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Nematode abundance at the oxygen minimum zone in the Arabian Sea

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Abstract

This paper supports the hypothesis that low oxygen does not influence deep-sea nematode abundance by investigating an oxygen minimum zone (OMZ) on the Oman slope in the Arabian Sea. Correlation with a number of environmental variables indicated that food quality (measured as the hydrogen index) rather than oxygen was the major predictor of nematode abundance. Nematode abundance was also positively correlated with abundance of total macrofauna, annelids, spionid polychaetes and macrofaunal tube builders. Comparison with published data showed Arabian Sea nematode abundance to be similar to that of the Porcupine Seabight and Bay of Biscay regions of the northeast Atlantic, which also receive significant quantities of phytodetritus but have no OMZ. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

Nematodes are the most abundant metazoan taxa in deep-sea sediments, becoming proportionately more important with increased depth (Carmen et al., 1987). Metazoan meiofauna tend to be more tolerant than macrofauna to anoxia (Giere, 1993), and nematodes are more tolerant than other meiofaunal taxa (Giere, 1993; Moodley

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Table 1
A summary of the characteristics of the four sites used in the analysis. Pearson correlations of the variables with nematode abundance and $\log_{10}$ nematode abundance are also shown. Adapted from Levin et al. (2000) and Gooday et al. (2000)

Description	OMZ (centre)	OMZ (inside)	OMZ (boundary)	Deep water (outside OMZ)	Pearson correlation with Nematode abundance	
					Un-transformed	Log_{10} transformed
Station	12695	12685	12725	12687		
Location (latitude & longitude)	19°22′N 58°16′E	19°19′N 58°16′E	19°14′N 58°31′E	19°00′N 59°00′E		
Mean nematode abundance (ind. 10 cm^{-2})	1700	2495	860	494		
Water depth (m)	400	700	1250	3400	−76.9	−88.3
Bottom water oxygen ($ml\,l^{-1}$)	0.13	0.16	0.52	2.99	−0.74	−0.85
% TOC {0–0.5 cm}	4.99	4.03	2.67	2.72	72.8	78.3
C : N {0–0.5 cm}	8.52	9.04	7.82	9.42	7.6	−10.7
Surface pigment {0–0.5 cm} ($\mu g\,g^{-1}$)	770	242	68	185	36.9	45.1
Hydrogen index {0–0.5 cm} (mg hydrocarbon/g TOC)	490	517	423	366	96.4	99.8
Sediment characteristics:						
% Sand	22.3	24.5	56.8	21.3	−32.4	−21.1
Mean grain size (μm)	42.2	46.4	79.0	42.8	−32.2	−21.6
Median grain size (μm)	28.7	34.3	42.1	26.5	5.9	14.5
% $CaCO_3$	55.1	56.7	66.1	39.5	33.5	47.3
Mean macrofaunal abundance (ind. m^{-2})	12363	19096	2354	4286	96.4	

Macrofauna tube builders (ind. m^{-2})	8184	14246	730	1119	98.1
Macrofauna burrowers (ind. m^{-2})	4179	4717	1608	3137	78.5
Macrofauna epifauna (ind. m^{-2})	0	134	16	30	69.6
Surface deposit feeders (ind. m^{-2})	12190	12298	1029	2173	90.4
Subsurface deposit feeders (ind. m^{-2})	173	1069	148	1556	− 12.3
Carnivorous feeders (ind. m^{-2})	0	0	1177	544	− 73.6
Macrofauna diversity (ES(100))	5.1	11.3	33.6	28.7	− 79.9
Annelida abundance (ind. m^{-2})	11930	17339	1690	1569	98.3
Spionidae abundance (ind. m^{-2})	7741	11569	339	163	98.3
Cirratulidae abundance (ind. m^{-2})	3829	3186	200	0	86.7
Ampharetidae abundance (ind. m^{-2})	0	469	70	11	79
Cossuridae abundance (ind. m^{-2})	248	1174	23	302	80.7
Sabellidae abundance (ind. m^{-2})	0	0	23	0	− 39.3
Mollusca abundance (ind. m^{-2})	0	0	530	724	− 93.1
Crustacea abundance (ind. m^{-2})	0	1757	66	1389	27.7
Mean macrofauna biomass (gm^{-2})	15.3	60	3.5	10.6	87.4
Foraminifera {>63 μm in 0–1 cm} Abundance (ind. 10 cm^{-2})	14700	N/A	N/A	586	N/A

