

Characterization of benthic habitat settings in a lagoonal ecosystem using free-living nematodes as proxy

Kapuli Gani Mohamed Thameemul Ansari · Ajit Kumar Pattnaik ·
Gurdeep Rastogi · Punyasloke Bhadury

Received: 3 January 2017 / Accepted: 1 August 2017 / Published online: 7 August 2017
© Springer Science+Business Media B.V. 2017

Abstract Free-living nematodes are sensitive to most of the disturbances and therefore have ability to reflect direct structural and functional changes in an ecosystem. We studied nematode assemblages of Chilika Lagoon, the largest lagoon of Asia, across spatio-temporal scales in link with environmental variables and evaluated nematode assemblages as a proxy to characterize lagoonal benthic habitat settings. Our results revealed that nematode communities showed significant variation spatially and temporally in terms of mean density (16–854/10 cm²) and mean number of species (7–74). Salinity is the key factor that controls nematode community structure across this lagoon and was strongly supported by statistical analyses. The observed nematode assemblages were

further used as a proxy to assign benthic habitats of Chilika into distinct biological, topographical and hydrological settings. This study showed that nematode assemblages could be effectively used for long term ecological monitoring of dynamic sedimentary environment of lagoons globally.

Keywords Nematodes · Assemblages · Ecosystem · Environmental variables · Habitat settings · Lagoon

Introduction

Structure and function within an ecosystem is measured as the integration between physico-chemical processes including biological diversity and prevailing geochemistry, which drive and/or sustain its overall performance as well as its delivery of ecosystem services (Edwards et al. 2014). In recent years, the importance of biological components and their role in ecosystem processes have drawn significant attention among researchers globally (e.g. Loreau et al. 2001). Moreover, marine ecosystems are subjected to intense natural and anthropogenic disturbances leading to extensive simultaneous effects (Halpern et al. 2008). Coastal ecosystems such as estuaries, lagoons and backwaters, are usually rich in nutrients mainly due to terrigenous inputs (Frontalini et al. 2011). Coastal lagoons are currently considered as vulnerable ecosystems owing to their unique characters such as shallow

Electronic supplementary material The online version of this article (doi:10.1007/s11273-017-9564-9) contains supplementary material, which is available to authorized users.

K. G. M. T. Ansari · P. Bhadury (✉)
Integrative Taxonomy and Microbial Ecology Research
Group, Department of Biological Sciences, Indian
Institute of Science Education and Research Kolkata
(IISERK), Mohanpur, Nadia, West Bengal, India
e-mail: pbhadury@iiserkol.ac.in

A. K. Pattnaik
Integrated Coastal Zone Management Project,
Suryanagar, Bhubaneswar, Odisha, India

G. Rastogi
Wetland Research and Training Centre, Chilika
Development Authority, Barkul, Balugaon, Odisha, India

depth, water intrusion, precipitation and sedimentation rate (Fabbrocini et al. 2005). Other than that, increased nutrient inputs may enhance primary production with increased organic matter which can subsequently settle in the sediments and in turn may lead to alterations in structure and function of biotic communities (Vanaverbeke et al. 2004, 2011). Benthic faunal communities play key roles in coastal ecosystems (Coull and Palmer 1984; Semprucci et al. 2010) and are characteristic of the habitat they occupy. Thus their sensitivity to natural or anthropogenic changes means that they can be effectively used to characterize benthic habitats in coastal environments. Natural disturbances such as inflow of organic debris (e.g. macroalgae, plankton), but also anthropogenic disturbances such as eutrophication and other forms of pollution can affect benthic community along temporal and spatial scales. For example, benthic macrofauna generally respond over larger spatial and more extended temporal scales than meiofauna owing to latter's shorter generation time and much smaller body size, despite the fact that meiofaunal species may be widespread over a range of habitats (Moens et al. 2013 for review). Therefore, this sensitivity on shorter spatial and temporal scales renders meiofauna as a reliable indicator of environmental changes. Among meiofauna, free-living nematodes are known to be prevalent across various marine geographical settings and they are widely considered as excellent indicators for ecosystem level monitoring (e.g. Alves et al. 2013, 2014; Moens et al. 2013; Semprucci et al. 2014a; Bianchelli et al. 2016). In addition to being highly abundant (Lamshead 2004) and diverse (Coomans 2002), they play important role as intermediates between microbial communities and larger organisms (Danovaro et al. 2007). Free-living nematodes represent the most complex metazoan form with many metabolic and developmental processes comparable to higher vertebrate taxa; they are also known to withstand stress and adverse conditions (see Tahseen 2012 for review). Their success across various biotopes (such as lagoon, estuary, inshore, offshore and deep sea) could be attributed to morphological plasticity, physiological adaptability and ecological diversity (see Giere 2009; Moens et al. 2013 for review). However, structure and function of free-living nematodes are mostly unknown across various coastal ecosystems from the Indian subcontinent (Ansari et al. 2016).

Benthic environments in the Bay of Bengal region receive huge inputs of nutrients (Gordon et al. 2002) and organic matter (Ittekkot et al. 1991) due to continuous freshwater discharge from major rivers (e.g. Ganga, Brahmaputra, Meghna, Mahanadi, Godavari, Krishna, Pennar, Cauvery). This region is also rich in various types of coastal biotopes such as lagoons and mangroves (Hirpa et al. 2013). Generally, lagoonal ecosystems exhibit dynamic environmental conditions (e.g. variable salinity, wave and wind actions, sedimentation) and thus organisms present in the sediment or water become adapted to prevailing conditions. One of such organismal groups is nematodes which are present in the benthic layers of lagoonal environment and can tolerate changes compared to other benthic fauna (Semprucci et al. 2014a). Nematode distribution and species diversity have been extensively investigated from European (Mediterranean) coastal lagoons (Colangelo and Ceccherelli 1994; Guerrini et al. 1998; Gambi et al. 2003; Fabbrocini et al. 2005; Frontalini et al. 2011; Moreno et al. 2011; Semprucci et al. 2014a) whereas information on nematode assemblages from coastal lagoons located in Indian Ocean is extremely sparse (Semprucci et al. 2010, 2014b; Ansari et al. 2015).

Chilika lagoon (latitudes 19°28' and 19°54'N and longitudes 085°05'–085°38'E) is the largest lagoonal ecosystem in Asia facing the north-west coast of the Bay of Bengal. It represents a shallow water body (<2 m water depth) with a large catchment basin (~3500 km²). In 1981, Chilika lagoon was declared as a RAMSAR site due to its rich biological diversity (Mohapatra et al. 2007) and socio-economic importance (shell and fin fishery resources). This lagoon is highly influenced by two important factors such as north-west monsoon (freshwater flow ca. 5.09×10^9 m³) and continuous siltation through littoral drift of sediments from catchment basin that has resulted in unremitting shrinkage over the last one century (see Ansari et al. 2015). Additionally, 52 rivulets empty their residue into the northern fringes of Chilika lagoon including from Daya, Nuna and Bhargavi which are tributaries of Mahanadi River (Ansari et al. 2017). There is also inflow of saline water from the Bay of Bengal through a narrow artificial mouth opening (near Satapada) in the lagoon (Panda and Mohanty 2008). Limited saline water influx and higher freshwater inflow has resulted in the formation of distinct salinity gradients and the lagoon represents a

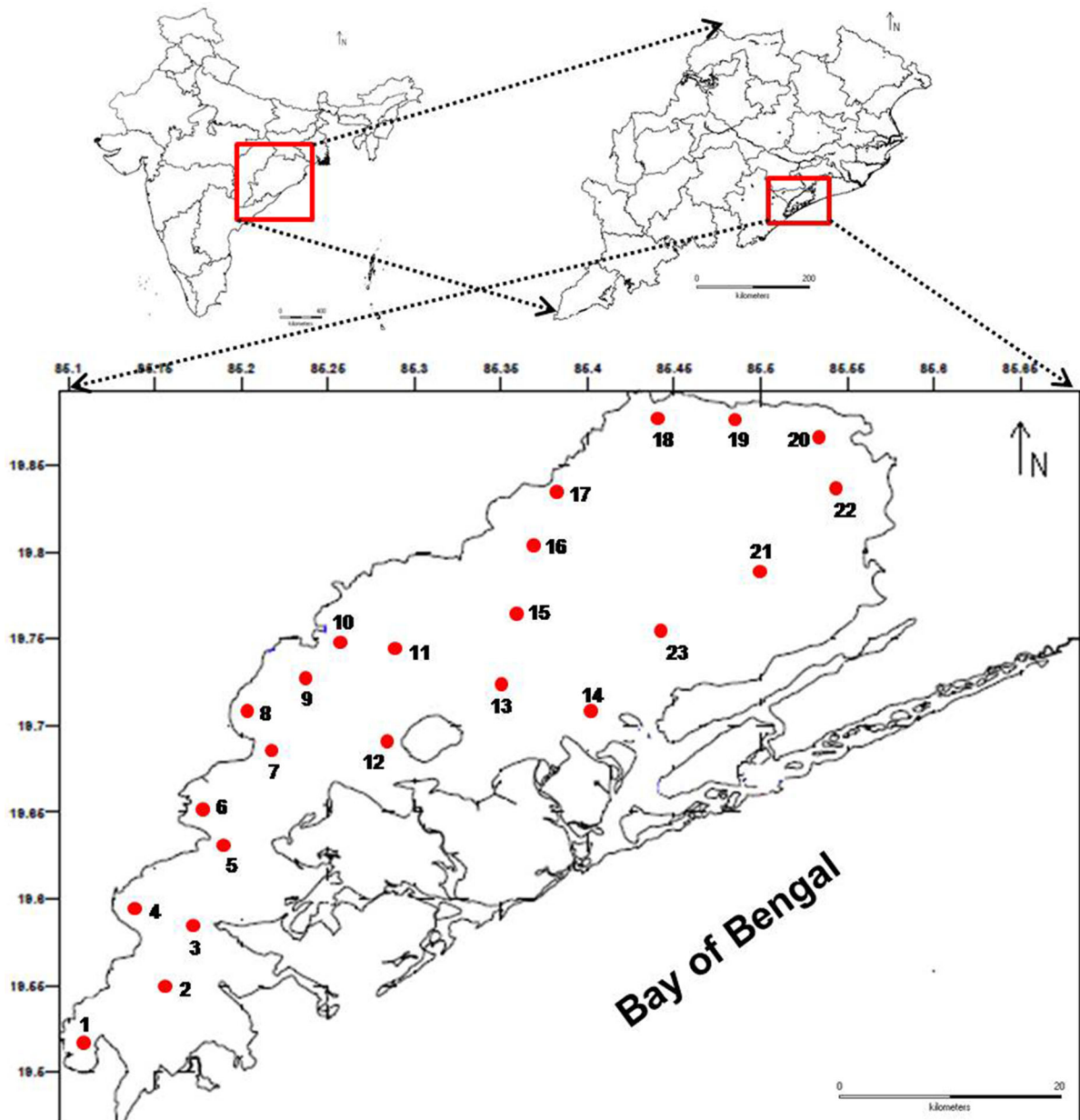


Fig. 1 Location of sampling stations across the Chilika lagoon studied over a period of 21 months

tropical monsoon-influenced brackish water ecosystem (Ansari et al. 2015); indeed hydrological conditions during monsoon season resemble that of a freshwater ecosystem (Jeong et al. 2008). Furthermore, Chilika lagoon is also subjected to natural (e.g. freshwater flow, sedimentation, seagrass bed, massive growth of macrophytes) and anthropogenic disturbances due to high population density residing on its

fringes and from regular fishing activity (Panigrahi et al. 2009). To date, only a handful of studies have been undertaken on benthic communities of Chilika lagoon; most of them are restricted to selective spatial and seasonal scaling, particularly nematode assemblage patterns in link with prevailing abiotic conditions are largely unknown (Ansari et al. 2015 and references therein).

