PERGAMON

Available online at www.sciencedirect.com

SCIENCE DIRECT

Deep-Sea Research I 50 (2003) 103–117

DEEP-SEA RESEARCH
PART I

www.elsevier.com/locate/dsr

Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench (South Pacific Ocean)

C. Gambi[a], A. Vanreusel[b], R. Danovaro[a,]*

[a] Istituto Scienze del Mare, Facoltà di Scienze, Università di Ancona, MMFFNN, Via Brecce Bianche, Monte D'Ago, Ancona 60131, Italy
[b] Ghent University, Marine Biology Section, Ledeganckstraat 35, B-9000 Ghent, Belgium

Received 27 November 2001; received in revised form 25 July 2002; accepted 15 October 2002

Abstract

Nematode assemblages were investigated (in terms of size spectra, sex ratio, Shannon diversity, trophic structure and diversity, rarefaction statistics, maturity index, taxonomic diversity and taxonomic distinctness) at bathyal and hadal depths (from 1050 to 7800 m) in the deepest trench of the South Pacific Ocean: the Trench of Atacama. This area, characterised by very high concentrations of nutritionally-rich organic matter also at 7800-m depth, displayed characteristics typical of eutrophic systems and revealed high nematode densities (> 6000 ind. 10 cm^{-2}). Nematode assemblages from the Atacama Trench displayed a different composition than at bathyal depths. At bathyal depths 95 genera and 119 species were found (Comesomatidae, Cyatholaimidae, Microlaimidae, Desmodoridae and Xyalidae being dominant), whereas in the Atacama Trench only 29 genera and 37 species were encountered (dominated by Monhysteridae, Chromadoridae, Microlaimidae, Oxystominidae and Xyalidae). The genus *Monhystera* (24.4%) strongly dominated at hadal depths and *Neochromadora*, and *Trileptium* were observed only in the Atacama Trench, but not at bathyal depths. A reduction of the mean nematode size (by ca. 67%) was observed between bathyal and hadal depths. Since food availability was not a limiting factor in the Atacama Trench sediments, other causes are likely to be responsible for the reduction of nematode species richness and body size. The presence of a restricted number of families and genera in the Atacama Trench might indicate that hadal sediments limited nematode colonisation. Most of the genera reaching very high densities in Trench sediments (e.g., *Monhystera*) are opportunistic and were responsible for the significant decrease of the maturity index. The dominance of opportunists, which are known to be characterised by small sizes, might have contributed to the reduced nematode size at hadal depths. Shannon diversity and species richness decreased in hadal water depth and this pattern was more evident at genus than at species level. Epistrate feeders dominated and increased their relevance, determining a reduction of the index of trophic diversity at hadal depths. According to trophic diversity, taxonomic diversity and distinctness also decreased with depth. All diversity indices from the Atacama Slope and Trench were lower than in other equally deep areas world wide (e.g. Puerto Rico Trench). We suggest that such reduction was related to the high nutrient loading observed in this system (up to two orders of magnitude higher than in typical oligotrophic deep-sea sediments).

Keywords: Nematode; Sex ratio; Diversity; Trophic structure; Bathyal and hadal sediments; Atacama Trench

---

*Corresponding author. Tel.: +39-071-2204654; fax: +39-071-2204650.
E-mail addresses: danovaro@unian.it (R. Danovaro).

PII: S0967-0637(02)00143-7

1. Introduction

Nematodes are generally the most abundant metazoan component of the deep-sea meiobenthos (Jensen, 1988; Tietjen, 1992) and their numerical dominance increases with water depth (up to more than 90%; Thiel, 1975; Heip et al., 1985; Vincx et al., 1994). As their feeding ecology can be inferred from the morphology of their mouth cavity (Wieser, 1953; Jensen, 1987), nematodes offer unique opportunities to examine the trophic features of the deep-sea meiobenthos (Soetaert and Heip, 1995). These factors make nematodes a useful tool for investigating both structural and functional diversity, especially in the deep sea.

However, despite their ubiquity and dominance, the knowledge of nematode biodiversity in the deep-sea is limited to few areas, such as the upper abyssal zone of the North and Central Atlantic, eastern central Pacific, the deep Western Mediterranean, the Arctic and the Weddell Sea (Antarctica; Tietjen, 1976, 1984, 1989; Dinet and Vivier, 1979; Thistle and Sherman, 1985; Jensen, 1988; Renaud-Mornant and Gourbault, 1990; Soetaert et al., 1991; Soetaert and Heip, 1995; Thistle et al., 1995; Vanreusel et al., 1997, 2000; Vanhove et al., 1999; Lambshead et al., 1983, 1994, 2000). Among deep-sea environments, hadal trenches are the most inaccessible ones and the knowledge of their fauna either have been insufficiently studied or have not been studied at all (Angel, 1982). This applies also to a larger extent to nematode biodiversity, as the only available information is limited to the Puerto Rico Trench (Tietjen, 1989).

