuarine Ecosystem*. UK, Blackie and Son Ltd. 215 pp.

MOKIEVSKY, V.O., TCHESUNOV, A.V., UDALOV, A.A. & NGUYEN DUY TOAN. 2011. Quantitative distribution of meiobenthos and the structure of the free-living nematode community of the mangrove intertidal zone in Nha Trang Bay (Vietnam) in the South China Sea. *Russian Journal of Marine Biology* 37: 272-283. DOI: 10.1134/S1063074011040109

MONTHUM, Y. & ARYUTHAKA, C. 2006. Spatial distribution of meiobenthic community in Tha Len seagrass bed, Krabi Province, Thailand. *Coastal Marine Science* 30: 146-153.

MUTHUMBI, A.W. & VINCX, M. 1998. Chromadoridae (Chromadorida: Nematoda) from the Indian Ocean: description of new and known species. *Hydrobiologia* 364: 119-153. DOI: 10.1023/A:1003109929194

NDARO, S. & OLAFSSON, E. 1999. Soft-bottom fauna with emphasis on nematode assemblage structure in a tropical intertidal lagoon in Zanzibar, eastern Africa: I. Spatial variability. *Hydrobiologia* 405: 133-148. DOI: 10.1023/A:1003874122971

NGO XUAN QUANG, VANREUSEL, A., NGUYEN VU THANH & SMOL, N. 2007. Biodiversity of meiofauna in the intertidal Khe Nhan mudflat, Can Gio mangrove forest, Vietnam, with special emphasis on free-living nematodes. *Ocean Science Journal* 42: 135-152. DOI: 10.1007/BF03020918

NGO XUAN QUANG, VANREUSEL A., SMOL, N. & NGUYEN NGOC CHAU. 2010. Meiobenthos assemblages in the Mekong estuarine system with special focus on free-living marine nematodes. *Ocean Science Journal* 45: 213-224. DOI: 10.1007/s12601-010-0020-5

NGO XUAN QUANG, SMOL, N. & VANREUSEL, A. 2013. The meiofauna distribution in correlation with environmental characteristics in five Mekong estuaries, Vietnam. *Cahiers de Biologie Marine* 54: 71-83.

NGUYEN DINH TU, SMOL, N., VANREUSEL, A. & NGUYEN VU THANH. 2011. Six new species of the genus *Onyx* Cobb, 1891 (Nematoda: Desmodoridae) from coastal areas in Vietnam. *Russian Journal of Nematology* 19: 1-20.

NGUYEN VU THANH. 2007. *Free Living Nematodes of Vietnam – Fauna of Vietnam*. Vietnam, Publishing House for Science & Technology. 458 pp.

NGUYEN VU THANH & NGUYEN DINH TU. 2003. Biodiversity of the marine nematodes in the coastline of Ha Long Bay and their use for the assessment and biomonitoring of water environment. *Journal of Marine Science and Technology* 32: 51-63.

NGUYEN VU THANH, NGUYEN DINH TU & NGUYEN XUAN DUC. 2002. [Biodiversity of the marine nematodes in the coastal sea area of the central part of Vietnam]. *Journal of Biology* – Tap Chi Sinh Hoc 24: 9-14 (in Vietnamese).

NICHOLAS, W.L., BIRD, A.F., BEECH, T.A. & STEWART, A.C. 1992. The nematode fauna of the Murray River estuary, South Australia; the effects of the barrages across its mouth. *Hydrobiologia* 234: 87-102. DOI: 10.1007/BF00010864

PAVLYUK, O.N. & TREBUKHOVA, YU.A. 2006. Meiobenthos in Nha Trang Bay of the South China Sea (Vietnam). *Ocean Science Journal* 41: 139-148. DOI: 10.1007/BF03022419

PAVLYUK, O.N, TREBUKHOVA, YU.A., NGUYEN VU THANH & NGUYEN DINH TU. 2008. Meiobenthos in estuary part of Ha Long Bay (Gulf of Tonkin, South China Sea, Vietnam). *Ocean Science Journal* 43: 153-160. DOI: 10.1007/BF03020696

PLATT, H.M. & WARWICK, R.M. 1988. *Free-Living Marine Nematodes. Part II: British Chromadorids. Synopses of the British Fauna (New Series), no. 38* (Series Eds: D.M. Kermack & R.S.K. Barnes). Leiden, The Netherlands, E.J. Brill/Dr. W. Backhuys. 502 pp.