Table 1 Mean environmental variables variations across the Chilika lagoon

Sampling stations	Depth (cm)	SD (cm)	Salinity	Temperature		DO (mg/l)		NO ₃ ⁻ (µg/l)		PO ₄ ³⁻ (µg/l)		SiO ₄ ²⁻ (µg/l)		NH ₄ ⁺ (µg/l)		Sand (%)	Silt/clay (%)	TOC (mg/g)
				SW	BW	SW	BW	SW	BW	SW	BW	SW	BW	SW	BW			
CNS 1	265.3	76.3	8.73	28.83	27.44	5.5	5.2	31.3	33.6	0.7	1.7	57.9	54.4	1.8	1.1	92.7	7.3	4.0
CNS 2	335.1	80.7	8.48	28.04	27.02	5.8	5.7	30.5	30.5	1.2	0.9	65.2	51.2	1.9	1.1	93.9	6.1	4.9
CNS 3	148.2	90.5	7.93	28.90	28.05	6.2	5.9	32.3	33.6	1.1	1.1	50.9	51.4	2.3	1.2	96.4	3.6	3.7
CNS 4	284.9	92.5	8.13	27.94	26.95	5.9	5.3	29.4	33.3	1.3	1.8	59.7	59.5	1.3	3.8	93.2	6.8	3.7
CNS 5	294.6	73.1	8.44	28.32	26.20	5.4	4.9	30.6	30.0	0.7	1.3	58.5	60.7	1.4	1.3	94.5	5.5	4.4
CNS 6	256.9	71.1	8.89	26.93	26.20	5.6	5.0	28.9	28.1	1.5	0.9	58.0	71.5	1.8	1.5	92.8	7.2	3.2
CNS 7	194.4	60.2	8.77	27.59	26.60	5.7	4.9	30.0	30.6	1.9	2.1	67.9	66.0	2.1	1.0	93.7	6.3	2.0
CNS 8	182.2	66.2	8.43	27.00	26.74	5.3	4.9	31.1	30.2	1.8	1.0	69.6	61.1	2.8	1.5	94.2	5.8	1.6
CNS 9	202.8	60.5	6.90	28.01	27.14	5.7	4.6	32.2	33.9	1.1	1.3	70.6	72.2	2.0	2.8	95.5	4.5	1.9
CNS 10	202.6	70.0	6.16	27.85	27.27	5.8	4.5	35.0	41.4	1.6	3.1	71.7	70.8	2.2	2.3	95.7	4.3	1.7
CNS 11	177.0	54.3	7.65	27.00	26.59	5.7	4.7	31.5	39.9	0.7	1.5	83.6	82.9	1.6	6.3	94.7	5.3	1.8
CNS 12	200.6	50.4	7.73	26.88	26.82	5.4	4.9	32.1	31.4	2.8	1.0	66.8	76.4	2.1	1.7	92.6	7.4	3.3
CNS 13	158.4	46.8	9.28	27.69	27.09	5.4	5.1	36.5	31.9	2.4	1.6	67.1	75.6	2.9	2.0	97.3	2.7	3.8
CNS 14	131.0	39.5	9.38	28.12	27.40	5.3	4.8	33.4	39.1	2.1	1.9	76.9	84.4	2.6	1.9	95.1	4.9	4.5
CNS 15	160.4	47.7	8.46	31.04	26.44	5.6	4.6	38.3	37.7	1.8	1.8	79.0	71.1	2.6	3.1	93.7	6.3	2.3
CNS 16	135.4	63.9	4.95	27.76	27.01	5.3	4.3	41.4	44.1	1.5	0.9	48.3	53.2	2.7	2.4	93.9	6.1	1.8
CNS 17	143.6	67.0	2.98	28.33	27.30	5.3	5.0	54.2	51.4	1.4	1.7	83.3	75.2	4.0	3.8	95.7	4.3	2.3
CNS 18	130.7	32.2	2.65	29.12	27.05	5.3	5.0	48.0	44.2	1.6	2.6	123.1	131.4	4.9	1.7	94.6	5.4	1.4
CNS 19	125.1	33.9	1.09	27.76	26.66	4.9	4.6	47.1	49.5	1.1	1.7	143.1	131.0	3.8	2.5	95.0	5.0	1.2
CNS 20	134.9	32.3	0.87	28.37	26.94	5.5	5.0	42.2	40.7	2.6	1.1	144.3	168.6	4.0	3.7	93.7	6.3	1.6
CNS 21	151.3	23.6	5.53	27.75	26.77	5.5	5.2	39.2	34.9	2.2	2.0	154.0	157.3	2.6	2.3	94.8	5.2	2.3
CNS 22	156.8	22.0	1.19	27.93	26.76	5.7	5.2	42.2	41.5	2.6	2.6	137.0	138.4	3.1	3.1	89.6	10.4	2.9
CNS 23	142.9	33.3	6.94	28.27	25.54	5.7	5.3	35.6	32.8	3.8	5.4	112.9	136.8	4.5	1.6	93.7	6.3	2.2

SD secchi depth, DO dissolved oxygen, NO₃⁻ dissolved nitrate, PO₄³⁻ dissolved phosphate, SiO₄²⁻ dissolved silicate, NH₄⁺ dissolved ammonium, TOC total organic carbon

Against this backdrop including uncertainty and knowledge gaps on benthic communities and their function in lagoonal ecosystems such as Chilika, we tested the hypothesis ‘does nematode community reflect habitat heterogeneity in an ecosystem?’ In doing so, the main aim was to increase our understanding of benthic habitat settings of a coastal lagoon (Chilika) using nematode community as a proxy. Three key questions were addressed as part of this aim: (1) how does nematode community structure vary spatio-temporally within a lagoonal ecosystem? (2) can nematode communities be used to distinguish benthic habitats with distinct ecological settings in a lagoonal ecosystem? and (3) whether environmental variables influence nematode assemblages in a lagoonal ecosystem?

Materials and methods

Field sampling and analysis

The present investigation focused on 444 sediment samples collected from 23 pre-fixed stations on a monthly basis between June 2013 and February 2015 within the Chilika lagoon (Fig. 1). The basis for selection of each sampling station has been thoroughly detailed by us as part of a previous study (see Ansari et al. 2015, 2017). It was not possible to collect samples from all the stations during some months; e.g. during dry season the water level decreased to 0.7 m and sampling could not be undertaken in some stations due to logistical constraints.

Water samples (surface and bottom water) were collected using a Niskin water sampler (5L, General Oceanic, USA) along with measurements of in situ environmental parameters like temperature, dissolved oxygen (DO 6 + meter), salinity (hand held refractometer, Erma, Japan) and pH (pH meter) from each station at the time of sampling. A quantitative sediment sampler, the Ponar grab was used for sediment sampling across Chilika lagoon owing to its shallow nature and to ensure collection of undisturbed samples (Elliott and Drake 1981; Nalepa et al. 1988). Triplicate sediment samples were collected using the grab (bite area of 0.025 m²); subsequently grab was hauled to the deck and two sub-samples (push-corer: inner diameter—3.5 cm and length of 10 cm) were collected for analysis of free-living

nematode community from each grab and one additional sub-sample was collected for undertaking sediment granulometry and total organic matter content analysis (e.g. Ansari et al. 2016). Rose Bengal solution (1 g in 1000 ml of distilled water) was added to sediment sub-samples (e.g. Ansari et al. 2014) and subsequently fixed using 4% buffered formalin (Heip et al. 1985). Sediment samples for grain size analysis were washed with distilled water and dried in an oven at 80°C for 24–36 h and successively sieved for 20 min through sets of sieves ranging from 1 mm to 0.045 mm mesh size (e.g. Blott and Pye 2001; Ansari et al. 2016). Sediment fractions were subsequently weighed in an analytical balance (Symmetry, PA220) and the weights were converted to percentages. Sediment fractions were defined according to the Wentworth size classes (Buchanan 1984). Total Organic Carbon content (TOC) of sediment was estimated using a chromic acid oxidation method, followed by titration with ammonium ferrous sulfate (Walkley–Black method) as modified by Gaudette et al. (1974). Additionally, collected water samples (both surface and bottom) were filtered (0.45 µm nitrocellulose filter paper) and subsequently analyzed for dissolved nutrients concentration following published methodologies (Strickland and Parsons 1984; Liddicoat et al. 1975; Finch et al. 1998; Turner et al. 1998) in the laboratory using a UV–Vis spectrophotometer (Hitachi-U2900).

Nematode extraction

In the laboratory for extraction of free-living nematodes, replicate core samples were subsequently processed separately and samples were rinsed with a gentle jet of freshwater through a 0.5 mm sieve to separate larger organisms (macrobenthos) and residues were collected from 0.063 mm mesh (Pfannkuche and Thiel 1988). The residual sediments were decanted more than five times for sorting nematodes following flotation technique which gives an accuracy of 95% (e.g. Armenteros et al. 2008). Sorted samples were enumerated under a stereo-zoom microscope (ZEISS-StemiDV4) and mounted onto glass slides following formalin-ethanol-glycerol technique of Seinhorst (1959). Subsequently, taxonomic identification to putative species level was undertaken under a compound microscope containing CCD camera (Olympus BX 53 under higher magnification of

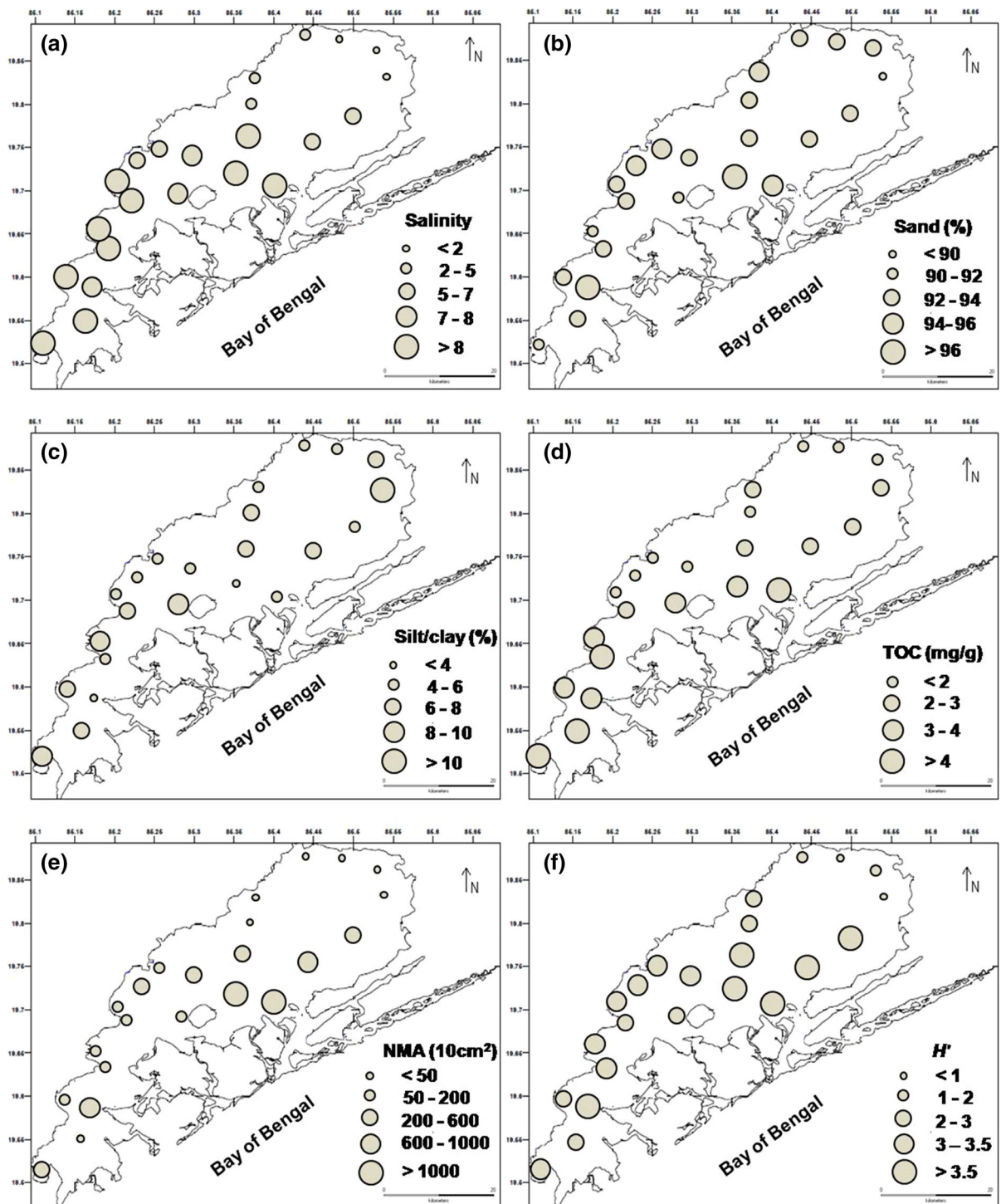


Fig. 2 Distribution of biotic and environmental variables across the Chilika lagoon **a** salinity; **b** sand content; **c** silt/clay content; **d** total organic carbon; **e** nematode mean abundance (NMA); **f** Shannon–Wiener diversity index (H')