Trenches characterised by high primary production on the surface (e.g., South Sandwich Trench, Kurile-Kamchatka Trench, Atacama Trench) display high macrobenthic biomass values and high meiofaunal density and biomass (Angel, 1982; Danovaro et al., 2002). The Atacama Trench, belonging to the Peru–Chile Trench, is the southernmost and deepest trench of the eastern Pacific Ocean. Here, meiobenthos is a key component of the fauna (reaching densities up to 6.4×10^3 ind. $10\,cm^{-2}$ and accounting for about 70% of the total benthic biomass), and nematodes largely dominate the meiobenthic assemblage (ca. 80% of total meiofauna; Danovaro et al., 2002). Atacama Trench sediments, receiving large primary production inputs from surface waters (Angel, 1982; Ahumada, 1989), are a model for testing the effects of extreme conditions (high pressure, low temperature) in a non-food limited environment (high quality and quantity of organic matter; Danovaro, 1999). This might have important consequences also for the adaptive strategies and biodiversity of the biota inhabiting the sea floor.

In this study we compared size spectra, sex ratio, Shannon diversity, rarefaction curves, trophic structure, maturity index, taxonomic diversity and distinctness of nematode assemblages inhabiting the Atacama Trench (7800 m) and three bathyal stations, selected along the continental slope facing the Atacama Trench (from 1050 to 1355 m depth), to provide information on the deep-sea biodiversity in extreme environments and to identify the environmental factors that are potentially responsible for depth related patterns.

2. Materials and methods

2.1. Study area

The Peru–Chile Trench is the largest trench worldwide, extending for about 5900 km with a mean width of 100 km. The maximum trench depth exceeds 8050 m and the minimum distance of land from 6000-m depth is 80 km. The Atacama Trench (extending from latitude 20° to 30°S) is the deepest trench of the South Pacific Ocean, with depths in excess of 8000 m at a distance of ca. 80 km from land. This trench is located in an area characterised by important up-welling events, which are responsible for very high primary production values (up to $9.9\,g\,C\,m^{-2}\,d^{-1}$; Fossing et al., 1995). There is no river input, but winds play an important role in transferring materials from the adjacent continental desert (Angel, 1982). Information on hydrological features during the sampling period are given by Sievers et al. (1999) and Della Croce et al. (1998).

2.2. Sampling

Samples were taken during the *Atacama Trench International Expedition* (A.T.I.E.) in the South Pacific on September 1997, aboard the R.V. *Vidal Gormaz*. Sampling station locations and depths are given in Table 1. Sampling procedures have been previously reported by Della Croce et al. (1998) and Danovaro et al. (2002). Sediment samples at hadal depths (i.e, from the inner part of the hadal trench: ca. 7800 m depth, station A1) were collected by means of 6 sediment corers connected to baited traps and penetrating ca. 6 cm into the sea floor and left on the bottom for 24 h before recovery to minimise resuspension (Della Croce et al., 1998). Three replicates displaying an undisturbed sediment surface were processed for meiofaunal analysis. Sediment samples at bathyal depths from the slope margin facing the Atacama Trench (1050, 1140, 1355 m, respectively for stations B1, B4, C7) were collected with an USNEL-type boxcorer. Six to ten replicate deployments were carried out at each site. Subsamples were taken from the inner part of box-corers showing a perfectly undisturbed sediment surface and three replicates were analysed for meiofauna. Sediment cores were sectioned into different layers (0–1, 1–2, 2–6, 6–10 and 10–15 cm). The top 6-cm layer was analysed for comparison between bathyal and hadal nematodes. Sediment samples were preserved in buffered 4% formalin solution and stained with Rose Bengal. Additional sediment samples were taken for grain size analysis, which was carried out by a dry sieve technique.

2.3. Meiofauna parameters

For meiofaunal extraction, sediment samples were passed through 1000 μm mesh and a 20-μm mesh was used to retain the smallest organisms. The fraction remaining on the latter sieve was re-suspended and centrifuged three times with Ludox HS 40 (density 1.31 g cm^{-3}) as described by Heip et al. (1985). From each of the three replicates 100 nematodes were randomly withdrawn and mounted on slides following the formalin–ethanol–glycerol technique described by Seinhorst (1959) to prevent dehydration. Nematode length (excluding filiform tail part) was measured to perform the size spectra analysis. All nematodes were identified to genus level according to Platt and Warwick (1983) and recent literature dealing with new nematode genera and species. The trophic composition was defined according to Wieser (1953). Nematodes were divided into four original groupings as follows: (1A) no buccal cavity or a fine tubular one-selective (bacterial) feeders; (1B) large but unarmed buccal cavity-non-selective deposit feeders; (2A) buccal-cavity with scraping tooth or teeth-epistrate or epigrowth (diatom) feeders; (2B) buccal cavity with large jaws-predators/omnivores. Moens and Vincx (1997) and Moens et al. (1999) recently proposed a modified feeding-type classification based on: (1) microvores, (2) ciliate feeders, (3) deposit feeders *sensu stricto*, (4) epigrowth feeders, (5) facultative predators and (6) predators. However, in the present study, Wieser's classification was preferred because it is still widely used and because no information was available for most genera encountered in deep-sea systems.