et al., 1997; Levin et al., 1991). Jensen (1987) investigated low oxygen conditions in sandy sediments at shallow depths and found that nematode abundance was unaffected by oxygen concentration. Similarly, nematodes were unaffected by severe seasonal hypoxia on the Louisiana shelf in the Gulf of Mexico (Murrell and Fleeger, 1989).

Levin et al. (1991) found no evidence that low oxygen (0.09–2.6 ml l^{-1}) affected nematode abundance at a site in the eastern Pacific Ocean and suggested that food supply, or biological interactions between the larger organisms and meiofauna, might be more important. Lambshead et al. (1994) found low nematode abundance in San Diego Trough where oxygen concentrations were also low, in the region of 15–60 μmol l^{-1} (compared to 6–23 μmol l^{-1} for the Arabesque OMZ stations). However, they concluded that this phenomenon was caused not by low oxygen but by high abundance of larger metazoans, notably ophiuroids.

This study tests the hypothesis that low oxygen conditions do not affect the abundance of deep-sea nematodes.

2. Materials and methods

Samples were collected during cruise 211 of RRS *Discovery* (9th October–11th November 1994) as part of the UK Natural Environment Research Council's (NERC) Indian Ocean campaign. Cores of 25.5 cm^2 were taken from separate deployments of an IOSDL multiple corer at four stations. Two were within the OMZ (at approximately 400 and 700 m depth), one at the lower boundary of the OMZ (approximately 1250 m depth) and one well below the influence of the OMZ (approximately 3400 m depth), Table 1. Three replicates were used from each depth station. The cores were sub-sampled into horizontal slices 1 cm thick as soon as they were returned to the ship, but only the 0–1 cm sub-sample was examined for this study. Each sub-sample was preserved in 5% formaldehyde buffered with borax. Samples were washed through 45 and 32 μm sieves to separate the two size fractions. Less than 3% of nematodes in this study passed through the larger mesh so the 32 μm mesh samples were abandoned. Nematodes were extracted using a modification of the 'LUDOX™' flotation technique (Somerfield and Warwick, 1996) for counting.

3. Results

The nematode abundance at the 700 m station was significantly higher than at the 1250 and 3400 m stations, but none of the other stations were significantly different to each other (Fig. 1, Table 2).

The correlation of mean nematode abundance and log mean nematode abundance with a number of environmental and biological variables are shown in Table 1. The log of abundance correlated better with depth than simple abundance, and a number of other environmental variables were expected to be depth-linked. Therefore, the log of nematode abundance, in addition to simple abundance, was used for analysis with environmental variables.

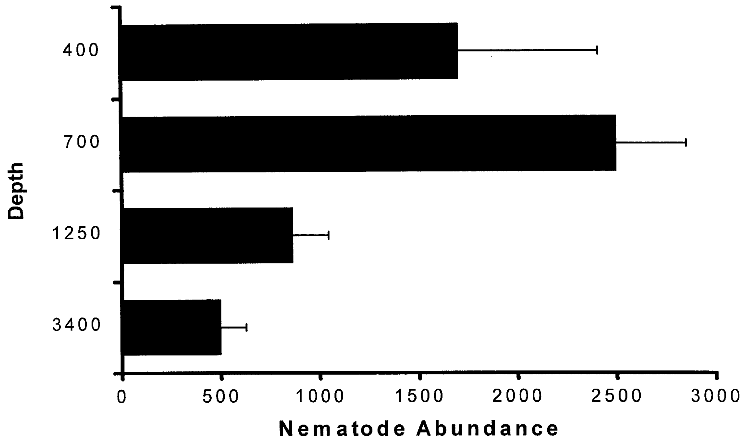

Fig. 1. Mean nematode abundance (> 45 μm), showing the 95% confidence of the mean, sampled at 4 water depths (m) on the Oman margin.

