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Deep-sea nematode assemblages from a commercially important polymetallic nodule area in the Central Indian Ocean Basin

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Abstract

The Central Indian Ocean Basin (CIOB) is an important area for prospective mining for polymetallic nodules. However, little is known about the biodiversity or community structure of abyssal benthic assemblages in the area. The aim of this study was to investigate nematode assemblages inhabiting nodule fields in the CIOB in terms of species composition, diversity, density, biomass, size spectra and sex ratio. Samples were collected by box corer from a depth of 5000–5100 m during the 39th cruise of RV *Akademik Boris Petrov* in 2009. In total, 1066 individuals were examined from 4 stations and 16 samples. The total average density of nematodes recorded in the CIOB was considerably lower than reported from other deep-sea regions (27.17 ± 2.7 inds/10 cm²). Nematode diversity was comparable with that of other deep-sea regions and the composition of the dominant taxa was typical for oceanic basins. A total of 284 morphotypes belonging to 113 genera and 30 families were identified. Chromadoridae (29.6%), Xyalidae (19.3%), Oxystominidae (6.6%) and Desmoscolecidae (5.0%) were the dominant families. Among the genera, *Acantholaimus* (23.2%), *Halalaimus* (5.7%), *Desmoscolex* (4.8%), *Theristus* (3.5%) and *Daptonema* (3.4%) were the most numerous. The majority of specimens had a body length in the range of 1000–1500 µm, which is also in accordance with other deep-sea studies. Females were three times more abundant than males at all CIOB stations. Average total nematode biomass (52.39 ± 10.0 mg/m²) was comparable with macrofauna biomass from the same area.

Key words: Central Indian Ocean Basin, deep sea, diversity, nematode assemblage, polymetallic nodule

Introduction

Nematodes are usually the dominant meiobenthic metazoans in the deep sea, and their numerical dominance increases with water depth with up to more than 90% in some cases (Heip et al. 1985; Vincx et al. 1994). Despite their dominance, the distribution and composition of deep-sea nematode assemblages is still scarcely studied (particularly at species level), and the Indian Ocean is one of the least-studied regions. Nevertheless, the area known as the Indian Ocean Nodule Field could be of high commercial importance because of its polymetallic nodule deposits, with an average abundance of about 4.5 kg/m² (Prasad 2007) in a 150,000 km² area of the Central Indian Ocean Basin (CIOB). Commercial deep-sea mining for polymetallic nodules has been

predicted to have a significant impact over huge areas of the seabed, owing to the widespread distribution of the nodules (Morgan 2000). Ideally, prior to the commencement of commercial nodule mining, environmental studies should be conducted to evaluate potential impacts to the biological assemblages inhabiting these areas. Although the essential first step is to determine any effects of mining on biological diversity, there are only a few studies dealing with the nematofauna of nodule fields. In fact, nematode assemblages from only two nodule-bearing regions, both in the Pacific Ocean, have been studied to date. One of these regions is the Clarion-Clipperton Nodule Province (CCNP, tropical NE Pacific) (Snider et al. 1984; Spiess et al. 1987; Renaud-Mornant & Gourbault 1990; Radziejewska et al. 2001; Lamshead et al. 2003; Miljutina et al.

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2010), for which a review of the published literature along with general conclusions has previously been undertaken (Miljutina et al. 2010). The other studied nodule-bearing region is in the Peru Basin, tropical SE Pacific (Bussau 1993; Thiel et al. 1993; Bussau et al. 1995). The majority of data regarding the ecology and taxonomy of nematode assemblages inhabiting the nodule fields in the Peru Basin were presented in the detailed work by Bussau (1993), including descriptions of many new species. Of particular importance was the discovery that the nematode assemblage inhabiting the surface and crevices of nodules differed from that in the surrounding soft sediments with regard to the composition of dominant taxa (Bussau 1993; Thiel et al. 1993). This is the first study to examine the Nematoda in the CIOB nodule field, although macrofaunal communities have been investigated (Ingole et al. 2005; Pavithran et al. 2009). The present study investigated the composition and distribution of the nematode assemblages inhabiting nodule fields in the CIOB and is the first to report species/genus level data including their biomass, sex ratio and body length for free-living nematodes from the Central Indian Ocean Basin. It can, therefore, be used as a reference data set for future environmental baseline studies in the Central Indian Ocean.

Material and methods

Study area

The CIOB is an abyssal area bounded by ridge systems on all but the northern side, where it is open towards the Indian peninsula. To the northwest it is bounded by the Chagos–Laccadive Ridge. The surface water primary production recorded in the CIOB ranges between 9.06 and 103.4 mg C/m²/day, which is considerably lower than that reported for other oceans (Matondkar et al. 2005). Sedimentary organic carbon content also appears to be lower in the Central Indian Ocean (0.07–0.41%) than in other deep-sea areas and has been attributed to low sediment accumulation rates (Pattan et al. 2005). Water temperature decreases from about 32°C at the surface to –2°C below 4500 m depth, and salinity profiles show a superficial thin layer of high salinity in the bottom water layer (34.72 PSU at 3000 m depth; Ingole et al. 2005). Nodules are found in an area of the Central Indian Ocean that extends from 10°S to 16°30'S and 72°E to 80°E (Mukhopadhyay et al. 2002; Prasad 2007). This area is identified as the Indian Ocean Nodule field, which has an average nodule content of 4.5 kg/m². The study area lies between 12°20'–13°00' S and 74°18'–75°30'E over a depth range of 5000–5300 m (Table I; Figure 1).