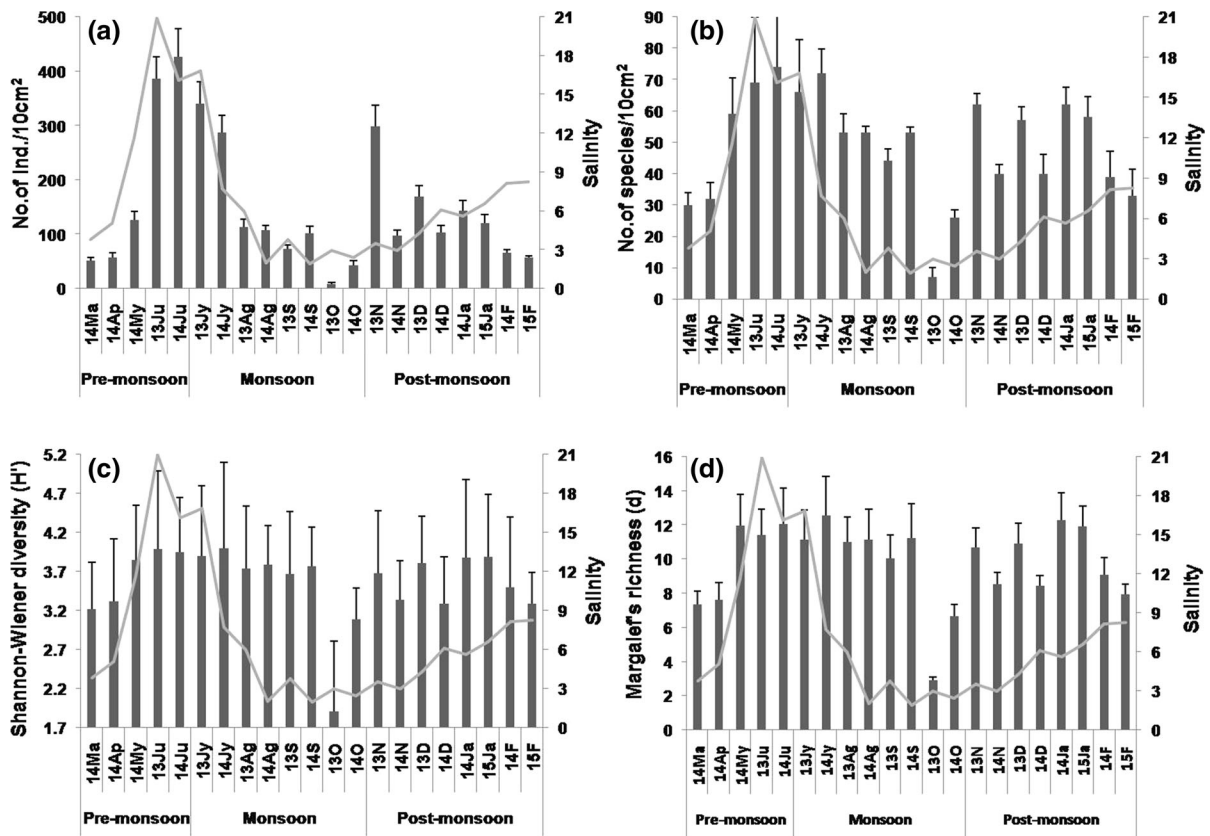


Fig. 3 Temporal variations of nematode community and salinity in this study area **a** mean abundance; **b** mean species composition; **c** Shannon–Wiener diversity index (H'); **d** Margalef's richness (d)

1000 \times) and photo-vouchered (with the help of CellSens standard software) based on standard pictorial keys (e.g. Platt and Warwick 1983, 1988; Warwick et al. 1998; Vanaverbeke et al. 2015). Trophic status of each nematode species was determined according to Wieser's classification (1953): 1A—selective deposit feeders, 1B—non-selective deposit feeders, 2A—epistratum feeders and 2B—predators/omnivorous.

Data analyses

Spatio-temporal variation of nematode assemblages was analyzed using univariate (Shannon–Weiner diversity— H' ; Margalef's richness— d) and multivariate approaches (PCA, nMDS, SIMPER) in PRIMER v6.0.2 and PERMANOVA (Clarke and Gorley 2006; Anderson et al. 2008). Redundancy analysis (RDA) was performed using CANOCO v4.53 (ter Braak 1986; ter Braak and Smilauer 2002) to evaluate

possible linear combinations between nematode assemblages (response variables) and environmental variables (explanatory variables) along spatio-temporal scales following a form of stepwise regression. To differentiate the sampling stations into distinct settings based on environmental variables, Principal Component Analysis (PCA) was used. Secondly, the significance of species–environment relationships was determined by Monte Carlo permutation test (unrestricted). All the multivariate analyses were undertaken following square-root transformation of data prior to construction of Bray–Curtis similarity matrix and Euclidean distance matrix (Clarke et al. 2006). Free-living nematode community assemblage from the study area was used as a matrix and subsequently subjected to hierarchical agglomerative method using group-average linking two-dimensional ordinations plot and non-metric multidimensional scaling (nMDS) along with their relative abundance. Observed

differences in individual species contribution were calculated using similarity percentage (SIMPER—75% cut-off) analysis. The obtained nematode species and their relative abundance data with measured environmental variables (without transformation of data) were used to construct relationship between biotic and environmental variables with the help of RDA ordination plot (CANOCO v4.53). Spatial representation of biotic and environmental variables was carried using ArcGIS (www.arcgis.com).

Results

Environmental variables

The mean values of measured environmental variables of the study area have been detailed in Table 1. For example, salinity showed spatial (average: 6.50; minimum: 0.87–maximum: 9.38) (Fig. 2a) and temporal (average: 6.98; 1.92–20.94) variability across the lagoon whereas variability was much lesser within seasons and between years (Fig. 3). Highest salinity values were encountered in stations close to the outer channel (e.g. CNS 13 and CNS 14), while lowest values were recorded at stations in close proximity to freshwater inflow (e.g. CNS 20 and CNS 22) (see Fig. 2a; Table 1). Salinity values reached peak during end of the pre-monsoon season (e.g. June) while there was a decreasing trend during monsoon (e.g. September) and gradually increased during post monsoon (see Fig. 3). Sediment texture values were generally homogenous across temporal and spatial scales in the studied lagoon (Table 1). Sediment nature was predominantly sandy (average: 94.21%; range: 89.6–97.3%) and silt/clay content was low (average: 5.79%; 2.7–10.4%) (Fig. 2b, c). On the other hand, total organic carbon (TOC) content showed significant variability; highest value (4.9 mg/g) was observed in stations with less freshwater water influx (e.g. CNS 2; average depth: 335.1 cm) while lowest value (1.2 mg/g) was found in stations with frequent freshwater influx (e.g. CNS 20) (Fig. 2d). No marked variation in environmental variables such as temperature, dissolved oxygen (DO), dissolved nitrate (NO_3^-), dissolved ortho-phosphate (PO_4^{3-}), dissolved silicate (SiO_4^{2-}) and dissolved ammonium (NH_4^+) were

found between surface and bottom water both spatially and temporally in the lagoon (Table 1).

Nematode distribution patterns

A total of 6364 specimens belonging to 76 species, 32 genera and 17 families were encountered as part of this study. The Order Chromadorida were predominant both in terms of abundance (2702 specimens) and species number (32 species), followed by Monhysterida (1752 specimens; 20 species) and Enoplida (1562 specimens; 16 species), and remaining 348 specimens were represented by 8 unidentified taxa. Spatially, significant variation was found in terms of nematode mean abundance (NMA) (2 to 1236 ind./10 cm²) and also in nematode species number (NS) (1 to 68 species). The NMA and NS values were highest close to the outer channel stations (CNS 13 and CNS 14) while lowest in stations located close to the Mahanadi tributaries (e.g. CNS 19 and CNS 22) (Fig. 2e, f). Significant variations were also noticed temporally and considerable differences were found between sampled months [in terms of mean abundance (16–854 ind./10 cm²) and mean species richness (7–74)]; while differences for H' and d values were lesser although exceptions were encountered in some months (Fig. 3).

The nematode family Comesomatidae was predominant in terms of abundance (1006 specimens) and represented by 4 genera and 11 species, followed by Oncholaimidae (886 specimens; 5 genera and 10 species) and Linhomoeidae (866 specimens; 3 genera and 7 species). Few of the nematode species were found to be widely distributed across the lagoon; for example, *Viscosia* sp. (19 stations), *Terschellingia longicaudata* (18 stations), *Daptonema normadicum* and *Metalinhomoeus filiformis* (17 stations each), *Viscosia viscosa* and *Paralongicyatholaimus* sp. (16 stations each) were also abundant. In contrast, *Oxytomina* sp. and *Rhynchonema* sp. were found only in 3 stations which are located in close proximity to saline water inputs. At the temporal scale, species such as *Viscosia viscosa*, *Paralongicyatholaimus* sp. and *Metalinhomoeus filiformis* were encountered in all months except in October 2013. However, based on trophic status (functional attribute) of nematode communities, there was domination of non-selective

Table 2 Descriptors of biotic and environmental variables used for classification of different benthic habitat settings