Table 2
Probability (P) of the mean nematode abundance at each of the depths being significantly different from each other (Student's t-test)

Water depth (m)	400	700	1250
700	$P = 0.19$		
1250	$P = 0.16$	$P = 0.015$	
3400	$P = 0.085$	$P = 0.0094$	$P = 0.056$

There was a strong correlation between nematode abundance and the hydrogen index (Fig. 2, regression $y = -4310 + 12.7x$, $r^2 = 93\%$, $P = 0.036$; Fig. 3, $\log y = 1.01 + 0.00458x$, $r^2 = 99.6\%$, $P = 0.002$). Other measures of organic matter, total organic carbon (TOC), carbon : nitrogen ratio and surface pigment, correlated badly with nematode abundance. The correlation of nematode abundance with oxygen levels was poor (Fig. 4, regression $\log y = 3.25 - 0.20x$, $r^2 = 72.8\%$, $P = 0.147$) as was the correlation with physical sediment characteristics ($P > 0.05$).

Nematode abundance showed a strong positive correlation with general macrofauna abundance (Fig. 5, regression $y = 323 + 0.112x$, $r^2 = 92.9\%$, $P = 0.036$) but not with macrofauna biomass or diversity. Of the macrofauna functional types, only 'tube-builders' showed a significant regression line (Fig. 6, $y = 560 + 0.136x$, $r^2 = 96.3\%$, $P = 0.019$). Nematode abundance showed a close correlation with annelid abundance (regression $y = 474 + 0.112x$, $r^2 = 96.6\%$, $P = 0.017$) and with the abundance of the most common polychaete family, the Spionidae (Fig. 7, $y = 616 + 0.156x$, $r^2 = 96.7\%$, $P = 0.017$). Regression lines for nematode abundance plotted against the abundance of other polychaete families were not significant. The

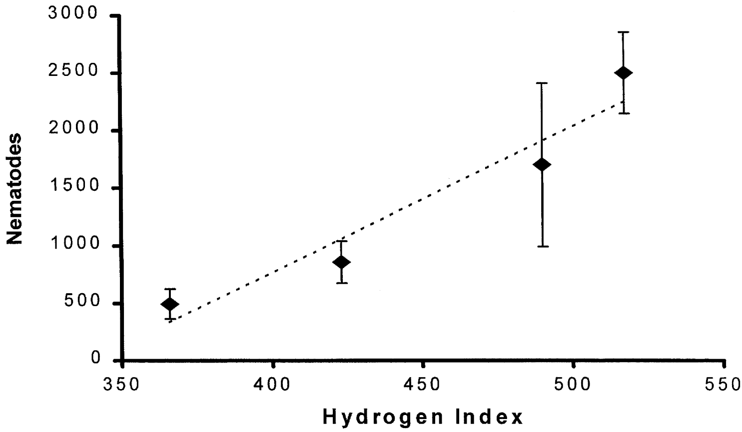

Fig. 2. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon, (individuals/10 cm^2), showing the 95% confidence of the means, against mean Hydrogen Index (mg hydrocarbon/g TOC).