Sample collection and laboratory analysis

Samples were collected during the IVBC 39 cruise (RV *Akademik Boris Petrov*, cruise No. 39) in September–October 2009. Sampling was performed at four stations (20A, 18F, 18D and 19D) using an USNEL box corer (50 cm × 50 cm) with a sampling area of 0.25 m². Each station represented one deployment of the box corer. Acrylic cores of 50 cm length and 5.7 cm diameter (Govaere & Thielemans 1979) were used to take subsamples from the sediment recovered by the box corer. Four sediment subsamples were taken for nematodes from each station/box core (in total, 16 subsamples). Subsamples consisted exclusively of soft sediment without any nodules. An additional subsample was taken from each station to determine sediment parameters (organic carbon, grain size, and chlorophyll *a*). Sediment grain size composition was determined by the dry-sieving method (Buchanan 1984). Initially, the silt–clay fraction was separated from the sediment samples and subjected to the pipette method based on Stokes' Law (Buchanan 1984). The remaining sand fraction was dried in an oven at 100°C for 24 h and then a known quantity of material was shaken through a series of stacked sieves (2000 to 20 µm) with an automatic shaker for 10 min. Chlorophyll *a* was estimated using an acetone extraction method (Holm-Hansen 1978). Organic carbon content was analysed by the wet oxidation method of El Wakeel & Riley (1957). Nematode assemblages were studied in the upper 10 cm layer of sediment. This was further subdivided into a superficial upper 0.5 cm thick layer, followed by 1 cm thick slices down to a depth of 5.5 cm, and then the remaining 5.5–10 cm layer of sediment was treated as a single slice. All material was preserved in 5% formaldehyde with Rose Bengal. In the laboratory all the material was sieved through a 32 µm mesh. The material was carefully examined under a stereo-microscope and all nematodes were counted, picked and permanently mounted on glass slides for taxonomic identification. They were identified to morphotype level with the aid of the pictorial keys of Platt & Warwick (1983, 1988), Warwick et al. (1998) and with reference to the NeMys database (Deprez et al. 2005). Each morphotype was sketched and measured using a camera lucida to identify it to the species level. Gender (female, male or juvenile) was determined for each individual. Total length, excluding tail, and maximum body diameter were measured for each specimen. In total, 1066 nematode individuals were examined. Nematode wet biomass was estimated by modifying Andrassy's formula (Andrassy 1956). It has been determined that Andrassy's formula is not suitable for deep-sea nematodes because many of them have long filiform

Table I. Details of the Central Indian Ocean Basin sampling stations, with number of nematode specimens examined from each core.

Date	Latitude, S	Longitude, E	Depth, m	Station	Number of examined nematodes in each of 4 cores (1, 2, 3, 4)
18.9.2009	12°59.381'	75°29.918'	5148	IVBC 19D	52, 96, 60, 61
21.9.2009	12°57.679'	74°28.520'	5041	IVBC 18D	55, 74, 67, 63
22.9.2009	12°58.842'	74°29.693'	5164	IVBC 20A	78, 54, 61, 38
24.9.2009	12°59.132'	74°29.77'	5065	IVBC 18F	86, 70, 64, 87

tails and very small internal volume. We therefore modified the formula by using the measurements of the body length without the tail and the average length of the conical part of the tail (thus excluding the filiform part) of 20 chosen individuals belonging to dominant families. The modified formula became:

$$V = L'W^2(a + 1)/1,600,000$$

where

V = individual body volume, nl;

L' = body length without tail, μm ;

a = ratio 'length of conical part of tail/body length without tail'; and

W = maximum diameter, μm .

The average value of a was 0.022. The individual volume (nl) was then converted to the individual dry biomass (in μg) using the specific factor for gravity of 1.13 (Wieser 1960). Total biomass (mg/m^2) was calculated by summarizing individual biomasses of the nematodes in the sample and then interpolating this value for 1 m^2 .