Table 1
Latitude, longitude, depth, silt-clay, median diameter, nematode male, female, juvenile percentages and sex ratio

Station	Latitude (S)	Longitude (W)	Depth (m)	Silt-clay	Median diam.	Nematode			
						Male (%)	Female (%)	Juvenile (%)	male:female
B1	23°30.5′	70°42.8′	1050	4.5	0.25	39.6	7.4	53.0	5.3
B4	23°46.6′	70°37.4′	1140	10.8	0.20	25.0	5.5	69.4	4.5
C7	23°15.0′	70°40.0′	1355	20.1	0.10	27.8	5.9	66.4	4.7
A1	23°15.0′	71°21.0′	7800	99.0	0.03	18.5	3.9	77.6	4.7

2.4. Statistical analysis and ecological indexes

Species diversity (H′, using log-base 2) was measured by Shannon–Wiener information function and evenness as J′ (Pielou, 1975). Species richness (SR) was estimated from Margalef's formula as $\mathrm{SR} = (\mathrm{S}-1)/\ln N$, where S is the number of species and N the number of individuals in a sample (Margalef, 1958) and the same formula was used to estimate genus richness, based on the number of genera encountered in each sample. Moreover, to make our samples comparable with others available in the literature, at each site the species-abundance data were converted into rarefaction diversity indices (Sanders, 1968, as modified by Hurlbert, 1971). The expected number of species for a theoretical sample of 51 individuals ES(51) was selected and applied both to our samples and to data available in the literature (data gathered from Lambshead et al., 2000). All analyses were performed at both genus and species level. To test the hypothesis of high similarities between the bathyal stations and the Atacama Trench, mean dissimilarities among replicates were carried out. SIMPER was used to identify the genera that are responsible for the differences observed between bathyal and hadal sediments.

The taxonomic diversity (Δ) and distinctness (Δ^*) were calculated to define the structure not only of the distribution of abundance amongst species but also the taxonomic relatedness of the species in each sample (Clarke and Warwick, 1998). All these analyses, as well as k-dominance curves and cluster analysis (using the Bray-Curtis similarity coefficient) were performed with the PRIMER programme (Plymouth Marine Laboratory; Clarke, 1993).

The maturity index (MI) was calculated according to the weighted mean of the individual genus scores: $\mathrm{MI} = \sum v(i)f(i)$, where v is the c–p value (colonisers–persisters) of genus i as given in the Appendix of Borgers et al. (1991) and $f(i)$ is the frequency of that genus.

The index of trophic diversity (ITD) was calculated as follows: $\mathrm{ITD} = \Sigma\theta^2$, where θ is the contribution of density of each trophic group to total nematode density. ITD ranges from 0.25 (highest trophic diversity; i.e., the four trophic guilds account for 25% each) to 1.0 (lowest diversity; i.e., one trophic guild accounts for 100% of nematode density; Heip et al., 1985).

3. Results

The Atacama Trench was characterised by silt-clay sediments (99%) whereas bathyal stations displayed a silt-clay composition (<62.5 μm) that accounted for 4.5–20.1% (at 1050 and 1355 m depth, respectively) of sediment dry weight (median diameter 0.1–0.25 mm, Table 1).

3.1. Nematode composition

Ninety-five nematode genera (belonging to 31 families) and 119 species were found in the present study (1048 nematodes identified, 773 and 275 for bathyal and hadal sediments, respectively). Twenty-eight families were encountered at 1050 m, 26 at 1140 m and 21 at 1355 m. At bathyal depths 90 genera were identified (51, 60, 55 genera at 1050 m, 1140 and 1355 m, respectively), whereas only 29 were found in the Atacama Trench. Comesomatidae (15.6%), Cyatholaimidae (13.1%), Microlaimidae (9.5%), Desmodoridae (8.9%), Xyalidae (8.2%), Chromadoridae (7.5%) were the most abundant families at bathyal stations, whereas only 15 families were encountered in the Atacama Trench and the most abundant were Monhysteridae (24.8%), Chromadoridae (22.9%), Microlaimidae (11.5%), Oxystominidae (8%) and Xyalidae (7.4%). At bathyal depths the number of genera ranged from 55 (1355 m) to 60 (1140 m) whereas the number of species ranged from 60 (1355 m) to 66 (1140 m; Fig. 1). In the Atacama Trench 29 genera and 37 species were identified. For each station, the genera displaying a mean relative abundance ⩾1% are reported in Table 2. *Molgolaimus* and *Pierrickia* showed the highest relative abundance (both 8.9%) at 1050 m depth, but their relative abundance decreased with increasing water depth. At 1140 m *Odontophora* (7.6%) was the most abundant genus but it disappeared in the Atacama Trench. *Microlaimus* was the second most important genus (7.2%) but it increased in relative