Settings	Biological settings			Topographical settings			Hydrological settings			
	UVS	PVS	VS	CR	MR	SR	SoS	CeS	NoS	
Depth (cm)	241.93	152.76	137.74	198.84	199.35	146.38	264.17	174.48	140.76	
Transparency (cm)	70.12	47.96	41.88	63.01	53.04	46.74	80.71	55.96	34.90	
Salinity	8.07	7.88	2.29	6.27	5.97	7.81	8.43	7.77	3.04	
Temperature (°C)	SW	27.74	28.39	28.21	27.94	28.17	28.14	28.16	27.89	28.22
	BW	26.84	26.84	26.95	26.94	26.72	26.97	26.98	26.91	26.72
DO (mg/l)	SW	5.63	5.62	5.32	5.50	5.56	5.60	5.75	5.53	5.40
	BW	4.98	5.08	4.84	4.89	4.91	5.24	5.32	4.73	5.03
NO ₃ ⁻ (µg/l)	SW	31.10	35.25	45.85	36.72	36.09	35.40	30.49	34.14	44.08
	BW	32.29	35.68	45.24	37.61	36.96	34.45	31.50	36.01	42.14
PO ₄ ³⁻ (µg/l)	SW	1.47	2.04	1.81	1.41	1.75	2.34	1.08	1.79	2.19
	BW	1.50	2.18	1.76	1.79	1.38	2.38	1.26	1.62	2.43
SiO ₄ ²⁻ (µg/l)	SW	64.59	89.19	113.17	80.49	85.34	92.34	58.36	70.15	128.23
	BW	64.38	94.21	116.30	79.32	87.82	101.09	58.12	71.37	134.10
NH ₄ ⁺ (µg/l)	SW	1.93	2.74	3.74	2.66	2.40	3.01	1.73	2.36	3.85
	BW	1.81	2.63	2.87	2.20	2.84	1.81	1.68	2.49	2.68
Sand (%)	93.88	95.08	93.75	94.31	93.32	95.44	93.92	94.64	93.85	
Silt/clay (%)	6.12	4.91	6.26	5.69	6.68	4.55	6.09	5.36	6.14	
TOC (mg/g)	3.06	2.95	1.85	2.29	2.87	3.31	5.99	2.47	1.97	
NA	142	336	47	139	72	425	112	181	101	
NS	37	55	9	27	21	61	30	38	21	
H'	2.72	3.65	1.35	2.58	2.53	3.74	3.15	3.28	1.87	

SD secchi depth, *DO* dissolved oxygen, *NO₃⁻* dissolved nitrate, *PO₄³⁻* dissolved phosphate, *SiO₄²⁻* dissolved silicate, *NH₄⁺* dissolved ammonium, *TOC* total organic carbon, *UVS* unvegetated sediments, *PVS* partially vegetated sediments, *VS* vegetated sediments, *CR* continental region, *MR* middle region, *SR* shore region, *SoS* southern sector, *CeS* central sector, *NoS* northern sector

deposit feeders—1B (32.66%), followed by epistatum feeders—2A (26.98%), selective deposit feeders—1A (20.20%) and predators—2B (20.16%). Similar patterns were also encountered at the temporal scale during this study (Fig. S1).

Nematode distributions supporting environmental discrimination of sampling stations

For visualization of the observed nematode pattern, results distinguished sampling stations into three important habitat settings within the lagoon namely, biological setting (based on presence of macrophytes and seagrasses across sampling stations—vegetation), topographical setting (based on stations situated across lagoon-region) and hydrological setting (based on freshwater inflow across lagoon-sector) (Fig. S2). This similar pattern has been also visualized by observed

environmental variables, which are also clearly discriminated different settings across lagoon in spatial scale (Table 2). The observed environmental variables have been further validated using PCA approach. The PCA plot showed a clear distinction in environmental variables between sampling stations which is also in agreement with the separation of habitat settings within the lagoon (Fig. 4). In PCA plot, the eigenvector values indicated that all environmental variables showed equal contribution to component 1 (explaining 58.6% of total variation), which marked the separation between lagoonal settings targeted as part of this study. Dissolved nutrients such as ammonium (0.328), silicate (0.327) and nitrate (0.325) along with water transparency (−0.320), water depth (−0.309) and salinity (−0.303) were the most important contributors to principal component 1 whereas sand (0.498), silt/clay (−0.487), dissolved ortho-phosphate

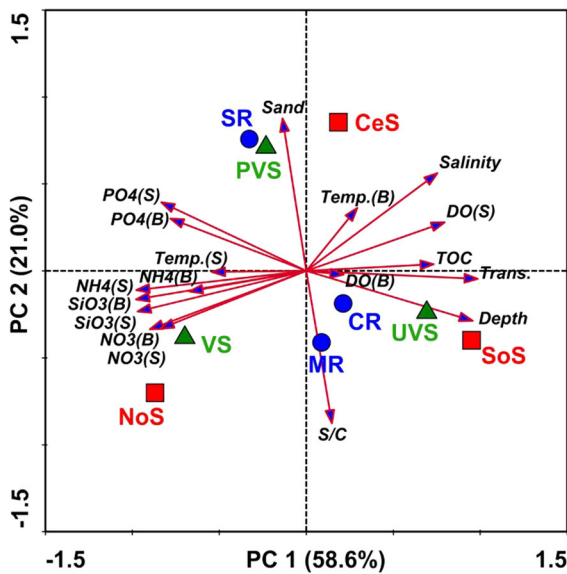


Fig. 4 Principal component analysis (PCA) to visualize patterns in response to whole set of environmental variables representing 23 stations

(−0.313) and dissolved oxygen (−0.268) contributed to component 2 and was also explained 21% of total variation.

The PCA analysis of environmental variables and classification (cluster) and ordination (nMDS) analyses of nematode assemblages were undertaken at the spatial level. Nematode abundance data has been applied into square root transformation followed by normalization to find out the marked variation between lagoonal habitat settings targeted as part of this study.

Biological settings

Similar to environmental variables (see Fig. 5), nematode community assemblage was also applied for distinguishing sampling stations representing the study area. The ordination plot (nMDS) showed clear classification of sampling stations based on biological setting (non-nematode group) using nematode assemblages from the lagoon (Fig. 5a). They were divided into three groups such as vegetated stations designated as VS (dominated by macrophytes), partially vegetated stations as PVS (dominated by seagrasses) and unvegetated bare sediment stations as UVS. Higher nematode assemblages (similarity level of ~53%) clearly split PVS (CNS 3, CNS 11, CNS 13–CNS 15,

CNS 21 and CNS 23) from the other two clusters. However, UVS (CNS 1, CNS 2, CNS 4–CNS 10 and CNS 12) showed moderate nematode density (similarity of ~46%) and comparatively lesser nematode density (similarity level of ~30%) was observed in VS (CNS 16–CNS 20 and CNS 22) with the exception of station CNS 19 where only one specimen was recorded (see Fig. 5a). Moreover, the seagrasses dominated PVS group was found to be inhabited by 55 nematode species with mean density of 336 ind./10 cm² and also had relatively coarse to medium sand, moderate TOC and DO concentrations. PERMANOVA results showed significant differences between biological habitat settings with respect to nematode assemblages and univariate descriptors (see Table S1). However, least variation was observed between UVS and PVS in terms of Shannon–Wiener index and Margalef’s richness. Furthermore, nematode trophic status also exhibited similar variations between biological habitat settings (see Table S2). On other hand, some nematode species such as *Metachromadora suecica*, *Neochromadora pseilosomoides*, *Desmodora sanguinea* and *Rhynchonema* sp. were found to be restricted in PVS group. The UVS group was characterized as having higher water depth with presence of fine sand to coarse silt, relatively high organic carbon and lesser dissolved nutrient concentrations along with lowest nematode abundance (142 ind./10 cm²) and diversity (37 species). Correlation between silt/clay and TOC content of UVS group showed clear agreement with dominance of selective deposit feeding nematodes (e.g. *Halalaimus longicaudata*). On the other hand, macrophytes dominated VS group showed least nematode abundance compared to UVS (>3 fold) and PVS (>5 fold); similar patterns were also observed in nematode diversity (see Table 2). The observed environmental variables of VS group can be explained mainly by lower salinity, TOC and water depth along with higher concentration of dissolved nitrate concentration. However, the epiphytic nematode *Hopperia* sp. was found to be dominant (24.45%) and restricted in VS group, which confirms the dominance of freshwater macrophytes.

Topographical setting

The nMDS ordination plot also classified sampling stations based on topographical setting (Fig. 5b) such

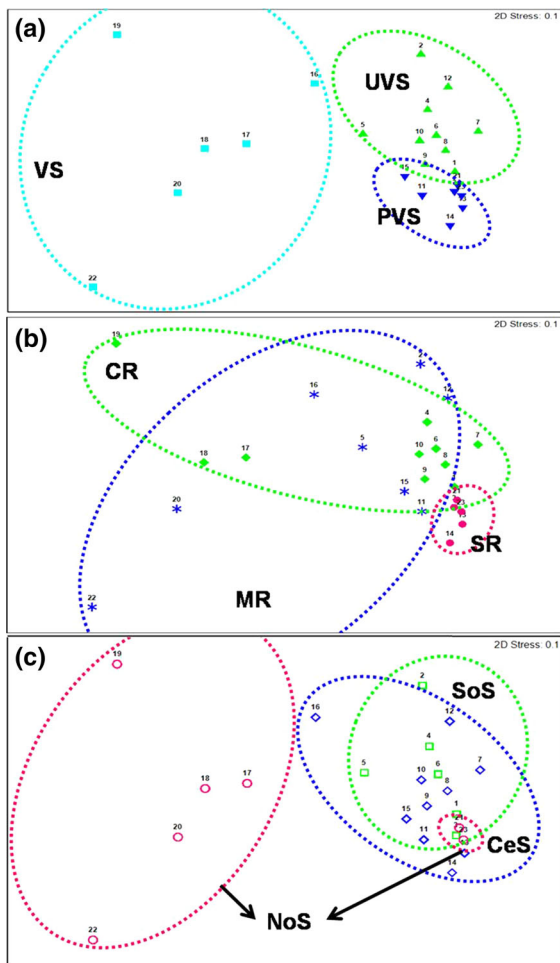


Fig. 5 Characterization of benthic habitat settings using ordination plot (nMDS) based on relative density of nematode community: **a** biological settings [UVS—unvegetated sediment; PVS—partially vegetated sediments; VS—vegetated]; **b** topographical settings [SR—shore regions; MR—middle region; CR—continental region]; **c** hydrological settings [SoS—southern sector; CeS—central sector; NoS—north sector]

as those situated (CNS 3, CNS 13, CNS 14, CNS 21, CNS 23) in close proximity to Bay of Bengal (shore region-SR), comprising of high nematodes assemblages (similarity ~63%) and clustered together. Other stations (CNS 1, CNS 4, CNS 6—CNS 10, CNS 17—CNS 19) located in the catchment area (continental region—CR with ~42% similarity) and in middle (CNS 2, CNS 5, CNS 11, CNS 12, CNS 15, CNS 16, CNS 20, CNS 22) of the lagoon (middle region—MR with ~30% similarity) formed two sub-clusters between themselves. There were some

exceptions such as closely related stations located in the middle of the lagoon (e.g. CNS 11, CNS 15) which did not cluster with other stations primarily due to higher nematode abundance and diversity (Fig. 5b). The stations represented by shore region (SR) had relatively higher nematode abundance (425 ind./10 cm²) and diversity (61 species) compared to continental region (CR) and middle region (MR) (see Table 2). The SR group was characterized by salinity dependent nematode species such as *Odonotophora longisetosa*, *Desmodora sanguinae*, *Rhynchonema* sp. and *Sabatieria praedatrix* along with higher values of salinity, TOC, sand content and moderate concentration of dissolved nutrient concentrations. The stations representing CR group was characterized by moderate concentration of dissolved nutrients along with continuous freshwater flow from surrounding rivers. Hence, TOC values were less which resulted in the dominance of deposit feeding species such as *Halalaimus longicaudatus* and *Terrellingia longicaudata*. Similarly, stations represented by MR group was characterized by increased mixing in the water column, relatively high silt, less salinity and moderate TOC values which resulted in the dominance of epistratum feeders such as *Ptycholaimellus* sp. and *Hopperia* sp. Nematode abundance and species composition displayed significant differences (PERMANOVA, $p < 0.05$) between topographically different habitat settings of Chilika whereas univariate descriptors (H' , d) did not vary significantly (see Table S1). Similarly large variations were also noticed in terms of trophic status of nematode community between topographical settings of Chilika, except in deposit feeders (1A + 1B) representing CR and SR (see results of PERMANOVA in Table S2).