Statistical analysis

PRIMER v.6 (Clarke & Gorley 2006) software and the PAST program (Hammer et al. 2001) were used for statistical analysis. The dissimilarity percentage program (SIMPER; Clarke 1993) was used to identify the species making the greatest contribution to differences. Diversity indices at family, genus, and species level were calculated using Margalef's index for species richness (d) (Margalef 1968), \log_2 Shannon–Wiener Index (H') for species diversity (Shannon & Weaver 1963) and Pielou's index (J') for species evenness (Pielou 1966). Total species richness was calculated by constructing a species rarefaction curve and a species dominance plot was constructed to determine which species were dominant throughout the study area. Two-way analysis of similarity (ANOSIM) was applied using standardized (percentage abundance) data to establish significant differences in relative abundance and composition between stations and subsamples at family, genus and species level. The list of valid genera found in the present study was compared with those from the two other studied nodule-bearing abyssal areas, the Clarion–Clipperton Fracture Zone, NE Pacific (Miljutina et al. 2010) and the Peru Basin, SE Pacific (Bussau 1993), the latter data set extracted from Miljutina et al. (2010). The CIOB genera list was also

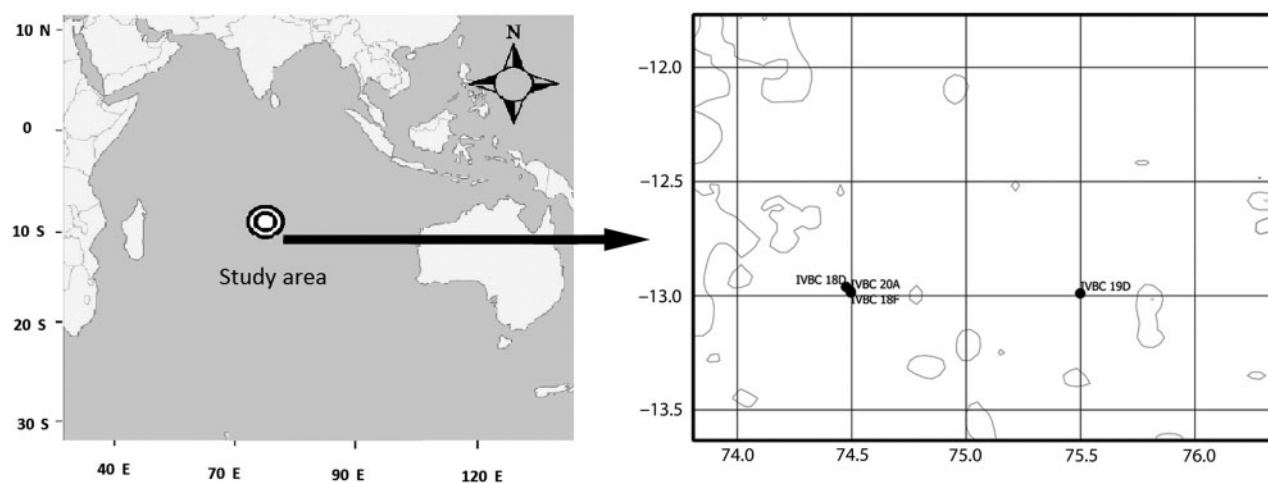


Figure 1. Map of the Central Indian Ocean Basin with details of the sampling locations.

Table II. Sediment parameters measured at each sampling station.

Station	Clay (%)	Silt (%)	Sand (%)	Chl- <i>a</i> ($\mu\text{g/g}$)	OC (organic carbon) (%)
IVBC 19D	34.38	54.56	11.06	0.12	0.81
IVBC 18D	32.77	56.21	11.02	0.17	0.72
IVBC 20A	29.08	55.32	15.60	0.03	0.02
IVBC 18F	25.38	59.27	15.35	0.18	0.70

compared with the list of valid abyssal nematode genera compiled by Miljutina et al. (2010).

Non-parametric Kruskal–Wallis and Mann–Whitney tests were used as global significance tests for differences in univariate parameters using the PAST program (Hammer et al. 2001). The linear correlation between environmental parameters and total density was also tested in PAST.

Results

Sediment parameters

Sediment granulometry was variable across the stations. Silt was dominant throughout the study area, with a range of 54.56–59.27%, followed by clay (25.38–34.38%). Sand was the minor sediment component ranging from 11.02% to 15.6% of total sediment weight (Table II). Values of sedimentary chlorophyll *a* varied greatly; the highest value, 0.18 $\mu\text{g/g}$, was recorded at station 18F and the lowest, 0.03 $\mu\text{g/g}$, recorded at station 20A (Table II). Sedimentary organic carbon (%) also varied and ranged on average from 0.02% (station 20A) to 0.81% (station 19D). In general, the content of

organic carbon was lower at stations 20A and 18F in comparison with stations 18D and 19D.

Total nematode density and biomass

The total average nematode density in the top 10-cm thick sediment layer was 23.99 ± 2.7 inds/10 cm^2 (Figure 2). Average density of nematodes was highest at station 18F (26.66 ± 2.1 inds/10 cm^2) followed by 20A (24.99 ± 3.6 inds/10 cm^2), 18D (23.23 ± 1.3 inds/10 cm^2) and 19D (21.07 ± 2.9 inds/10 cm^2). The Kruskal–Wallis test indicated no significant differences between the nematode densities from different stations and no significant correlations were found between total density and sediment parameters (maximum correlation was 0.396; $p > 0.128$). Averaged across the four stations, nematode biomass was 52.39 ± 10.0 mg/m^2 . It was highest at stations 18D (72.48 mg/m^2) followed by 18F (56.79 mg/m^2) in comparison to 19D (50.79 mg/m^2) and 20A (29.49 mg/m^2) (Figure 2). The Mann–Whitney tests indicated significant differences in nematode biomass between all four stations (maximum $p = 0.028$), but no significant correlation was observed between biomass and sediment parameters ($p > 0.05$).