RALPH, P.J., TOMASKO, D., MOORE, K., SEDDON, S. & MACINNIS-NG, C.M.O. 2006. Human impacts on seagrasses: eutrophication, sedimentation, and contamination. In: *Seagrasses: Biology, Ecology and Conservation* (A.W.D Larkum, R.J. Orth & C.M. Duarte Eds). pp. 567-593. Dordrecht, The Netherlands, Springer.

REMANE, A. 1934. Brackwasserfauna. *Zoologisher Anzeiger* 7: 34-74.

RIEMANN, F. 1966. Die interstitielle Fauna im Elbe-Aestuar. Verbreitung und Systematik. *Archiv für Hydrobiologie* 31 (Supplementband 1-2): 1-279.

SHORT, F.T., SHORT, C.A. & NOVAK, A. 2016. Seagrasses. In: *The Wetland Book* (C.M. Finlayson, G.R. Milton, R.C. Prentice & N.C. Davidson Eds). pp. 1-18. Dordrecht, The Netherlands, Springer Science + Business Media. DOI: 10.1007/978-94-007-6173-5_262-1

SMOL, N., WILLEMS, K.A., GOVAERE, J.C.R. & SANDEE, A.J.J. 1994. Composition, distribution, biomass of meiobenthos in the Oosterschelde estuary (SW Netherlands). *Hydrobiologia* 282: 197-217. DOI: 10.1007/978-94-011-1174-4_16

SOETAERT, K., VINCX, M., WITTOECK, J. & TULKENS, M. 1995. Meiobenthic distribution and nematode community structure in five European estuaries. *Hydrobiologia* 311: 185-206. DOI: 10.1007/BF00008580

SPALDING, M., TAYLOR, M., RAVILIOUS, C., SHORT, F. & GREEN, E. 2003. Global overview: the distribution and status of seagrasses. In: *World Atlas of Seagrasses* (E.P. Green & F.T. Short Eds). pp. 5-26. Berkeley (CA), USA, University of California Press.

TIETJEN, J.H. 1969. The ecology of shallow water meiofauna in two New England Estuaries. *Oecologia* 2: 251-291.

TIMM, R.W. 1961. The marine nematodes of the Bay of Bengal. *Proceedings of the Pakistan Academy of Science* 1: 25-88.

TITA, G., DESROSIERS, G., VINCX, M. & CLEMENT, M. 2002. Intertidal meiofauna of the St Lawrence estuary (Quebec, Canada): diversity, biomass and feeding structure of nematode assemblages. *Journal of the Marine Biological Association of the United Kingdom* 82: 779-791. DOI: 10.1017/S0025315402006148

TRAN THANH THAI, NGUYEN LE QUE LAM, NGO XUAN QUANG & HA HOANG HIEU. 2018A. Seasonal and spatial variations of meiofauna communities in correlation to environmental characteristics in the organic shrimp farms of Tam Giang commune, Nam Can district, Ca Mau province. *VNU Journal of Science: Natural Sciences and Technology* 34: 55-64. DOI: 10.25073/2588-1140/vnunst.4715

TRAN THAI TRAN, NGUYEN LE QUE LAM, LE HAI DANG, NGUEN THI MY YEN & NGO XUAN QUANG. 2018B. Intertidal meiofaunal communities in relation to salinity gradients in the Ba Lai River, Vietnam. *Journal of Vietnamese Environment* 10: 138-150. DOI: 10.13141/jve.vol10.no2.pp138-150

UDALOV, A.A., MOKIEVSKII, V.O. & CHERTOPRUD, E.S. 2005. Influence of the salinity gradient on the distribution of meiobenthos in the Chernaya River Estuary (White Sea). *Oceanology* 45: 680-688.