Hydrological setting

The nMDS ordination plot also showed groups of stations based on hydrological settings (Fig. 5c). The sampling stations could be clustered into two major groups: high freshwater influenced stations (northern sector—NoS: CNS 17—CNS 23) and low freshwater influenced stations (CNS 1—CNS 16). The cluster consisting of low freshwater influenced stations can be further sub divided into two sub-clusters, namely moderate (central sector—CeS: CNS 7—CNS 16) and

very low (southern sector—SoS: CNS 1—CNS 6) freshwater influenced stations. Higher nematode assemblages were noticed in SoS (~60%) and CeS (~54%) sectors, whereas lower nematode assemblages were found in NoS sector (~30%). Similar patterns of nematode assemblages of SoS and CeS groups can be mainly explained by higher salinity, TOC values and water depth compared to stations constituting the northern sector (NoS) group which had higher concentration of dissolved nutrients and relatively low salinity and water depth. However, stations such as CNS21 and CNS23 of NoS showed relatively higher nematode abundance and diversity (see Fig. 5c). Nematode species composition also showed significant relationship with salinity. Genera such as *Viscosia*, *Sabatieria*, *Halalaimus*, *Daptonema* and *Terschellingia* were observed mostly in high salinity stations whereas genera such as *Hopperia* and *Dorylaimopsis* were found in low salinity stations. The sectoral distribution (hydrological settings) of nematode assemblages (e.g. abundance, species composition) showed considerable variations (PERMANOVA, $p < 0.05$) while H' and d did not display any significant variation (see Table S1). Nematode trophic status also showed large variations (PERMANOVA, $p < 0.05$) between hydrological settings of Chilika (see Table S2).

Stations classified based on nematode density at the species level were pooled together and analyzed using SIMPER (similarity percentage—75% cut-off) analysis. The obtained nematode species composition was calculated as relative abundance to investigate the importance of nematode species-wise contribution for observed spatial patterns in different habitat settings of studied lagoon. Out of 76 species, 26 species separated the stations based on biological settings, whereas 9 species and 8 species separated stations based on topographical and hydrological settings respectively (Table 3). In total, 37 nematode species were identified as important species for explaining habitat settings across the lagoon based on SIMPER analysis (see Table 3). The RDA ordination plot (Fig. 6) clearly showed that first two main axes explained 69.3% of observed variations between nematode assemblage and environmental variables and was also confirmed using Monte Carlo permutation (forward selection) tests ($p < 0.001$).

Discussion

Benthic organisms play vital role in mediating coastal ecosystem processes (Carrico et al. 2013); in particular free-living nematodes are considered as a key component owing to their high abundance, diversity and rapid turnover rates (Schratzberger and Ingels 2017 for review). In the present study, nematodes contributed 89.2% of total meiofaunal density, and rest were represented by other meiofaunal groups such as Harpacticoid copepoda, Ostracoda, Kinorhyncha and live Foraminifera (data not shown). The results clearly show the importance of nematodes and their contribution within the meiofaunal community of Chilika lagoon as reported by other studies conducted in lagoons globally (e.g. Colangelo and Ceccherelli 1994; Gambi et al. 2003; Cibic et al. 2012; Semprucci et al. 2014a). However, numerical mean abundance of nematodes encountered in Chilika lagoon was lower (2–1236 ind/10 cm²) compared to other lagoonal environments and the observed value could be also due to sampling efforts/methods adopted as part of our study (e.g., number of samples collected, sampling periods, type of grabs used such as Ponar grab). Similar trends in nematode abundance based on sampling methodology (e.g. type of grab) have been reported in other ecosystems (e.g. Vanreusel et al. 2010; Ansari et al. 2015, 2017).

Results obtained from our study showed significant heterogeneity in nematode abundance and diversity both spatially and temporally across the lagoon and thereby confirming the patchy distribution patterns and colonization of nematode community as recorded across different marine habitats (Ansari et al. 2016 reference within). In total, 76 species of nematodes were recorded in this study and there was dominance of families namely, Comesomatidae, Oncholaimidae, Linhomoeidae and Chromadoridae. These families have been also found to dominate in lagoons located in the Mediterranean region (e.g. Boufahja et al. 2014; Semprucci et al. 2014b; Jouili et al. 2017) as well as in other coastal habitats (see Moens et al. 2013 for review). The dominance of brackish water nematode genera such as *Viscosia*, *Daptonema* and *Terschellingia* were observed across the Chilika; it could be attributed due to their large size (Fleeger and

Table 3 Mean relative abundance of selected nematode species (identified by SIMPER—75% cut-off) and affinity group of different benthic habitat settings. Highlighted values and species indicate the distinctiveness of different settings

Nematode species	Abbreviations	Feeding types	Biological settings				Topographical settings				Hydrological settings			
			UVS	PVS	VS	MR	SR	CR	MR	SoS	CeS	NoS		
<i>Oxystomina</i> sp.	<i>Oxy.sp.</i>	1A	0.65			0.57	0.28		0.45	0.11				
<i>Halalaimus longicaudatus</i>	<i>H.longi.</i>	1A	7.60	2.00		1.88	2.54		7.74	2.11				1.84
<i>Metachromadora</i> sp.	<i>Meta.sp.</i>	2A	2.33	0.72		0.61	2.41		3.27	0.55				0.43
<i>Sphaerolaimus</i> sp.	<i>Spha.sp.</i>	2B	2.07	0.47		0.47	1.84		0.74	0.83				0.99
<i>Metachromadora suecica</i>	<i>Meta.suec.</i>	2A		3.32		1.84	2.26		0.30	2.22				0.71
<i>Neochromadora psilosomoides</i>	<i>Neo.pseil.</i>	2A		1.91		1.65	2.82		0.30	2.38				
<i>Desmadora sanguinea</i>	<i>Des.sang.</i>	2A		1.02		1.08	0.28		0.45	1.11				0.14
<i>Rhynchonema</i> sp.	<i>Rhyn.sp.</i>	1A		0.17		0.19	0.17		0.17	0.17				0.14
<i>Odontophora</i> sp.1	<i>Odonto.sp.1</i>	1B		0.17		0.14	0.28		0.15	0.17				0.14
<i>Spilophorella candida</i>	<i>Spilo.cand.</i>	2A	1.03	3.65		3.67	0.71		0.30	4.04				2.70
<i>Sphaerolaimus gracilis</i>	<i>Spha.grac.</i>	2B	0.39	1.40		1.27	0.14		1.64	1.05				0.85
<i>Odontophora longisetosa</i>	<i>Odonto.longi.</i>	1B	0.13	1.23		1.37	0.14		1.05	1.56				1.28
Unidentified Sp.2	UI sp.2	2A	0.13	0.93		1.04	0.14		0.89	0.44				1.28
<i>Sabatieria celtica</i>	<i>Saba.cel.</i>	1B	0.13	0.89		0.75	1.69		0.30	0.61				0.14
<i>Daptonema oxycerca</i>	<i>Dapto.oxyc.</i>	1B	0.13	0.81		0.66	1.69		0.89	0.72				0.14
Unidentified Sp.3	UI sp.3	2A	0.13	0.81		0.80	0.14		0.15	0.78				0.71
<i>Desmodora sculzhi</i>	<i>Des.scul.</i>	2A	0.13	0.76		0.75	0.85		0.15	1.00				0.85
<i>Daptonema setosum</i>	<i>Dapto.seto.</i>	1B	0.13	0.55		0.42	0.14		0.44	0.44				0.85
<i>Viscostia viscosa</i>	<i>V. vis.</i>	2B	6.34	4.84		4.66	6.10		3.87	6.04				3.97
<i>Sabatieria praedatrix</i>	<i>Saba.praed.</i>	1B	0.26	0.72		0.80	0.28		0.30	0.83				0.28
<i>Axonolaimus</i> sp.	<i>Axono.sp.</i>	1B	0.91	0.25		0.28	0.99		0.30	0.50				0.28
<i>Metoncholaimus</i> sp.	<i>Meton.sp.</i>	2A	0.39	0.25		0.28	0.28		1.04	0.06				0.14
<i>Viscostia abyssorum</i>	<i>V.abys.</i>	2B	0.65	0.76		0.71	0.71		0.60	0.22				2.13
Unidentified Sp.7	UI sp.7	1A	0.26	0.68		0.71	0.14		0.15	0.28				1.70
<i>Hopperia</i> sp.	<i>Hopp.sp.</i>	1B			25.45	0.89	1.70		1.83	1.99				1.99
<i>Daptonema</i> sp.	<i>Dapto.sp.</i>	1B	0.91	0.93	12.73	0.94	1.42		1.34	0.78				1.84
<i>Sabatieria</i> sp.1	<i>Saba.sp.1</i>	1B	1.68	1.74	5.45	1.65	1.84		3.13	1.61				0.99
<i>Pycholaimellus</i> sp.	<i>Pty.sp.</i>	1B	1.03	2.17	5.45	1.74	1.13		0.74	2.33				2.13
<i>Oxystomina elongata</i>	<i>Oxy.elong.</i>	1A	1.29	1.23	3.64	1.32	1.42		2.83	0.44				1.99
<i>Pomponema</i> sp.	<i>Pompo.sp.</i>	2A	0.65	0.89	3.64	0.61	0.85		0.60	1.05				0.71
<i>Aponema</i> sp.	<i>Apo.sp.</i>	2A	0.39	0.59	1.82	0.66	0.43		1.04	0.44				0.43

Table 3 continued

Nematode species	Abbreviations	Feeding types	Biological settings			Topographical settings			Hydrological settings		
			UVS	PVS	VS	SR	CR	MR	SoS	CeS	NoS
<i>Sabatieria</i> sp.2	<i>Saba.sp.2</i>	1B	0.39	0.42	1.82	0.47	0.43	0.28	0.45	0.22	0.99
<i>Terschellingia longicaudata</i>	<i>Ter.longi.</i>	1B	5.82	4.80	1.82	5.04	6.24	2.26	5.06	4.99	4.96
<i>Daptonema normandicum</i>	<i>Dapto.nor.</i>	1B	4.79	4.25	1.82	4.29	4.68	3.95	4.61	4.38	3.97
<i>Dorylaimopsis punctata</i>	<i>Dory.pun.</i>	2A	4.27	2.89	1.82	2.97	4.40	2.26	4.46	3.05	2.41
<i>Paratolngicyatholaimus</i> sp.	<i>Parato.sp.</i>	2A	3.62	3.53	1.82	3.82	3.40	1.98	4.46	3.66	2.27
<i>Metatlnhomoeus filiformis</i>	<i>Metal.fil.</i>	1B	2.85	3.78	3.64	3.77	2.98	3.39	3.57	3.60	3.40

UVS unvegetated sediments, PVS partially vegetated sediments, VS vegetated sediments, CR continental region, MR middle region, SR shore region, SoS southern sector, CeS central sector, NoS northern sector

Carman 2011), faster locomotion (Heip et al. 1985) and also because of habitat preference mainly sandy sediments (see Tahseen 2012 for review; Losi et al. 2013; Netto and Fonseca 2017). At the same time, observation of nematode genera such as *Hopperia* and *Camacolaimus* indicate possible association with aquatic macrophytes (e.g. *Potamageton*) which are found in plentiful in the northern sector of Chilika lagoon. Such association has been also reported in other coastal ecosystems (Colangelo and Ceccherelli 1994; Netto and Fonseca 2017). Nematode species identified in this study clearly showed patterns similar to global trends and more specifically in relation to environmental variations such as salinity, sediment nature and anthropogenic inputs (Colangelo and Ceccherelli 1994; Cibic et al. 2012; Semprucci et al. 2014a; Boufahja et al. 2015; Netto and Fonseca 2017).