Composition of the nematode community

Two-way ANOSIM found no significant differences in the composition of nematode assemblages between the stations either at the species, genus or family level. Chromadoridae (29.7%), Xyalidae (19.4%), Oncholaimidae (11.2%), and Desmoscolecidae (5.0%) were the most dominant families, while at the genus level, *Acantholaimus* (22.3%), *Halalaimus* (5.8%), *Desmoscolex* (4.4%), *Daptonema* (3.8%) and *Theristus* (3.6%) were dominant. The morphotypes *Acantholaimus* sp. 1 (4.8%) and *Acantholaimus*

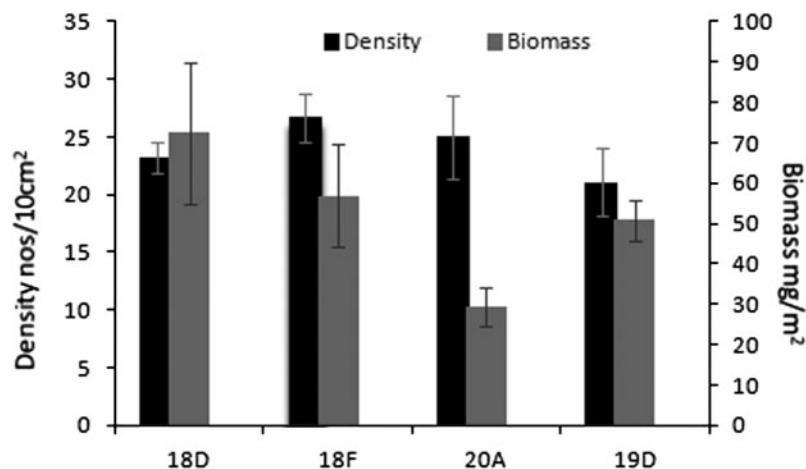


Figure 2. Average biomass and density of nematodes. Error bars indicate standard deviation 95% confidence interval.

sp. 2 (4.3%) were co-dominant, followed by *Halalaimus* sp. 1 (2.5%), although these percentages represent a very low level of dominance. The top 20 most abundant families, genera and species are listed in Table III.

Diversity indices and estimation of species number

A total of 284 morphotypes belonging to 113 genera and 30 families were identified. Detailed information on families, genera and number of species found in each genus are given as supplementary material (Table SI). The most species rich genus was *Acantholaimus* (33), followed by *Halalaimus* (9), *Sabatieria* (8) and *Daptonema* (8). Among families, Xyalidae was represented by the most genera (16), followed by Chromadoridae (13) and Cyatholaimidae (12). Some of the specimens of *Acantholaimus* sp. and *Theristus* sp. are identified up to valid species level. Among them *Acantholaimus akvavitus* Gerlach, Schrage & Freeman, 1979 (1.8% abundance), *A. barbatus* Miljutina & Miljutin, 2012 (1.3% abundance), *A. iubilus* Gerlach, Schrage & Freeman, 1979 (1.31% abundance) and *Theristus discolensis* Bussau, 1993 (0.94% abundance) were abundant. The list of valid species, their average density and percent abundance is given as supplementary material (Table SII). The average and standard deviation values of diversity indices at family, genus and species level are given in Table IV. Most diversity indices of the nematode assemblages from the different stations at family, genus and species levels varied insignificantly (Kruskal–Wallis test: $p > 0.05$).

The species rarefaction curve did not reach an asymptote (Figure 3).

Size spectra and sex ratios

Females were most abundant (66.3%) averaged across all samples, while the proportions of males and juveniles were 22.4% and 11.3%, respectively. Averaged across all specimens, 50.1% had a body length in the range of 1000–1500 μm ; 21% had a body length of 500–1000 μm (Figure 4). Excluding juveniles, the trend was similar with 52.7% of adults being 1000–1500 μm in length and 17.9% being 500–1000 μm in length. About 11.8% of specimens or 12.0% of adults had body lengths in the range of 1500–2000 μm . Similarly, 10.7% of specimens or 11.7% of adults were 2500–3000 μm in length. Nematodes of other body lengths were very rare. The average lengths of adults at stations 18D and 19D were 1597.9 μm and 1489.3 μm , respectively; at stations 20A and 18F, it was 1271.6 μm and 1394.6 μm , respectively. A student *t*-test and a Mann–Whitney test revealed a significant difference in the average body lengths between the four stations ($p = 0.04$).