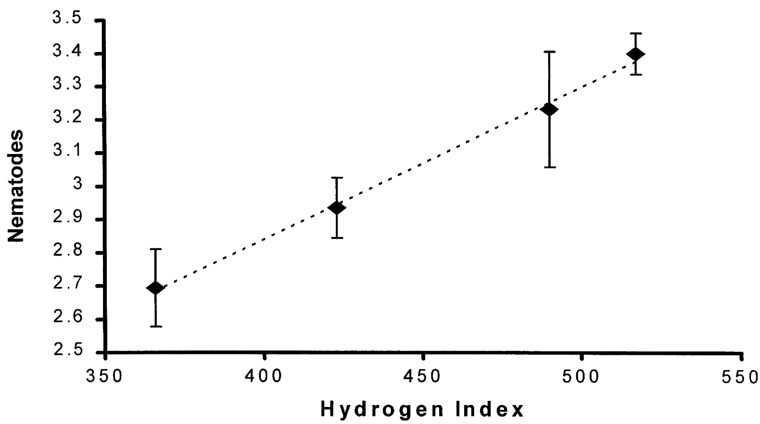

Fig. 3. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon (individuals/10 cm^2), plotted on a $\log_{10}$ scale, showing the 95% confidence of the means, against mean Hydrogen Index (mg hydrocarbon/g TOC).

regression line for molluscs was only significant for log nematode abundance ($\log y = 3.32 - 0.000817x$, $r^2 = 94.0\%$, $P = 0.03$).

4. Discussion

There was no evidence that nematode abundance was dependent on oxygen concentration. We, therefore, accept the hypothesis that low oxygen down to 0.13 ml l^{-1} does not affect the abundance of deep-sea nematodes. These results

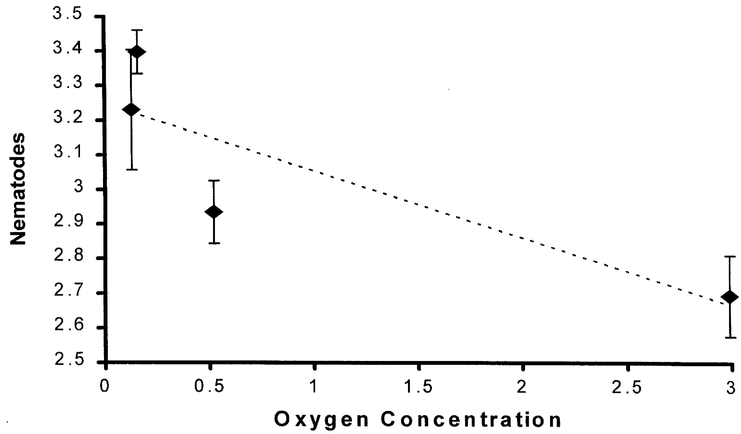

Fig. 4. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon (individuals/10 cm^2), plotted on a $\log_{10}$ scale, showing the 95% confidence of the means, against mean oxygen concentration (ml l^{-1}).

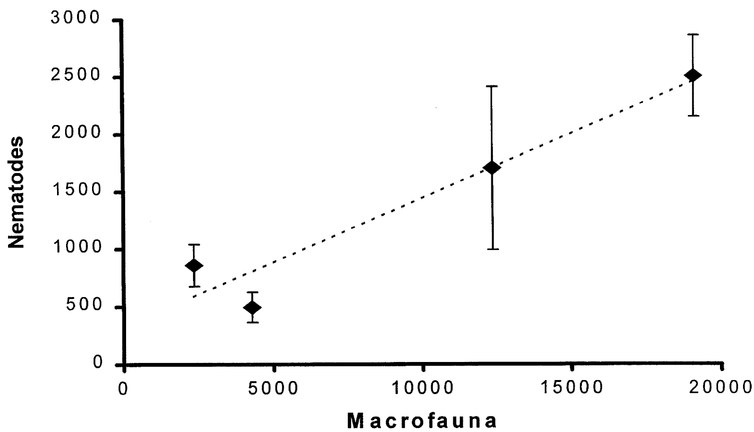

Fig. 5. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon, (individuals/10 cm^2), showing the 95% confidence of the means, against mean macrofauna abundance (individuals/m^2).

confirm that nematodes are highly tolerant to low oxygen conditions (0.1–0.2 ml l^{-1}). Gooday et al. (2000) notes that nematodes were the only metazoan meiofaunal taxa at the 400 m station whereas the 3400 m station contained other meiofaunal taxa, suggesting that nematodes are the most tolerant metazoan meiofaunal taxa to low oxygen.