Characterization of benthic habitat settings using nematode communities and associated environmental variables

Chilika lagoon has been relatively well studied in many aspects especially in terms of water quality, phytoplankton, macrophytes and benthic community (e.g. Panda and Mohanty 2008; Panigrahi et al. 2009; Srichandan et al. 2015a, b; Ansari et al. 2015, 2017; Mohanty et al. 2016; Barik et al. 2017). However, to the best of our knowledge sectoral level differences in Chilika lagoon have not been investigated mainly using biotic communities. A recent study undertaken by us showed patchiness of macrofaunal communities in multiple scales throughout Chilika lagoon (Ansari et al. 2017). Based on this broad background, the present study has been undertaken to evaluate the effectiveness of free-living nematodes as proxy for characterizing sampling stations of Chilika lagoon into different habitat settings in link with environmental variables. Statistical analyses (classification, ordination and PERMANOVA) undertaken in our study support our observation (both nematode and environmental variables) and clearly explained habitat settings namely, biological (vegetation), topographical (region) and hydrological (sector) settings across Chilika lagoon (see Figs. 5; Supplementary Material S2).

The patchy distribution pattern of nematode community structure within lagoonal systems was supported by ordination plot (nMDS) with clear

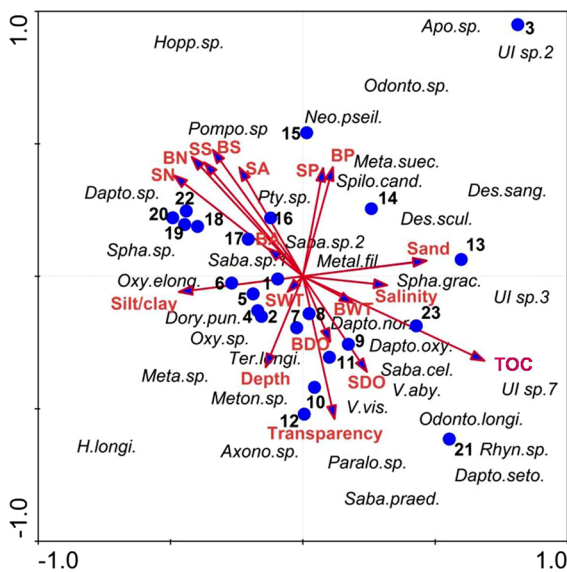


Fig. 6 Redundancy analyses (RDA) for selected nematode species (obtained from SIMPER analysis) and environmental variables across the Chilika lagoon. (species abbreviation—see in Table 3; S & B—surface and bottom water of each parameter; WT—water temperature; DO—dissolved oxygen; TOC—total organic carbon; N—dissolved nitrate; P—dissolved orthophosphate; S—dissolved silicate; A—dissolved ammonium)

separation of sampling stations (Fig. 5). The seagrass dominated partially vegetated stations (PVS) of Chilika lagoon clearly separated due to higher nematode density and diversity and represented by relatively coarse to medium sand as well as moderate TOC and DO concentrations. On the contrary freshwater macrophyte dominated vegetated stations (VS) and bare sediment stations (UVS) contributed to low nematode density and diversity. The patchy distribution of nematode community structure across Chilika was initially reported before (Ansari et al. 2015); nevertheless the importance of vegetation in influencing the observed nematode assemblages has been reported for the first time as part of this study. Similarly, Gambi et al. (2009) and Liao et al. (2015) reported higher nematode abundance in seagrass meadows compared to bare sediments and the authors stated that seagrass meadows can enhance organic matter content in the sediment which can ultimately end up in the deeper layers. This in turn can promote higher abundance of nematodes, in particular, deposit feeders (1A + 1B) in deeper layers and epistratum feeders (2A) in upper layers (Gambi et al. 2009; Liao et al. 2015). Interestingly, in our study some of the nematode species

which are deposit feeders such as *Metachromadora suecica*, *Neochromadora pseilosomoides*, *Desmodora sanguinea* and *Rhynchonema* sp. were found to be restricted in seagrass habitats of Chilika lagoon (see Table 3). Although, the bare sediments stations were also rich in organic matter and relatively higher silt/clay content but nematode density and diversity were moderate. There was dominance of selective deposit feeders (e.g. *Halalaimus longicaudata*) in these stations and the morphological characteristics of this species include elongated body shape and long tail. PERMANOVA results on nematode trophic status clearly supported the observed large variation found between biological settings (see Table S2). Interestingly, in some of the bare sediment stations, dissolved oxygen concentration was found to be low although TOC was high and as a result nematode abundance and diversity was lowest. Such abiotic conditions can facilitate production of hydrogen sulphide which can ultimately lead to sedimentary hypoxia/anoxia in shallow coastal ecosystems (Guerrini et al. 1998; Khan et al. 2012). However, nematode communities are known to be highly tolerant to hypoxic/anoxic conditions compared to other meiofaunal groups (Cook et al. 2000; Vanaverbeke et al. 2004; Gambi et al. 2009; Bhadury and Austen 2010; Ürkmez et al. 2015). Freshwater macrophyte dominated stations showed very low nematode density and diversity. Liao et al. (2015) reported that huge amount of freshwater flow can possibly trigger dominance of freshwater nematode community than their marine counterparts. Our results also showed low salinity and huge sedimentation can promote lush growth of freshwater macrophytes with dominance of epiphytic nematode genus *Hopperia* (24.45%) along with the persistence of freshwater nematode taxa (e.g. Order Dorylaimida; data not included in this study) in vegetated part of Chilika (see Table 3). Generally, in vegetated ecosystems epiphytic nematode communities can dominate compared to sedimentary free-living forms (Jensen 1984; Da Rocha et al. 2006; Adão et al. 2009; Ansari et al. 2015; Pérez-García et al. 2015).

Our results further showed another important habitat setting based on topographical nature of lagoon. The ordination plot (nMDS) clearly separated sampling stations (shore region—SR) which had higher nematode density and diversity with the prevalence of salinity dependent nematode species such as *Odontophora longisetosa*, *Desmodora*

sanguinae, *Rhynchonema* sp. and *Sabatieria praedatrix*. Moreover, in these stations TOC and dissolved nutrient concentrations were found to be higher. These conditions provide a unique habitat for observed nematode communities to flourish as reported by others (Mahmoudi et al. 2005; Moreno et al. 2011). The higher abundance and diversity of nematodes could be due to intrusion of fresh and saline water which brings both marine and brackish water nematode community (Adão et al. 2009). Nevertheless, the inner part of lagoon also showed unique nematode community patterns representing both continental (CR) and middle (MR) regions (e.g. *Odontophora longisetosa*, *Rhynchonema* sp.). The observed environmental variables also supported the habitats settings with moderate concentration of dissolved nutrients and TOC thereby promoting the dominance of deposit feeding nematodes (e.g. *Halalaimus longicaudatus* and *Terschellingia longicaudata*). Similar trends of nematode composition have been also reported from other lagoons globally (e.g. Beyrem et al. 2011; Semprucci et al. 2011).

We found relevant interaction of nematode community assemblages within sectoral settings of Chilika lagoon (Srichandan et al. 2015a, b; Mohanty et al. 2016; Ansari et al. 2017; Barik et al. 2017). Sector-wise distribution of nematode community assemblages could be clearly distinguished by nMDS plot (see Fig. 4c). However, some level of overlapping was observed between southern (SoS) and central sectors (CeS). Salinity is the factor which played an important role in influencing the observed pattern of nematode community in SoS and CeS, as evident by the dominance of brackish water nematodes (*Viscosia*, *Sabatieria*, *Halalaimus*, *Daptonema* and *Terschellingia*) in our studied lagoon. However, in NoS there was dominance of freshwater nematode genera such as *Hopperia* and *Dorylaimopsis* (Netto and Fonseca 2017) whereas CNS21 and CNS23 stations showed the presence of brackish water to marine nematodes. The observed pattern could have been due to the artificially dredged channel which brings enormous amount of sea water into the Chilika lagoon (Panigrahi et al. 2009; Ansari et al. 2015; Srichandan et al. 2015a). Such variations in nematode community distribution have been widely documented in global lagoonal ecosystems (Gambi et al. 2003; Beyrem et al. 2011; Boufahja et al. 2014; Semprucci et al. 2014a; Majdi and Traunspurger 2015). Moreover, species

such as *Terschellingia longicaudata*, which is usually considered as a cosmopolitan species (Bhadury et al. 2008), was found to be prevalent (in terms of abundance) in the Chilika lagoon as also reported by us previously (Ansari et al. 2015).

The observed habitat settings of Chilika lagoon based on nematode community structure also showed link with prevailing environmental variables. We observed clear discrimination between the spatial stations based on environmental variables using principal component analysis (PCA) (Fig. 4) and some of these patterns have discussed in a recent publication (see Fig. S1 of Ansari et al. 2017). The overwhelming dominance of marine nematodes clearly indicates salinity is an important environmental variable which controls the structure and functioning of nematodes across the studied lagoon. It also provides detailed insight to investigation of nematode community as a tool for ecosystem monitoring mainly in salinity dependent environments including lagoons and estuaries.

Conclusion

As part of this study we undertook extensive sampling based on specific lagoonal habitat settings across space and time. We observed that different habitat settings mutually provide various biological community patterns including that of nematodes along with associated environmental variables and observed patterns can be successfully applied to characterize a lagoon into three major settings (biological, topographical and hydrological). Chilika lagoon is strongly influenced by natural and anthropogenic factors and these are known to influence biotic and abiotic changes as observed in our study. Statistical analysis undertaken in our study showed that prevailing salinity provided key insight in terms of distribution and diversity of nematodes, many of which are largely dependent on salinity compared to freshwater counterparts. Overall this study clearly show that nematode communities could be used to assign benthic habitat settings within a lagoon and can prove to be a key tool for long term ecological monitoring of coastal ecosystems globally including Chilika lagoon.

Acknowledgements This work is supported by a grant awarded to Punyasloke Bhadury by Chilika Development

Authority (CDA) through the financial support received from the World Bank supported Integrated Coastal Zone Management Project (ICZMP) of Odisha. We are also grateful to Integrative Taxonomy and Microbial Ecology Research Group members for helping us during field work.