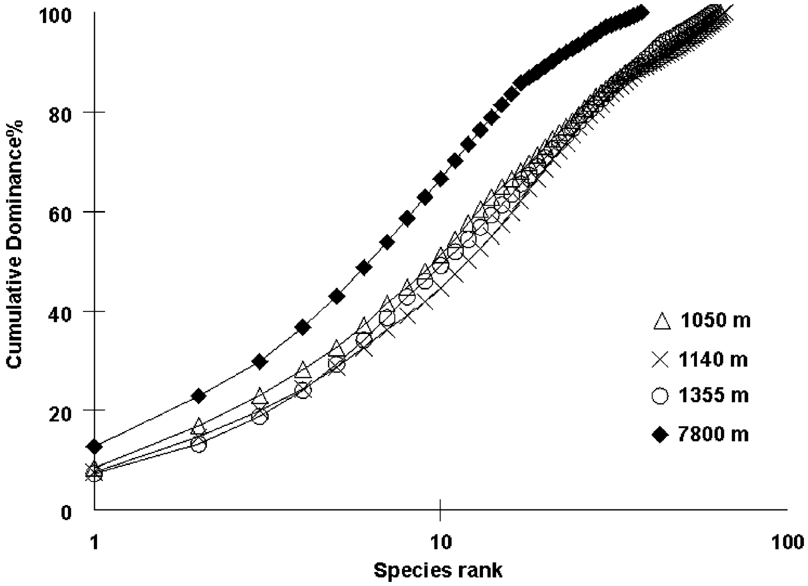

Fig. 1. Comparison of K-dominance curves of nematode genera from the sampling stations.

abundance (8.7%) in the trench sediments. At 1355-m depth the genus *Metacomesoma* showed the highest relative abundance (7.4%), but this genus was completely absent at all other sampling stations. *Desmodora* and *Pierrickia* each accounted for 6.7% and their relative abundance decreased with increasing water depth. In the Atacama Trench, *Monhystera* (24.4%) and *Acantholaimus* (11.3%) dominated and *Halalaimus*, *Prochromodorella*, *Trefusia* displayed relative abundances about twice those at bathyal depths. *Campylaimus*, *Halichoanolaimus*, *Longicyatholaimus*, *Metalinhomoeus*, *Molgolaimus*, *Odontophora*, *Pomponema*, *Sabatiera*, *Sphaerolaimus*, *Trichoteristus*, *Vasostoma*, *Viscosia* were found at all bathyal stations, but were completely lacking from the Trench sediments. Conversely, *Neochromadora* and *Trileptium* were encountered only in trench sediments. SIMPER analysis identified *Daptonema*, *Pierrickia*, *Odontophora*, *Desmodora*, *Microlaimus*, *Aponema* and *Halalaimus* as the main genera responsible for the similarity among replicates at bathyal depths (the sum of their relative contribution is ca. 52%). In the Atacama Trench, *Monhystera*, *Acantholaimus* and *Microlaimus* accounted for ca. 70% of the similarity among replicates. SIMPER analysis identified *Monhystera* and *Odontophora*, *Trefusia* and *Acantholaimus* as the main genera responsible for differences observed between bathyal and Atacama Trench assemblages (average dissimilarity ca. 60%).

The trophic structure of nematode assemblages at bathyal and hadal depths is reported in Fig. 2. Deposit feeders (1A + 1B) cumulatively dominated at all stations, accounting for more than 50% of nematode assemblages. Selective deposit feeders (1A) included 32 genera and accounted for ca. 23% (at 7800 m) to 34% (at 1050 m) of the total nematode abundance. Non-selective deposit feeders (1B) included 21 genera and accounted for ca. 21% (1140 m) to 32% (7800 m). Epistrate feeders (2A, 29 genera) were the dominant feeding type at all stations, except at 1050-m depth, accounting for 31% (1355 m) to 44% (7800 m). Predator-omnivores (2B) were composed of 12 genera and their relative importance was low at each station, ranging from 1% (at 7800 m) to 12% (at 1050 m).

3.2. Nematode size spectra and sex ratio

The length-frequency distribution patterns and sex ratio are reported in Fig. 3 and Table 1,

Table 2
Check list of the dominant nematode genera encountered in bathyal and trench sediments