The hydrogen index proved to be the best environmental predictor of nematode abundance, whereas oxygen concentration proved to be the significant predictor of macrofauna abundance (Levin et al., 2000). The hydrogen index is a measure of food

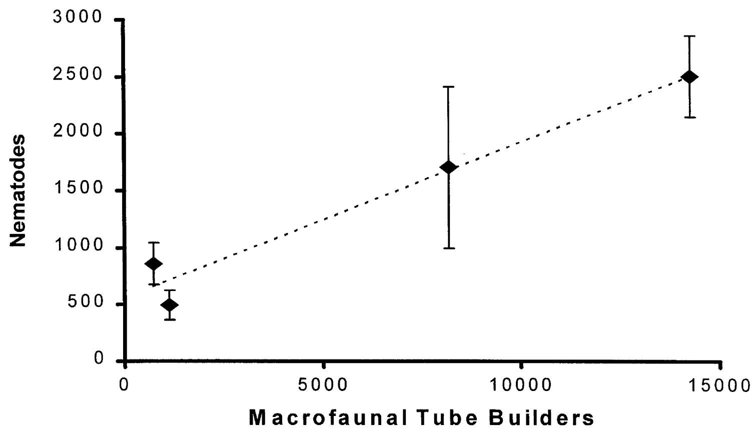

Fig. 6. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon, (individuals/10 cm^2), showing the 95% confidence of the means, against mean number of macrofauna tube builders (individuals/10 cm^2).

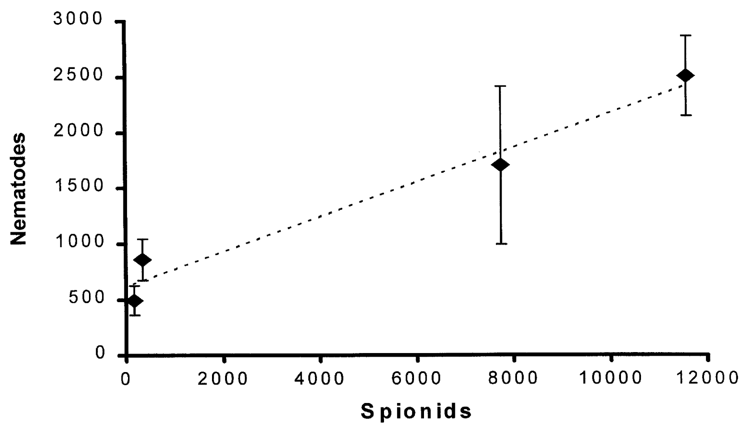

Fig. 7. Linear regression of mean nematode abundance in the 0–1 cm sediment horizon, (individuals/10 cm^2), showing the 95% confidence of the means, against mean number of Spionids (individuals/10 cm^2).

quality (Patience and Gage, unpublished). The closer correlation between a food-quality index and nematode rather than macrofauna abundance implies a closer coupling between nematodes and food input.

Nematode abundance correlated well with macrofauna abundance; in particular it correlated with tube-builders, the dominant functional group, and the Spionidae, the dominant polychaete family at the stations tested here. As this family is dominant, it probably causes the significant correlation with abundance of Annelida. It is difficult to interpret this relationship because spionoids are tube builders so the two correlations are interlinked.

There was poor correlation between nematode abundance and the abundance of any macrofaunal feeding type, despite spionids being surface deposit-feeders, so it seems possible that tube-building is the key parameter. A relationship between meiofauna abundance and tube-building polychaetes has been reported in tidal sediments (Reise, 1981).

European coastal research led scientists to consider physical sediment characteristics to be a 'super-factor', highly correlated with nematode abundance and diversity (Platt and Warwick, 1983). A large-scale analysis by Boucher and Lambshead (1995) found little evidence that such sediment characteristics were correlated with diversity. Physical sediment characteristics had little correlation with nematode abundance in this paper.