Discussion

Sediment parameters

The sediment granulometry of the Central Indian Ocean, as measured in the present study, in general showed less variation than in previously published data. In the present study, silt was dominant

Table III. List of the 20 most abundant families, genera and species recorded across the study area and their average percentage abundance.

Abundant families	%	Abundant genera	%	Abundant species	%
Chromadoridae	29.7	<i>Acantholaimus</i>	22.3	<i>Acantholaimus</i> sp. 1	4.8
Xyalidae	19.4	<i>Halalaimus</i>	5.8	<i>Acantholaimus</i> sp. 2	4.3
Oncholaimidae	11.2	<i>Desmoscolex</i>	4.4	<i>Halalaimus</i> sp. 1	2.5
Desmoscolecidae	5.0	<i>Daptonema</i>	3.8	Xyalidae Genus 2 sp. 1	2.3
Desmodoridae	4.9	<i>Theristus</i>	3.6	<i>Acantholaimus akvavitus</i> Gerlach, Schrage & Riemann, 1979	1.8
Comesomatidae	4.1	<i>Marisalbinema</i>	3.3	<i>Marisalbinema</i> sp. 2	1.7
Diplopeltidae	4.1	<i>Diplopeltula</i>	3.1	<i>Syringolaimus</i> sp. 3	1.4
Ironidae	3.0	<i>Syringolaimus</i>	3.0	<i>Acantholaimus barbatus</i> Miljutina & Miljutin, 2012	1.3
Monhysteridae	2.6	<i>Viscosia</i>	2.5	<i>Acantholaimus iubilus</i> Gerlach, Schrage & Riemann, 1979	1.3
Cyatholaimidae	2.3	<i>Desmodora</i>	2.3	<i>Acantholaimus</i> sp. 7	1.3
Anticomidae	2.2	<i>Thalassomonhystera</i>	2.3	<i>Daptonema</i> sp. 3	1.3
Enchelidiidae	1.6	Xyalidae genus 2	2.3	<i>Desmoscolex</i> sp. 4	1.2
Leptolaimidae	1.6	<i>Chromadorita</i>	2.1	<i>Theristus</i> sp. 2	1.2
Ceramonematidae	1.0	<i>Sabatieria</i>	1.9	<i>Acantholaimus</i> sp. 3	1.1
Microlaimidae	0.8	<i>Chromadora</i>	1.8	<i>Syringolaimus</i> sp. 2	1.1
Axonolaimidae	0.5	<i>Manganonema</i>	1.8	<i>Thalassomonhystera</i> sp. 2	1.1
Linhomoeidae	0.5	<i>Mesacanthion</i>	1.7	<i>Chromadorita</i> sp. 2	1.0
Aegialoalaimidae	0.4	<i>Actinonema</i>	1.6	<i>Desmoscolex</i> sp. 2	1.0
Leptosomatidae	0.4	<i>Anticoma</i>	1.5	<i>Diplopeltula</i> sp. 3	1.0
Benthimermithidae	0.3	<i>Oncholaimus</i>	1.2	<i>Viscosia</i> sp.1	1.0

Table IV. Mean and standard deviation for diversity indices of the nematode communities at species, genus and family level. Margalef's index for species richness (d), Pielou's index for species evenness (J'), ES (51) = estimated total number of species, \log_2 Shannon–Wiener Index for species diversity (H').

Index	Species level	Genus level	Family level
d	10.1 \pm 2.3	6.0 \pm 1.8	3.1 \pm 0.8
J'	0.954 \pm 0.017	0.869 \pm 0.047	0.791 \pm 0.072
ES (51)	35.3 \pm 4.5	22.4 \pm 4.7	12.7 \pm 2.7
H'	5.1 \pm 0.4	4.0 \pm 0.5	3.0 \pm 0.5

followed by clay and sand, while in the same study area Khadge (1992) observed an average sand fraction of 16% with average clay and silt fractions of 52% and 32%, respectively. Similar results were observed by Khadge in (1998), with silt, clay and sand fractions of 57%, 41% and 2%, respectively.

In fact, no significant correlations were found between nematode assemblage parameters and the abiotic factors analysed. Nevertheless, significant differences in nematode density and body length were found between different stations. Possibly, these distinctions were caused by other factors which result in the segregation of the sediment surface into too many microhabitats. Low primary production is attributed to low sedimentary organic carbon in CIOB. The surface water primary production (PP) values in the CIOB ranged between 9.06 and 103.4 mgC/m²/day, which is lower than in other oceans (for review, see Matondkar et al. 2005; Pavithran et al. 2009). The organic carbon values recorded in the present study (0.02–0.81%) are therefore in agreement with previous data. Pavithran et al. (2009) reported organic carbon values of 0.07–0.41%, while Khadge (1992) reported 0.19–0.8% and Pattan et al. (2005) reported 0.1–0.6%.