B1-1050 m		B4-1140 m		C7-1355 m		A1-7800 m	
Genera	%	Genera	%	Genera	%	Genera	%
Molgolaimus	8.0	Odontophora	7.6	Metacomesoma	7.4	Monhystera	24.4
Pierrickia	8.9	Microlaimus	7.2	Desmodora	6.7	Acantholaimus	11.3
Odontophora	6.3	Desmodora	5.6	Pierrickia	6.7	Microlaimus	8.7
Paralongicyatholaimus	5.5	Acantholaimus	5.2	Daptonema	6.0	Halalaimus	7.6
Daptonema	5.1	Daptonema	4.4	Odontophora	5.6	Daptonema	6.2
Aponema	4.6	Halalaimus	4.4	Microlaimus	5.3	Paralongicyatholaimus	5.5
Pomponema	4.6	Pierrickia	4.4	Aponema	4.6	Prochromodorella	4.7
Desmodora	3.8	Dichromadora	3.6	Pselionema	4.2	Trefusia	4.4
Acantholaimus	3.4	Aponema	2.8	Chromadorina	3.2	Actinonema	3.6
Longicyatholaimus	3.4	Desmoscolex	2.8	Metacyatholaimus	3.2	Desmoscolex	3.3
Microlaimus	3.4	Halichoanolaimus	2.8	Desmoscolex	2.8	Pselionema	2.9
Stylotheristus	3.4	Pselionema	2.8	Aegialoalaimus	2.5	Aponema	2.5
Metalinhomoeus	3.0	Vasostoma	2.8	Longicyatholaimus	2.5	Chromadorina	2.5
Halalaimus	2.5	Campylaimus	2.4	Pomponema	2.5	Paramesonchium	2.5
Viscosia	2.1	Leptolaimus	2.4	Halalaimus	2.1	Pierrickia	1.1
Chromadorina	1.7	Longicyatholaimus	2.4	Metalinhomoeus	2.1	Tricoma	1.1
Metacyatholaimus	1.7	Metacyatholaimus	2.4	Paracomesoma	2.1		
Pselionema	1.7	Tricoma	2.4	Paralongicyatholaimus	2.1		
Sabatiera	1.7	Chromadorina	2.0	Halichoanolaimus	1.8		
Trefusia	1.7	Metalinhomoeus	2.0	Vasostoma	1.8		
Vasostoma	1.7	Paralongicyatholaimus	2.0	Diplopeltula	1.4		
Campylaimus	1.3	Ceramonema	1.6	Monhystera	1.4		
Diplopeltula	1.3	Molgolaimus	1.6	Oxystomina	1.4		
Halichoanolaimus	1.3	Pomponema	1.6	Terschellingia	1.4		
Synonchus	1.3	Nannolaimus	1.2	Campylaimus	1.1		
		Paracyatholaimus	1.2	Comesoma	1.1		
		Paramesonchium	1.2	Dorylaimopsis	1.1		
		Viscosia	1.2				

Only genera with mean relative abundance >1% of the total number of individuals are reported.

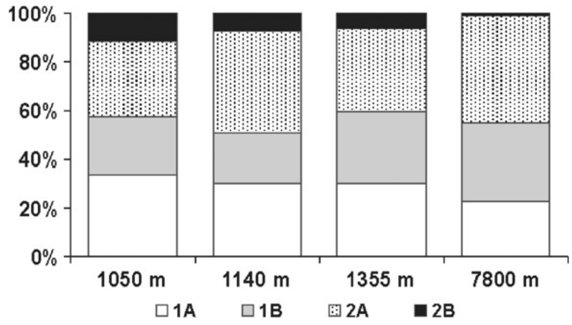

Fig. 2. Trophic structure of nematode assemblages from the Atacama Slope and Trench.

respectively. The nematode length varied from 0.318 to 4.288 mm at 1050 m, from 0.288 to 5.030 mm at 1140 m and from 0.175 to 3.963 mm at 1355 m. In the Atacama Trench, the length ranged from 0.163 to 3.125 mm. The length–frequency curve showed that the bathyal stations presented a larger length–frequency interval (0.10–4.9 mm) than the hadal sediments, where most of nematode lengths (ca. 90%) are restricted to a small range (0.10–3.25 mm).

Juveniles dominated at all stations, increasing their relative importance with increasing depth from 53% (at 1050 m) to 78% (at 7800 m). Both males and females decreased from 1050 m to the Atacama Trench (from 40% to 19% for males and from 7% to 4% for females; Table 1). The male to female ratio ranged from 4.5 to 5.3 at 1140 and 1050 m, respectively whereas in the Atacama Trench it was 4.7.