References

- Adão H, Alves AS, Patrício J, Neto JM, Costa MJ, Marques JC (2009) Spatial distribution of subtidal Nematoda communities along the salinity gradient in southern European estuaries. *Acta Oecol* 35:287–300. doi:[10.1016/j.actao.2008.11.007](https://doi.org/10.1016/j.actao.2008.11.007)
- Alves AS, Adão H, Ferrero TJ, Marques JC, Costa MJ, Patrício J (2013) Benthic meiofauna as indicator of ecological changes in estuarine ecosystems: the use of nematodes in ecological quality assessment. *Ecol Indic* 24:462–475. doi:[10.1016/j.ecolind.2012.07.013](https://doi.org/10.1016/j.ecolind.2012.07.013)
- Alves AS, Veríssimo H, Costa MJ, Marques JC (2014) Taxonomic resolution and biological traits analysis (BTA) approaches in estuarine free-living nematodes. *Estuar Coast Shelf Sci* 138:69–78. doi:[10.1016/j.ecss.2013.12.014](https://doi.org/10.1016/j.ecss.2013.12.014)
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Ansari KGMT, Manokaran S, Raja S, Lyla PS, Ajmal Khan S (2014) Interaction of free-living marine nematodes in the artificial mangrove environment (southeast coast of India). *Environ Monit Assess* 186:293–305. doi:[10.1007/s10661-013-3374-1](https://doi.org/10.1007/s10661-013-3374-1)
- Ansari KGMT, Pattnaik AK, Rastogi G, Bhadury P (2015) An inventory of free-living marine nematodes from Asia's largest coastal lagoon, Chilika, India. *Wetlands Ecol Manage* 23:881–890. doi:[10.1007/s11273-015-9426-2](https://doi.org/10.1007/s11273-015-9426-2)
- Ansari KGMT, Lyla PS, Ajmal Khan S, Bhadury P (2016) Diversity patterns of free-living marine nematodes in the southwest continental shelf of Bay of Bengal and their link to abiotic variables. *Mar Ecol* 37:631–644. doi:[10.1111/maec.12332](https://doi.org/10.1111/maec.12332)
- Ansari KGMT, Lyla PS, Ajmal Khan S, Bhadury P (2017) Multiple spatial scale analysis provide an understanding of benthic macro-invertebrate community structure across a lagoonal ecosystem. *Wetlands* 37:277–287. doi:[10.1007/s13157-016-0866-0](https://doi.org/10.1007/s13157-016-0866-0)
- Armenteros M, Perez-Garcia JA, Perez-Angulo A, Williams JP (2008) Efficiency of extraction of meiofauna from sandy and muddy marine sediments. *Rev Investiga Mar* 29:113–118
- Barik SK, Muduli PR, Mohanty B, Behara AT, Mallick S, Das A et al (2017). Spatio-temporal variability and the impact of Phailin on water quality of Chilika lagoon. *Cont Shelf Res* 136:39–56. doi:[10.1016/j.csr.2017.01.019](https://doi.org/10.1016/j.csr.2017.01.019)
- Beyrem H, Boufahja F, Hedfi A, Essid N, Aïssa P, Mohmoudi E (2011) Laboratory study on individual and combined effects of Cobalt and Zinc-Spiked sediment on meiobenthic nematodes. *Biol Trace Elem Res* 144:790–803. doi:[10.1007/s12011-011-9032-y](https://doi.org/10.1007/s12011-011-9032-y)
- Bhadury P, Austen MC (2010) Barcoding marine nematodes- an improved set of nematode 18S rRNA primers to overcome eukaryotic co-interference. *Hydrobiologia* 641:245–251. doi:[10.1007/s10750-009-0088-z](https://doi.org/10.1007/s10750-009-0088-z)
- Bhadury P, Austen MC, Bilton DT, Lamshead PJD, Rogers AD, Smerdon GR (2008) Evaluation of combined morphological and molecular techniques for marine nematode (*Terschellingia* spp.) identification. *Mar Biol* 154:509–518. doi:[10.1007/s00227-008-0945-8](https://doi.org/10.1007/s00227-008-0945-8)
- Bianchelli S, Pusceddu A, Buschi E, Danovaro R (2016) Trophic status and meiofauna biodiversity in the Northern Adriatic Sea: insights for the assessment of good environmental status. *Mar Environ Res* 113:18–30. doi:[10.1016/j.marenvres.2015.10.010](https://doi.org/10.1016/j.marenvres.2015.10.010)
- Blott SJ, Pye K (2001) GRADISTAT: a grain size distribution statistic package for the analysis of unconsolidated sediments. *Earth Surf Proc Land* 26:1237–1248. doi:[10.1002/esp.261](https://doi.org/10.1002/esp.261)
- Boufahja F, Vitiello P, Aïssa P (2014) More than 35 years of studies on marine nematodes from Tunisia: a checklist of species and their distribution. *Zootaxa* 3786:269–300. doi:[10.11646/zootaxa.3786.3.3](https://doi.org/10.11646/zootaxa.3786.3.3)
- Boufahja F, Semprucci F, Beyrem H, Bhadury P (2015) Marine nematode taxonomy in Africa: promising prospects against scarcity of information. *J Nematol* 47:198–206
- Buchanan JB (1984) Sediment analysis. In: Holme NA, McIntyre AD (eds) *Methods for the study of marine benthos*. Blackwell Scientific Publications, London, pp 41–65
- Carriço R, Zeppilli D, Quillien N, Grall J (2013) Can meiofauna be a good biological indicator of the impacts of eutrophication caused by green macroalgal blooms? *Les cahiers naturalistes de l'Observatoire marin* 2:9–16
- Cibic T, Franzo A, Celussi M, Fabbro C, Del Negro P (2012) Benthic ecosystem functioning in hydrocarbon and heavy-metal contaminated sediments of an Adriatic lagoon. *Mar Ecol Prog Ser* 458:69–87. doi:[10.3354/meps09741](https://doi.org/10.3354/meps09741)
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/Tutorial. PRIMER-E, Plymouth
- Clarke KR, Somerfield PJ, Airoldi L, Warwick RM (2006) Exploring interaction by second-stage community analysis. *J Exp Mar Biol Ecol* 338:179–192. doi:[10.1016/j.jembe.2006.06.019](https://doi.org/10.1016/j.jembe.2006.06.019)
- Colangelo MA, Ceccherelli UV (1994) Meiofaunal recolonization of azoic sediment in a Po Delta lagoon (Sacca di Goro). *Boll Zool* 61:335–342. doi:[10.1080/11250009409355904](https://doi.org/10.1080/11250009409355904)
- Cook AA, Lamshead PJD, Hawkins LE, Mitchell N, Levin LA (2000) Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Res II* 47:75–85. doi:[10.1016/S0967-0645\(99\)00097-1](https://doi.org/10.1016/S0967-0645(99)00097-1)
- Coomans A (2002) Present status and future of nematode systematics. *Nematology* 5:573–582. doi:[10.1163/15685410260438836](https://doi.org/10.1163/15685410260438836)
- Coull BC, Palmer MA (1984) Field experimentation in meiofaunal ecology. *Hydrobiologia* 118:1–19. doi:[10.1007/BF00031783](https://doi.org/10.1007/BF00031783)
- Da Rocha CMC, Venekey V, Bezerra TNC, Souza JRB (2006) Phytal marine nematode assemblages and their relation with the macrophytes structural complexity in a Brazilian tropical rocky beach. *Hydrobiologia* 553:219–230. doi:[10.1007/s10750-005-0923-9](https://doi.org/10.1007/s10750-005-0923-9)

- Danovaro R, Scopa M, Gambi C, Frascchetti S (2007) Tropic importance of subtidal metazoan meiofauna: evidence from in situ exclusion experiments on soft and rocky substrates. *Mar Biol* 152:339–350. doi:[10.1007/s00227-007-0696-y](https://doi.org/10.1007/s00227-007-0696-y)
- Edwards DP, Tobias JA, Sheil D, Meijaard E, Laurance WF (2014) Maintaining ecosystem function and services in logged tropical forests. *Trends Ecol Evol* 29:511–520. doi:[10.1016/j.tree.2014.07.003](https://doi.org/10.1016/j.tree.2014.07.003)
- Elliott JM, Drake CM (1981) A comparative study of seven grabs for sampling benthic macrinvertebrates in rivers. *Freshwat Biol* 11:99–120
- Fabbrocini A, Guarino A, Scirocco T, Franchi M, D'adamo R (2005) Integrated bio-monitoring assessment of the Lesina Lagoon (Southern Adriatic Coast, Italy): preliminary results. *Chem Ecol* 21:479–489. doi:[10.1080/02757540500438623](https://doi.org/10.1080/02757540500438623)
- Finch MS, Hydes DJ, Clayson CH, Weigl B, Dakin J, Gwilliam P (1998) A low power ultra violet spectrophotometer for measurement of nitrate in seawater: introduction, calibration and initial sea trials. *Anal Chim Acta* 377:167–177. doi:[10.1016/S0003-2670\(98\)00616-3](https://doi.org/10.1016/S0003-2670(98)00616-3)
- Fleeger JW, Carman KR (2011) Experimental and genetic studies of meiofauna assess environmental quality and reveal mechanisms of pollution fate and effects. *Vie Milieu* 61:1–26
- Fonseca G, Maria TF, Kandravicius N, Venekey V, Gheller PF, Gallucci F (2014) Testing for nematode-granulometry relationships. *Mar Biodiv* 44:435–442. doi:[10.1007/s12526-014-0241-4](https://doi.org/10.1007/s12526-014-0241-4)
- Frontalini F, Semprucci F, Coccioni R, Balsamo M, Bittoni P, Covazzi-Harriague A (2011) On the quantitative distribution and community structure of the meio and macrofaunal communities in the coastal area of the central Adriatic Sea (Italy). *Environ Monit Assess* 180:325–344. doi:[10.1007/s10661-010-1791-y](https://doi.org/10.1007/s10661-010-1791-y)
- Gambi C, Totti C, Manini E (2003) Impact of organic loads and environmental gradients on microphytobenthos and meiofaunal distribution in a coastal lagoon. *Chem Ecol* 19:207–223. doi:[10.1080/0275754031000119951](https://doi.org/10.1080/0275754031000119951)
- Gambi C, Bianchelli S, Perez M, Invers O, Ruiz RM, Danovaro R (2009) Biodiversity response to experimental induced hypoxic-anoxic conditions in seagrass sediments. *Biodivers Conserv* 18:33–54. doi:[10.1007/s10531-008-9433-1](https://doi.org/10.1007/s10531-008-9433-1)
- Gaudette HE, Flight WR, Lois T, Folger DW (1974) An inexpensive titration method for determination of organic carbon in recent sediments. *J Sediment Petrol* 44:249–253. doi:[10.1306/74D729D7-2B21-11D7-8648000102C1865D](https://doi.org/10.1306/74D729D7-2B21-11D7-8648000102C1865D)
- Giere O (2009) *Meiobenthology: the microscopic motile fauna of aquatic sediments*, 2nd edn. Springer, Berlin. doi:[10.1007/978-3-540-68661-3](https://doi.org/10.1007/978-3-540-68661-3)
- Gordon AL, Claudia FG, Takahashi T, Sutherland S, Morrison J, Olson D (2002) Bay of Bengal nutrient-rich benthic layer. *Deep-Sea Res II* 49:1411–1421. doi:[10.1016/S0967-0645\(01\)00161-8](https://doi.org/10.1016/S0967-0645(01)00161-8)
- Guerrini A, Colangelo MA, Ceccherelli UV (1998) Recolonization patterns of meiobenthic communities in the brackish vegetated and unvegetated habitats after induced hypoxia/anoxia. *Hydrobiologia* 375(376):73–87. doi:[10.1023/A:1017096603808](https://doi.org/10.1023/A:1017096603808)
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C et al (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952. doi:[10.1126/science.1149345](https://doi.org/10.1126/science.1149345)
- Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. *Oceanogr Mar Biol Ann Rev* 23:399–489
- Hirpa FA, Hopson TM, De Groeve T, Brakenridge GR, Gebremichael M, Restrepo PJ (2013) Upstream satellite remote sensing for river discharge forecasting: application to major rivers in South Asia. *Remote Sens Environ* 131:140–151. doi:[10.1016/j.rse.2012.11.013](https://doi.org/10.1016/j.rse.2012.11.013)
- Ittekkot V, Nair RR, Honjo S, Ramaswamy V, Bartsch M, Manganini S, Desai BN (1991) Enhanced particle fluxes in Bay of Bengal induced by injection of fresh water. *Nature* 351:385–387. doi:[10.1038/351385a0](https://doi.org/10.1038/351385a0)
- Jensen P (1984) Ecology of benthic and epiphytic nematodes in brackish waters. *Hydrobiologia* 108:201–217. doi:[10.1007/BF00006329](https://doi.org/10.1007/BF00006329)
- Jeong KS, Kim DK, Pattnaik A, Bhatta K, Bhandari B, Joo GJ (2008) Patterning limnological characteristics of the Chilika lagoon (India) using a self-organizing map. *Limnology* 9:231–242. doi:[10.1007/s10201-008-0243-7](https://doi.org/10.1007/s10201-008-0243-7)
- Jouili S, Essid N, Semprucci F, Boufahja F (2017) Environmental quality assessment of El Bibane lagoon (Tunisia) using taxonomic and functional diversity of meiofauna and nematodes. *J Mar Biol Assoc UK*. doi:[10.1017/S0025315416000990](https://doi.org/10.1017/S0025315416000990)
- Khan SA, Ansari KGMT, Lyla PS (2012) Organic matter content of sediments in continental shelf area of southeast coast of India. *Environ Monit Assess* 184:7247–7256. doi:[10.1007/s10661-011-2494-8](https://doi.org/10.1007/s10661-011-2494-8)
- Lambhead PJD (2004) Marine nematode biodiversity. In: Chen ZX, Chen Y, Chen SY, Dickson DW (eds) *Nematology: advances and perspectives*, vol 1. Nematode morphology, physiology and ecology. CABI Publishing, Wallingford, pp 436–467
- Liao JX, Yeh HM, Mok HK (2015) Meiofaunal communities in a tropical seagrass bed and adjacent unvegetated sediments with note on sufficient sample size for determining local diversity indices. *Zool Stud* 54:14. doi:[10.1186/s40555-014-0101-8](https://doi.org/10.1186/s40555-014-0101-8)
- Liddicoat MI, Tribbitts S, Butler EI (1975) The determination of ammonia in seawater. *Limnol Oceanogr* 20:131–132
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808. doi:[10.1126/science.1064088](https://doi.org/10.1126/science.1064088)
- Losi V, Ferrero TJ, Moreno M, Gaozza L, Rovere A, Firpo M, Marques JC, Albertelli G (2013) The use of nematodes in assessing ecological conditions in shallow waters surrounding a Mediterranean harbor facility. *Estuar Coast Shelf Sci* 130:209–221. doi:[10.1016/j.ecss.2013.02.017](https://doi.org/10.1016/j.ecss.2013.02.017)
- Mahmoudi E, Essid N, Beyrem H, Hedfi A, Boufahja F, Vitiello P, Aïssa P (2005) Effects of hydrocarbon contamination on a free-living marine nematode community: results from microcosm experiments. *Mar Pollut Bull* 50:1197–1204. doi:[10.1016/j.marpolbul.2005.04.018](https://doi.org/10.1016/j.marpolbul.2005.04.018)
- Majdi N, Traunsperger W (2015) Free-living nematodes in the freshwater food web: a review. *J Nematol* 47:28–44