Nematode density and biomass

The total average density of nematodes in this study area was 27.17 inds/10 cm², which corresponds well with previous studies in the CIOB (Ingole et al. 2000, 2005). Moreover, Ingole et al. also used a box corer for sampling (12–53 inds/10 cm²). However, these values are much lower than the average densities observed by Muthumbi et al. (2004) in the Western Indian Ocean off the Kenyan coast (867 inds/10 cm² at coastal stations, 424.5 inds/10 cm² at shelf stations and 419 inds/10 cm² at depths greater than 2000 m). Nematode abundance in the CIOB was also much lower than recorded in other deep-sea tropical and temperate regions (Table V). It is possible that the low densities recorded could be due to the lower primary productivity in the surface waters of the CIOB (Matondkar et al. 2005), as discussed above. A decline in benthic abundance has been correlated with distance from productive coastal waters and the rate and seasonal pattern of nutrient inputs from overlying surface water production (Falkowski et al. 1998; Rex et al. 2000, 2006). Another possible reason may be an effect of using a box corer. Ingole et al. (2001, 2005) highlighted the limitations of box corers in deep-sea benthic studies and Bett et al. (1994) and Shirayama & Fukushima (1995) have shown that meiobenthic density estimates from box corer samples can be half that of multi-corer samples. However, even if we were to double the total densities recorded here in order to minimize this potential sampling bias, the density values would still be very low. The abiotic parameters studied here were not statistically significant for nematode density and this raises the question of appropriate sampling pattern. Owing to the relatively small number of samples available, we were not able to draw any conclusions from the effect of the measured abiotic parameters on the nematofauna.

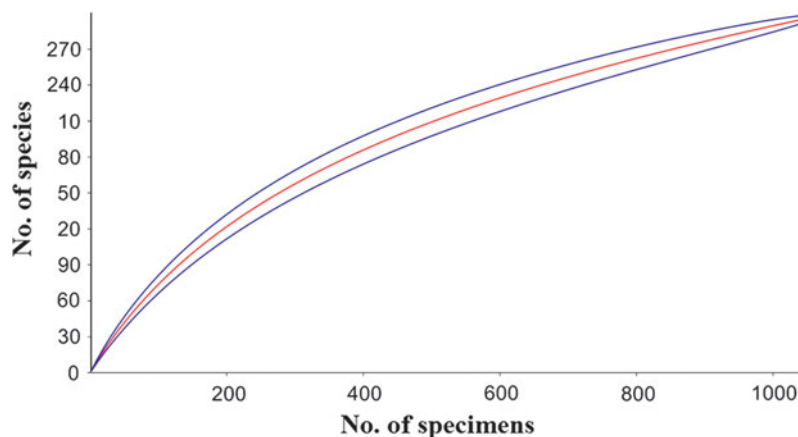


Figure 3. Species rarefaction plot.

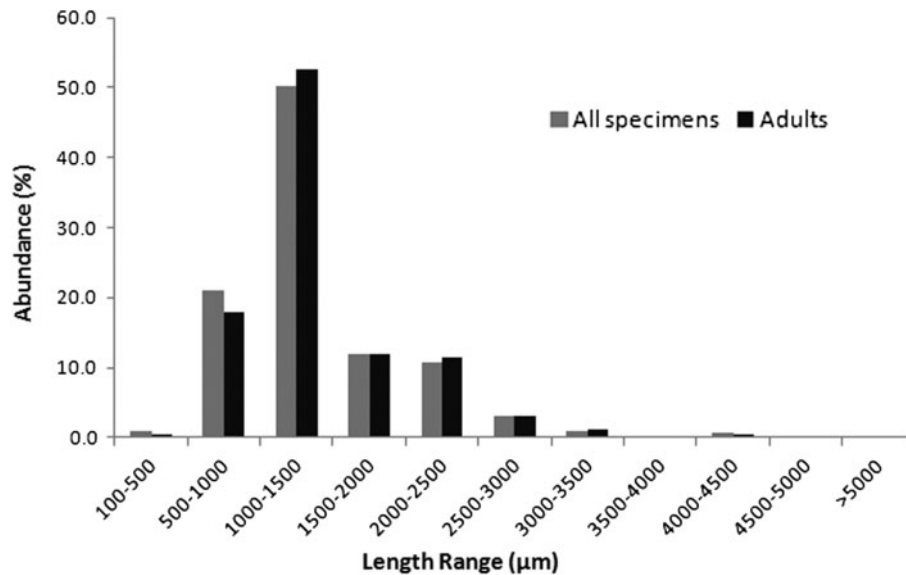


Figure 4. Plot of nematode percentage abundance within size classes. Grey columns, all specimens; black columns, adult specimens only.

In the present study, average nematode biomass ($52.39 \pm 10.0 \text{ mg/m}^2$) was higher than or comparable to other regions (e.g. $8\text{--}54 \text{ mg/m}^2$ in the Porcupine Abyssal plain (Vanreusel et al. 1995); 7.8 mg/m^2 in the Central Equatorial Pacific (Brown et al. 2001); and 57.2 mg/m^2 in the Peru Basin (Bussau 1993). Unfortunately, data on deep-sea nematode biomass are still very scarce. The nematode biomass values recorded in the CIOB in this study were, however, comparable with known macrofauna biomass ($4.6\text{--}69.3 \text{ mg/m}^2$) from the same area (Ingole et al. 2001). This highlights the

importance of nematode assemblages in the trophic structure of the CIOB.