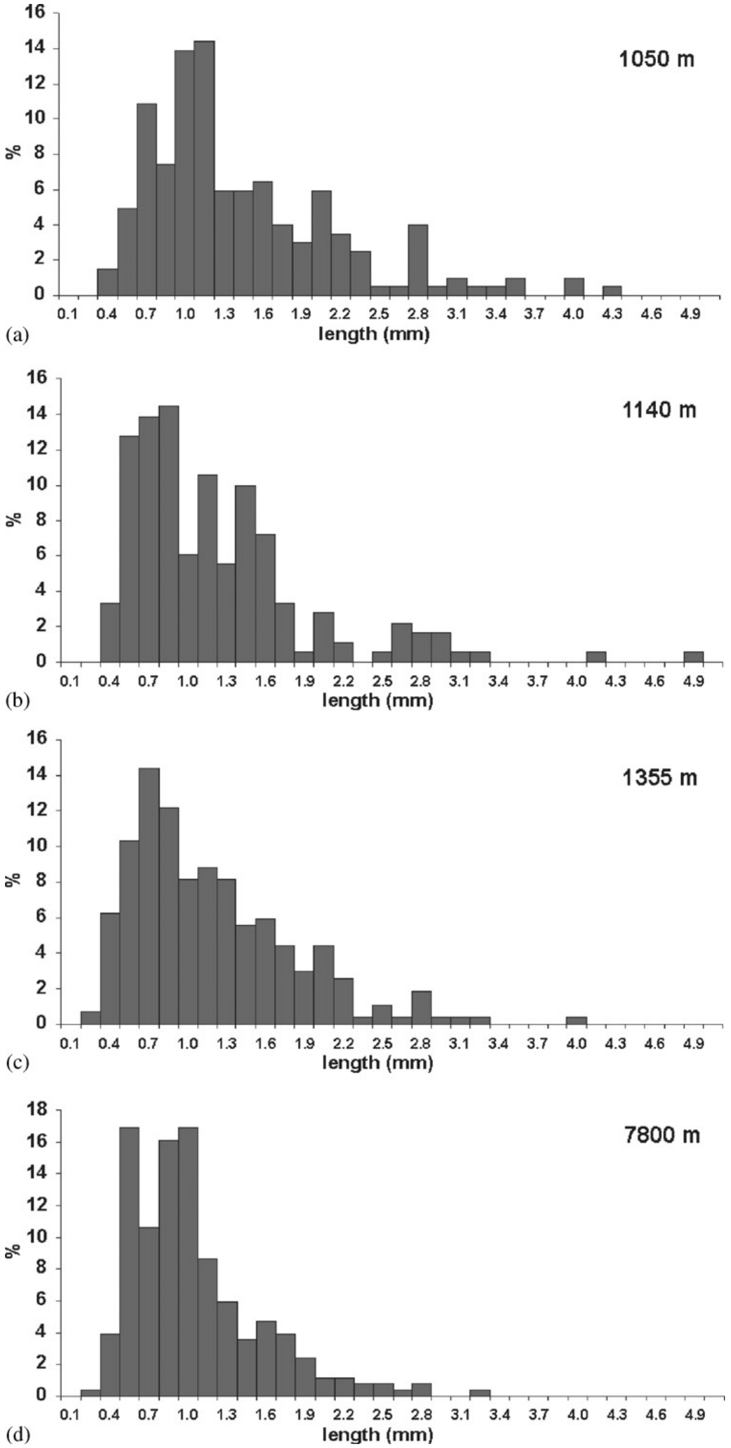

Fig. 3. Nematode length–frequency distribution patterns at (a) 1050 m; (b) 1140 m; (c) 1355 m; (d) 7800 m.

Table 3
Diversity (H′), evenness (J), genus and species richness (GR and SR) calculated at genus and species level

Station	Depth (m)	H′		J		GR	SR
		Genus	Species	Genus	Species	Genus	Species
B1	1050	3.0	3.1	0.874	0.878	12.6	14.1
B4	1140	3.2	3.2	0.895	0.897	13.1	14.5
C7	1355	3.2	3.2	0.888	0.897	11.7	13.0
A1	7800	2.5	2.7	0.805	0.862	5.8	7.9

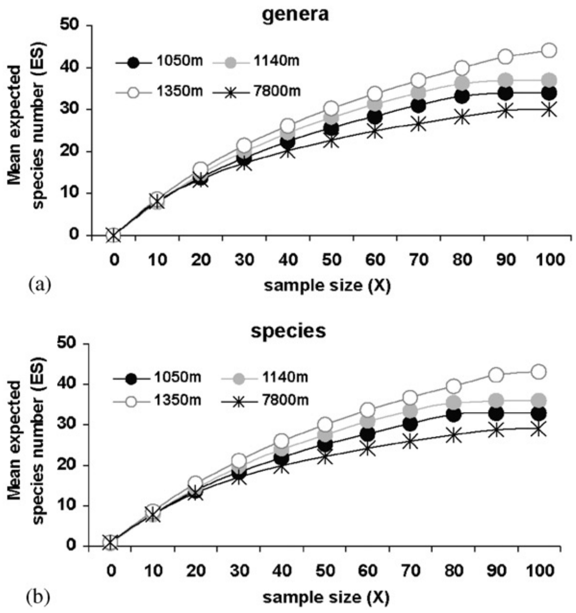

Fig. 4. Composite rarefaction curves for the three bathyal sites and the hadal stations. Reported are: curves created from genera abundance (a) and for species abundance (b).

3.3. Nematode diversity

Diversity parameters are reported in Table 3. Both species and genus diversity decreased significantly with depth (ANOVA, both $p<0.01$), ranging from 3.2±0.1 to 2.7±0.2 at bathyal depths and 3.2±0.1 to 2.5±0.1 at hadal depth. Also genus and species richness decreased significantly (ANOVA, $p<0.01$) from bathyal stations to the Atacama Trench. Evenness decreased (not significantly, $p=0.505$) from bathyal to hadal stations and reflected the same pattern reported for diversity and genus and species richness.

The rarefaction curves are illustrated in Fig. 4. The expected number of genera (Fig. 4a) and species (Fig. 4b) displayed the same pattern, increasing from 1050 to 1350 m, but then decreasing significantly in Trench sediments (ANOVA, $p<0.01$).