- Moens T, Braeckman U, Derycke S, Fonseca G, Gallucci F, Gingold R et al (2013) Ecology of free-living marine nematodes. In: Schmidt-Rhaesa A (ed) Handbook of zoology. De Gruyter, Berlin, pp 109–152. doi:[10.1515/9783110274257.109](https://doi.org/10.1515/9783110274257.109)
- Mohanty B, Muduli PR, Behera AT, Mahapatro D, Barik SK, Nag SK et al (2016) Assessment of petroleum hydrocarbon in a tropical brackish water lagoon: Chilika, India. doi:[10.1080/02757540.2016.1177521](https://doi.org/10.1080/02757540.2016.1177521)
- Mohapatra A, Mohanty RK, Mohanty SK, Bhatta KS, Das NR (2007) Fisheries enhancement and biodiversity assessment of fish, prawn and mud crab in Chilika lagoon through hydrological intervention. *Wetlands Ecol Manage* 15:229–251. doi:[10.1007/s11273-006-9025-3](https://doi.org/10.1007/s11273-006-9025-3)
- Moreno M, Semprucci F, Vezzulli L, Balsamo M (2011) The use of nematodes in assessing ecological quality status in the Mediterranean coastal ecosystems. *Ecol Indic* 11:328–336. doi:[10.1016/j.ecolind.2010.05.011](https://doi.org/10.1016/j.ecolind.2010.05.011)
- Nalepa TF, Quigley MA, Ziegler RW (1988) Sampling efficiency of the Ponar grab in two different benthic environments. *J Great Lakes Res* 14:89–93
- Netto SA, Fonseca G (2017) Regime shifts in coastal lagoons: evidence from free-living marine nematodes. *PLoS ONE* 12(2):e0172366. doi:[10.1371/journal.pone.0172366](https://doi.org/10.1371/journal.pone.0172366)
- Panda US, Mohanty PK (2008) Monitoring and modeling of Chilika environment using remote sensing data. In: Sengupta M, Dalwani R (eds) Proceedings of Taal2007: the 12th world lake conference, Jaipur, India, pp 617–638
- Panigrahi S, Wikner J, Panigrahy RC, Satapathy KK, Acharya BC (2009) Variability of nutrients and phytoplankton biomass in a shallow brackish water ecosystem (Chilika lagoon, India). *Limnology* 10:73–85. doi:[10.1007/s12011-009-0262-z](https://doi.org/10.1007/s12011-009-0262-z)
- Pérez-García JA, Ruiz-Abierno A, Armenteros M (2015) Does morphology of host marine macroalgae drive the ecological structure of epiphytic meiofauna? *J Mar Biol Oceanogr* 4:1. doi:[10.4172/2324-8661.1000139](https://doi.org/10.4172/2324-8661.1000139)
- Pfannkuche O, Thiel H (1988) Sample Processing. In: Higgins RP, Thiel H (eds) Introduction to the study of Meiofauna. Smithsonian Institution Press, Washington DC, pp 134–145
- Platt HM, Warwick RM (1983) Free living marine nematodes, Part I, British Enoplids, Pictorial key to world genera and notes for the identification of British species. In: Kermack DM, Barnes RSK (eds) Synopses of the British Fauna, vol 28. Cambridge University Press, Cambridge, pp 1–307
- Platt HM, Warwick RM (1988) Free living marine nematodes, Part II, British Chromodorids, Pictorial key to world genera and notes for the identification of British species. In: Kermack DM, Barnes RSK (eds) Synopses of the British Fauna (new series), vol 38. Brill/Backhuys, Leiden, pp 1–502
- Schratzberger M, Ingels J (2017) Meiofauna matters: the role of meiofauna in benthic ecosystems. *J Exp Mar Biol Ecol*. doi:[10.1016/j.jembe.2017.01.007](https://doi.org/10.1016/j.jembe.2017.01.007)
- Seinhorst JW (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. *Nematologica* 4:67–69. doi:[10.1163/187529259X00381](https://doi.org/10.1163/187529259X00381)
- Semprucci F, Colantoni P, Baldelli G, Rocchi M, Balsoma M (2010) The distribution of meiofauna on back-reef sandy platforms in the Maldives (Indian Ocean). *Mar Ecol* 31:592–607. doi:[10.1111/j.1439-0485.2010.00383.x](https://doi.org/10.1111/j.1439-0485.2010.00383.x)
- Semprucci F, Colantoni P, Sbrocca C, Baldelli G, Rocchi M, Balsamo M (2011) Meiofauna in sandy back-reef platforms differently exposed to the monsoons in the Maldives (Indian Ocean). *J Mar Syst* 87:208–221. doi:[10.1016/j.jmarsys.2011.04.002](https://doi.org/10.1016/j.jmarsys.2011.04.002)
- Semprucci F, Balsoma M, Frontalini F (2014a) The nematode assemblage of a coastal lagoon (Lake Varano, southern Italy): ecology and biodiversity patterns. *Sci Mar* 78:579–588. <http://dx.doi.org/10.3989/scimar.04018.02A>
- Semprucci F, Colantoni P, Sbrocca C, Baldelli G, Balsamo M (2014b) Spatial patterns of distribution of meiofaunal and nematode assemblages in the Huvadhoo lagoon (Maldives, Indian Ocean). *J Mar Biol Assoc UK* 94:1377–1385. doi:[10.1017/S002531541400068X](https://doi.org/10.1017/S002531541400068X)
- Srichandan S, Kim JY, Bhadury P, Barik SK, Muduli PR, Samal RN, Pattnaik AK, Rastogi G (2015a) Spatiotemporal distribution and composition of phytoplankton assemblages in a coastal tropical lagoon: Chilika, India. *Environ Monit Assess* 187:47. doi:[10.1007/s10661-014-4212-9](https://doi.org/10.1007/s10661-014-4212-9)
- Srichandan S, Kim JY, Kumar A, Mishra DR, Bhadury P, Muduli PR, Pattnaik AK, Rastogi G (2015b) Interannual and cyclone-driven variability in phytoplankton communities of a tropical coastal lagoon. *Mar Pollut Bull* 101:39–52. doi:[10.1016/j.marpolbul.2015.11.030](https://doi.org/10.1016/j.marpolbul.2015.11.030)
- Strickland JDH, Parsons TR (1984) A practical handbook of seawater analysis. Bulletin (vol. 167), Fisheries Research Board of Canada, Queen's Printer, Ottawa
- Tahseen Q (2012) Nematodes in aquatic environments: adaptations and survival strategies. *Biodiver J* 3:13–40
- ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179. doi:[10.2307/1938672](https://doi.org/10.2307/1938672)
- ter Braak CJF, Smilauer P (2002) CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4.53). Micro-computer power, Ithaca, New York
- Turner RE, Qureshi N, Rabalais NN (1998) Fluctuating silicate: nitrate ratios and coastal plankton food webs. *Proc Natl Acad Sci USA* 95:13048–13051. doi:[10.1073/pnas.95.22.13048](https://doi.org/10.1073/pnas.95.22.13048)
- Ürkmez D, Brennan ML, Sezgin M, Bat L (2015) A brief look at the free-living nematoda of the oxic/anoxic interface with a new genus record (Trefusia) for the Black Sea. *Oceanol Hydrol Stud* 44:539–551. doi:[10.1515/ohs-2015-0051](https://doi.org/10.1515/ohs-2015-0051)
- Vanaverbeke J, Steyaert M, Soetaert K, Rousseau V, Gansbeke DV, Parent J, Vincx M (2004) Changes in structural and functional diversity of nematode community during spring phytoplankton bloom in the southern North Sea. *J Sea Res* 52:281–292. doi:[10.1016/j.seares.2004.02.004](https://doi.org/10.1016/j.seares.2004.02.004)
- Vanaverbeke J, Merckx B, Degraer S, Vincx M (2011) Sediment-related distribution patterns of nematodes and macrofauna: two sides of the benthic coin? *Mar Environ Res* 71:31–40. doi:[10.1016/j.marenvres.2010.09.006](https://doi.org/10.1016/j.marenvres.2010.09.006)
- Vanaverbeke J, Bezerra TN, Braeckman U, De Groot A, De Meester N, Deprez T et al (2015). NeMys: world database of free-living marine nematodes at <http://www.nemys.ugent.be/aphia.php?p=taxadetails&id=2132> added on 02.03.2015
- Vanreusel A, Fonseca G, Danovaro R, Da Silva MC, Esteves AM, Ferrero T et al (2010) The contribution of deep-sea

- macrohabitat heterogeneity to global nematode diversity. *Mar Ecol* 31:6–20. doi:[10.1111/j.1439-0485.2009.00352.x](https://doi.org/10.1111/j.1439-0485.2009.00352.x)
- Warwick RM, Platt HM, Somerfield PJD (1998) Free-living marine nematodes, Part III, Monhysterids, Pictorial key to world genera and notes for the identification of British species. In: Kermack DM, Barnes RSK (eds) *Synopses of the British Fauna (new series)*. Field Studies Council, Shrewsbury, pp 1–296
- Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. *Arkiv für Zoologi* 4:439–484