Composition of nematode assemblages

The composition of the dominant nematode genera and families in the CIOB was in general similar to that recorded in two other nodule fields, the Clarion-Clipperton Fracture Zone in the tropical NE Pacific (Miljutina et al. 2010) and the Peru Basin in the tropical SE Pacific (Bussau 1993). The dominant families in the present study area, like

Table V. Comparison of nematode abundances previously published for various deep-sea oceanic locations.

Location	Depth (m)	Abundance (no. inds/10 cm ²)	Reference	Sampling gear
Atlantic Ocean				
Porcupine Seabight, NE Atlantic	4167–4850	345 ± 103	Pfannkuche (1985)	Multiple corer
Porcupine Abyssal Plain, NE Atlantic	4843–4850	118 ± 35	Lambshead et al. (1995)	Multiple corer
BIOTRANS, NE Atlantic	4330–4561	117 ± 63	Soltwedel et al. (1996)	Box corer and multiple corer
Pacific Ocean				
Western Pacific	5580–5820	145 ± 108	Shirayama (1984)	Box corer
Clarion Clipperton Fracture Zone, Eastern Central Pacific	4905–5140	35 ± 15	Renaud-Mornant & Gourbault (1990)	Box corer
Peru Basin, Eastern South Pacific	4100–4200	133	Bussau (1993)	Multiple corer
Peru Basin, Eastern South Pacific	4100–4200	121	Bussau et al. (1995)	Multiple corer
HOT Station, Central Pacific	4871–4884	40 ± 9	Brown et al. (2001)	Multiple corer
JGOFS Eq.Pac.transsect 9°N, Equatorial Pacific	4986–4994	45 ± 38	Brown et al. (2001)	Box corer
NE Pacific Basin, CCNP, 14°N, NN site	4983–5042	137 ± 28	Miljutina et al. (2010)	Multiple corer
NE Pacific Basin, CCNP, 14°N, NB site	4947–5000	69 ± 19	Miljutina et al. (2010)	Multiple corer
Indian Ocean				
Central Indian Ocean Basin	5300–5330	52 ± 27	Ingole et al. (2000)	Box corer
South West Indian Ocean	2007–2053	251–406	Muthumbi et al. (2004)	Box corer
Central Indian Ocean Basin	5200–5300	12.00 ± 5.2	Ingole et al. (2005)	Box corer
Central Indian Ocean Basin	5000–5200	27.17 ± 2.7	Present study	Box corer

Chromadoridae, Xyalidae and Desmoscolecidae, were also found to be dominant in the two above mentioned nodule fields.

It can be postulated that the sampling area is inhabited by a single, homogeneously spread, nematode assemblage. It is known that the nematofauna of nodule fields is the same as in other abyssal regions, with nematode genera exhibiting a relatively uniform distribution across different deep-sea regions (Thistle & Sherman 1985; Vanreusel et al. 2010). Yet, the nematofauna of two neighbouring nodule areas can be very different. For instance, Radziejewska et al. (2001) found *Terschellingia*, *Desmoscolex* and *Pareudesmoscolex* to be dominant in the eastern part of the Clarion–Clipperton Nodule Province (CCNP), whereas in the central part of the CCNP, Miljutina et al. (2010) reported *Thalassomonhystera*, *Theristus* and *Acantholaimus* as the dominant genera. Nematofaunal assemblages may also vary over decadal scales. Thus, *Syringolaimus* and *Molgo-laimus* were the most abundant genera at one CCNP site in 1986 (Renaud-Mornant & Gourbault 1990), but were replaced by *Thalassomonhystera*, *Theristus*, and *Acantholaimus* in 2004 (Miljutina et al. 2010). This may be explained by variation in geological activity across the CCNP, which could have a knock-on effect on the benthic community structure (Miljutina et al. 2010). The composition of the dominant genera in the CIOB also corresponds well with many other deep-sea studies (see e.g. Dinert & Vivier 1979; Tietjen 1984; Soetaert & Heip 1995; Gambi et al. 2003; Muthumbi et al. 2004; Vanreusel et al. 2010; Hasemann & Soltwedel 2011) and can hence be considered typical for vast deep-sea regions. Additionally, a two-way ANOSIM showed that there were no significant differences in the composition of nematode assemblages from the different stations.

Diversity

In the present study, most nematode assemblage diversity values were not significantly different (Kruskal–Wallis test: $p > 0.05$). However, the species rarefaction plot failed to reach an asymptote, indicating that more samples would be required to allow a complete understanding of the area. Diversity indices (species richness, evenness, diversity) indicated that nematode assemblages in the CIOB were comparable with those in other deep-sea regions (for review see Table VI). In comparison to the present study, Bussau (1993) examined more nematode individuals and identified more species morphotypes, but recorded a comparable number of families and fewer genera from the Peru Basin (1066 CIOB vs. 2623 Peru individuals, 284 vs. 324

Table VI. Comparison of species abundance, diversity, evenness and ES (51) published for nematode assemblages from various deep sea locations. Abbreviation: n.a., information is not available.