Data relative to the index of trophic diversity (ITD), taxonomic diversity (Δ), distinctness (Δ^*) and maturity index (MI) are reported in Table 4. The index of trophic diversity barely increased from 0.275 at 1050 m to 0.337 at 7800 m. The taxonomic diversity (Δ) and distinctness (Δ^*) displayed a non-significant decrease ($p=0.07$ and 0.200, respectively) with increasing water depth. Also the maturity index slightly decreased, though not significantly ($p=0.399$), from 2.7 at 1050 m to 2.4 in the Atacama Trench.

4. Discussion

Bett et al. (1994), comparing sampling efficiency of box-corer and multiple corer at abyssal depths, suggested that box-corer might underestimate meiofaunal counts by up to 50%. Unfortunately, we have no information on the sampling efficiency of the instruments we deployed at bathyal and hadal depths, but differences in meiofaunal densities between hadal and bathyal depth are too large to be accounted for the use of different samplers. Sampling bias should be more relevant in samples recovered from 7800-m depth than from bathyal depths, but the high meiofaunal densities and the abundance of copepods in hadal sediments (Danovaro et al., 2002) are elements suggesting a high sampling quality.

Table 4
Index of trophic diversity, taxonomic diversity and distinctness and maturity index

Station	Depth (m)	ITD	Taxonomic		Maturity index
			Diversity	Distinctness	
B1	1050	0.275	95.6	98.1	2.7
B4	1140	0.308	96.5	98.4	2.6
C7	1355	0.283	95.3	97.6	2.5
A1	7800	0.337	90.5	95.2	2.4

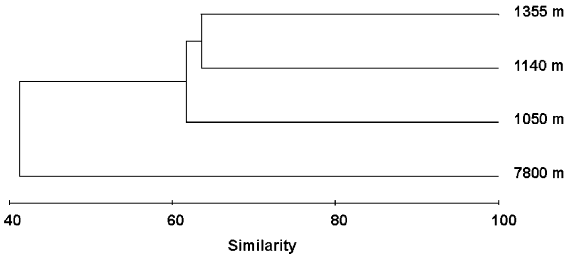

Fig. 5. Cluster analysis reported from sampling stations based on the nematode genus composition.

4.1. Nematode assemblage composition

Tietjen (1989), comparing bathyal and hadal sediments in the Puerto Rico Trench, reported a low affinity index. This was not due to the presence or absence of certain families/genera, but rather to the different percent compositions of nematode assemblages at different depths. Also in our study nematode assemblages displayed a low affinity index, but contrary to what Tietjen reported, this was due to a different composition at bathyal and hadal depths (Fig. 5). At the bathyal stations the most abundant families were: Comesomatidae, Cyatholaimidae, Microlaimidae, Desmodoridae and Xyalidae whereas in the Atacama Trench the most abundant were Monhysteridae (24% at hadal depths vs. <1% at bathyal depths), Chromadoridae, Microlaimidae, Oxystominidae and Xyalidae. Moreover, the genus *Monhystera* dominated the Trench sediments and *Neochromadora* and *Trileptium* were exclusively observed in the Atacama Trench. Also in other studies carried out at bathyal depths in the Mediterranean, Atlantic and Weddell Sea (Soetaert and Heip, 1995; Vanhove et al., 1999), Comesomatidae, Microlaimidae and Xyalidae were the most abundant families. Similarly, the dominant families in the Atacama Trench were also dominant in other deep-sea studies at depths between 3000 and 5000 m (the Gulf of Gascony, Dinet and Vivier, 1979; Venezuela basin, Tietjen, 1984; Scotian Rise, Thiestle and Sherman, 1985; eastern central Pacific, Renaud-Mornant and Gourbault, 1990; Soetaert and Heip, 1995). Comparing the Atacama Trench with the only study available for hadal depths (i.e., the Puerto Rico Trench; Tietjen, 1989) we found that the dominant families were the same: Monhysteridae, Chromadoridae, Oxystominidae and Xyalidae, but the relative importance of Monhysteridae (5% in the Puerto Rico vs. 24% in the Atacama Trench) and Xyalidae (17.4% in the Puerto Rico vs. 7.4% in the Atacama Trench) changed. Another peculiarity of the nematode assemblage from the Atacama Trench was that the family Cyatholaimidae, particularly abundant in both Trench and Slope sediments (6.3% and 13.1%, respectively), accounted only for a minor fraction of nematode assemblages in all other deep-sea studies (<1% in the Puerto Rico Trench, Tietjen, 1989; <2% in the deep Mediterranean, Soetaert and Heip, 1995; 3.0% in the Weddell Sea (Antarctica), Vanhove et al., 1999).

The SIMPER analysis carried out at the genus level indicated that the main differences in the nematode composition between the Trench sediments and the bathyal stations were due principally to the genera *Monhystera* and *Acantholaimus*, which largely dominated the Atacama Trench but were rare at bathyal depths. Conversely, *Pierrickia* and *Odontophora* dominated at bathyal depths, but were lacking (*Odontophora*) or extremely reduced (*Pierrickia*) in the Trench sediments.