VAN LUONG CAO, VAN THAO NGUYEN, KOMATSU TERUHISA, DAC VE NGUYEN & DUC TIEN DAM. 2012. Status and threats on seagrass beds using GIS in Vietnam. *Proceedings of SPIE* 8525: 852512. DOI: 10.1117/12.977277

WARWICK, R.M., PLATT, H.M. & SOMERFIELD, P.J. 1998. *Free-Living Marine Nematodes. Part III: Monhysterids. Synopses of the British Fauna (New Series), no. 53* (Series Eds: R.S.K. Barnes & J.H. Crothers). Kerkwerve, The Netherlands, Backhuys Publishers. 296 pp.

WAYCOTT, M., DUARTE, C.M., CARRUTHERS, T.J.B., ORTH, R.J., DENNISON, W.C., OLYARNIK, S.,

CALLADINE, A., FOURQUREAN, J.W., HECK JR., K.L., HUGHES, A.R., KENDRICK, G.A., KENWORTHY, W.J., SHORT, F.T. & WILLIAMS, S.L. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106: 12377-12381. DOI: 10.1073/pnas.0905620106

WIESER, W. 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden: eine ökologisch-morphologische Studie. *Arkiv för Zoologi* 4: 439-484.

XU, W.Z., CHEUNG, S.G., ZHANG, Z.N. & SHIN, P.K.S. 2018. Dual isotope assessment of trophic dynamics of an intertidal infaunal community with seasonal shifts in food sources. *Marine Biology* 165: 21. DOI: 10.1007/s00227-017-3278-7

ZOGRAF, J.K., PAVLYUK, O.N., TREBUKHOVA, YU.A. & NGUYEN DINH TU. 2017. Revision of the genus *Parasphaerolaimus* (Nematoda: Sphaerolaimidae) with description of new species. *Zootaxa* 4232: 58-70. DOI: 10.11646/zootaxa.4232.1.4

ZOGRAF, J.K., PAVLYUK, O.N., TREBUKHOVA, YU.A. & NGUYEN DINH TU. 2020. Description of three new *Sphaerolaimus* species (Nematoda: Sphaerolaimidae) form the South China Sea. *Zootaxa* 4755: 491-514. DOI: 10.11646/zootaxa.4755.3.3

O.N. Pavlyuk, Yu.A. Trebukhova, V.V. Mordukhovich, J.K. Zograf, V.V. Yushin, Nguyen Dinh Tu, Nguyen Vu Thanh and Cao Van Luong. Пространственно-временная изменчивость сообществ нематод в районах развития морских трав эстуария реки Тьен Йен (Вьетнам, провинция Куангнинь).

Резюме. Изучены сезонные изменения плотности поселения, видового разнообразия и трофической структуры сообществ свободноживущих морских нематод в тропических лугах морских трав эстуария реки Тянь-Йен (Тонкинский залив, Южно-Китайское море). Выявлены значительные вариации изучаемых параметров сообществ нематод как в пространстве, так и во времени. В сезон дождей (октябрь) плотность поселения нематод заметно снижалась, по сравнению с апрелем значительно менялись видовой состав и набор доминирующих видов, а также в целом разнообразие и структура сообществ. В общей сложности в исследуемой акватории зарегистрирован 71 вид нематод, но лишь четыре вида были обнаружены на всех станциях и в апреле, и в октябре. Основными причинами наблюдаемых различий в сообществах, по всей видимости, являются высокая пространственная неоднородность условий окружающей среды и их выраженные сезонные колебания. Гранулометрический состав донных отложений, температура и соленость воды характеризовались выраженными различиями между станциями и временами года. При этом основным фактором, ответственным за сезонные изменения в литоральной зоне, выступают проливные дожди.