Location	Depth (m)	Total number of examined individuals	No. of species found	Diversity (H')	Evenness (J')	ES (51)	Reference
Venezuela Basin	3858	n.a.	53	3.4	0.93	27.2 ± 2.0	Tietjen (1984)
Venezuela Basin	3517	n.a.	85	4.0	0.95	32.1 ± 1.0	Tietjen (1984)
Venezuela Basin	5054	1004	75	3.6	0.85	31.8 ± 2.2	Tietjen (1984)
NE Atlantic, Norwegian deep-sea	3062	n.a.	93	3.8–5.0	0.85–0.94	n.a.	Jensen (1988)
Hatteras Plain	5411	507	116	4.1	0.87	30.0 ± 1.1	Tietjen (1989)
Puerto Rico Trench	7460	n.a.	82	3.6	0.87	25.4 ± 1.0	Tietjen (1989)
SE Pacific, Peru Basin, nodule area	4100–4201	2623	324	n.a.	n.a.	n.a.	Bussau (1993)
NE Atlantic, Porcupine Plain (1991)	4850	1428	156	n.a.	n.a.	28.8	Santos et al. (1994)
Central Pacific Basin and NE Pacific Basin (CCNP)	4301–4994	2059	200	n.a.	n.a.	28–34	Lambhead et al. (2003)
Atacama Trench	7800	1048	37	2.7	0.81	18.4 ± 0.2	Gambi et al. (2003)
Arctic Ocean, Amerasian Basin	1000–3890	≈400	n.a.	n.a.	n.a.	n.a.	Renaud et al. (2006)
NE Pacific Basin	4877–5046	2174	325	4.3–5.9	0.85–0.96	27–41	Miljutina et al. (2010)
Central Indian Ocean Basin	5000–5200	1066	285	5.1 ± 0.4	0.95 ± 0.0	35.3 ± 4.5	Present study

morphotypes, 113 vs. 66 genera and 30 vs. 35 families). Similarly, Miljutina et al. (2010) distinguished 325 species morphotypes (from 2174 individuals) belonging to 33 families and 96 genera from the NE Pacific Basin. From the Atacama slope and trench of the South Pacific Ocean, however, Gambi et al. (2003) noted fewer genera (95) but a similar number of families (31) with fewer individuals (1048) and distinguished fewer species (119). In this CIOB study, the most species-rich genera were *Acantholaimus*, *Desmoscolex* and *Halalaimus*, which corresponds well with other studies on deep-sea nematode assemblages (Bussau 1993; Lamshead et al. 2003; Mesel et al. 2006; Miljutina et al. 2010).

Size spectra and sex ratios

The majority of specimens (53%) had a body length in the range of 1000–1500 µm, which is similar to that found in the Atacama Trench by Gambi et al. (2003), who observed that 50–70% of nematodes were < 1.5 mm in length. Bussau (1993) also reported that 51% of nematodes were in the length range of 501–1500 µm in the Peru Basin. The nematodes from the present study, however, differ in having, on average, a greater body biomass than the nematodes from the abyss (Udalov et al. 2005). A possible explanation for this could be the low abundance of juveniles, about 11%, in the study area, compared with 53–78% in the Atacama Trench (Gambi et al. 2003) and 46% in the abyss of the Clarion–Clipperton Fracture Zone (Miljutina et al. 2010).

Females were three times more abundant than males at all CIOB stations. This is in contrast to the Atacama Trench, where males were five times more abundant than females (Gambi et al. 2003), while in the CCFZ females also dominated (Miljutina et al. 2010). Such a high proportion of females may be a strategy to minimize the energetic investment required for reproduction.

Conclusion

The composition and diversity of nematode genera from the CIOB generally corresponds well with the nematofauna from other deep-sea regions. The CIOB is inhabited by cosmopolitan nematode genera like *Acantholaimus*, *Halalaimus* and *Desmoscolex*. The density of nematodes was considerably lower than reported for other oceans; this could be explained by the low level of primary productivity in surface waters, although the use of a box corer for sampling may be a contributory factor. Nevertheless, the total nematode biomass was comparable with the biomass of macrobenthos in this area. The nematode

diversity was comparable with that of other deep-sea regions. Previous studies conducted in the Central Indian Ocean Basin focused on the macro- and meiofauna groups (major taxa level). This is the first study that has contributed the much needed information regarding density, diversity, sex ratio, size and biomass of nematofauna from the unexplored Central Indian Ocean. Thus, the present study can serve as a reference for future investigations of nematofauna in this region.

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Supplementary material

Supplementary material for this article is available via the Supplemental tab of the article's online page at <http://dx.doi.org/10.1080/17451000.2013.866251>

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