Fig. 8 compares the results of this study with published data (Vincx et al., 1994; Lambshead et al., 1994; Teitjen et al., 1989) from the 0–1 cm sediment horizon. The sieve size used in these studies ranged from 32 to 50 μm, which was not considered to invalidate the results (Vincx et al., 1994). Some of the published studies employed box corers whilst others used multiple corers, as in the present study. Bett et al. (1994) investigated the effect of sampler bias in the study of the deep-sea nematodes, reporting that box corers were only 41% efficient compared to multiple corers for the surface 1 cm. Sampling efficiency is affected by a number of factors including sediment type and the presence or absence of phytodetritus (Bett et al., 1994), but, on balance, standardisation of box corer results by multiplying by 2.45 probably allows for a better comparison between the two sampling methods.

Fig. 9 shows the standardised data with abundance plotted against depth on a log scale to produce linear lines of best fit, as it is assumed that the quantity and quality of

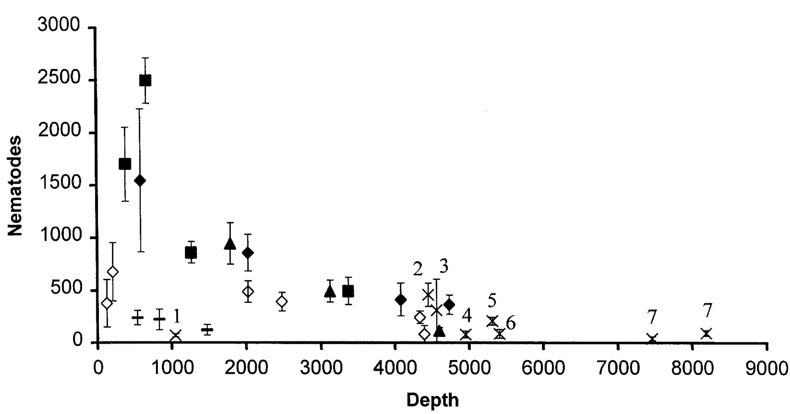

Fig. 8. Mean nematode abundance at different depths (m) showing 95% confidence of the mean. The sites are, Arabesque (■), Bay of Biscay (◇), Porcupine Seabight (◆), Eumeli (▲), Rockall (–) and various other sites (×). The various other sites are, [1]San Diego Trough, [2]DORA, [3]BIOTRANS, [4]Madeira Abyssal plain, [5]Iberic Sea, [6]Hatteras plain and [7]Puerto Rico trench. See text for sources of data.

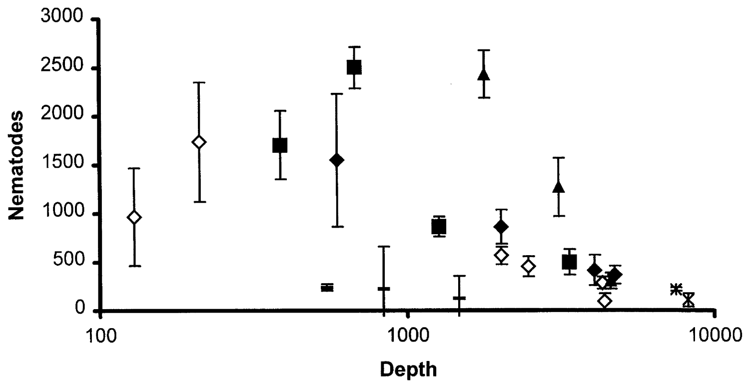

Fig. 9. Mean nematode abundance, box cores adjusted (assuming 41% efficiency), at different depths (m, log scale) showing 95% confidence of the mean. The sites shown are, Arabesque (■), Bay of Biscay (◇), Porcupine Seabight (◆), Eumeli (▲) and Rockall (–). See text for sources of data.

organic matter reaching the benthos decreases exponentially with depth. Singleton points have been removed.

The abundance at the 700 m station was high, but not greatly different from previously published data (Fig. 9). After standardisation, nematode abundance was indistinguishable from other phytodetritus-influenced sites at similar depths (Porcupine Seabight and Bay of Biscay) that are unaffected by an OMZ, again suggesting that food input rather than oxygen concentration is a better predictor of nematode abundance.

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