The Atacama Trench displayed characteristics typical of eutrophic systems, being characterised by very high concentrations of nutritionally rich organic matter (Danovaro, 1999). These characteristics are opposite to those described for the Puerto Rico Trench (Tietjen et al., 1989). In the Atacama Trench, chlorophyll-a concentrations in the sediment were high at both bathyal and hadal depths, and chloroplastic pigment equivalents (as the sum of chlorophyll-a and phaeopigments; CPE) displayed concentrations among the highest reported for other equally deep-sea sediment worldwide (Danovaro et al., 1999b). Proteins were the dominant biochemical class of organic compounds and organic matter quality surprisingly increased with water depth (Danovaro et al., 1999a), so that meiofaunal abundance in hadal sediments was 10-fold higher than at bathyal depths (Danovaro et al., 2002). The different trophic conditions observed between Atacama and other trenches might have contributed to the differences in the structure of nematode assemblages.

Recently Bongers (1990) and Bongers et al. (1991) proposed a classification for nematodes into "colonisers" (comparable to r-strategists, characterised by short life-cycle, high colonisation ability and tolerance to disturbance, eutrophication and anoxybiosis) and "persisters" (with opposite characteristics, K-strategist with low reproduction rate, long life-cycle, low colonisation ability and tolerance to disturbance). Bongers and Ferris (1999) also distinguished two types of opportunists: enrichment- and general opportunists. Enrichment-opportunists colonise food-enriched conditions and are classified as $c-p=1$; general opportunists are classified as $c-p=2$. The genus *Monhystera* (family Monhysteridae), which largely dominates the Atacama Trench, is an enrichment opportunist (coloniser, Bongers and Ferris, 1999). Also most of the other genera reaching high densities in Trench sediments were opportunistic (Bongers, 1990). Caution must be used when the maturity index is applied to deep-sea nematodes, as the MI is based on findings from shallow water species (Bongers, 1990). Nonetheless the results of the present study indicate that this index might provide additional insights to the analysis of the characteristics of nematode assemblages in the deep sea.

4.2. Nematode size spectra, sex ratio and trophic structure

Size spectra of organisms are useful descriptors for ecosystem structures and functioning. Previous studies on deep-sea nematodes found higher numbers of individuals in the smaller size fractions with increasing water depth (Pfannkuche, 1985; Soetaert and Heip, 1989) and decreasing food availability (Vanreusel et al., 1995; Soltwedel et al., 1996). In our study we observed that the nematode size spectrum at bathyal and hadal depths was different: at 7800-m depth ca. 80% of nematodes were <1.5 mm length, whereas at bathyal depths only ca. 50–70% of nematodes fell in this size range. We observed that between bathyal and hadal depths, despite the fact that the percentage of juveniles barely increased, mean nematode length was reduced by 67%. Since, the Atacama Trench was rich in organic matter of high nutritional quality, the hypothesis of nematode dwarfism due to the increasing "oligotrophy" with depth (Schewe and Soltwedel, 1998) can be rejected and other explanations have to be considered.

In this regard the analysis of the maturity index (MI) revealed decreasing values with increasing depth. Lower values indicate that nematode assemblages in Trench sediments are increasingly dominated by "colonisers". MI values reported in the present study are significantly lower than those calculated by Bongers et al. (1991) for the deep-sea nematodes of the Hatteras Abyssal Plain and Puerto Rico Trench (range 2.80–2.93; from data reported by Tietjen, 1989; *t*-test, $p<0.05$). The reduction of the nematode size in the Atacama Trench could be therefore related to the dominance of colonisers (opportunists), which are known to be small size. If we assume that the classification into colonisers vs. persisters, proposed by Bongers and Ferris (1999), can apply also to the deep sea, data reported here suggest that the community structure of hadal nematodes is characterised by a higher fraction of colonisers (opportunistic behaviour) than at bathyal depths.

The male:female ratio was similar at all stations, suggesting a common nematode sex ratio in all investigated deep-sea sediments. At the same time, the ratio was apparently high, since males were ca. five times more abundant than female. However, the limited information on this does not allow to be drawn conclusions about the ecological significance of these sex ratios in deep-sea sediments.

The quantity and variety of organic matter allow the co-existence of different feeding types (Jensen, 1987; Moens and Vincx, 1997). In the study area, at all depths, epistrate feeders (i.e., nematodes feeding on diatoms and other microalgae) were the dominant feeding guild (>30% at bathyal depths and >40% in the Atacama Trench). This is unusual for most deep-sea systems, but not in a highly productive system, as the Peru-Chile upwelling area, in which large amounts of primary organic matter (microalgae and phytodetritus) are supplied to the bottom. This was also confirmed by the extremely high chlorophyll-a and phytopigment concentrations ($>30\,\mu g\,g^{-1}$ of sediment) reported at both bathyal and hadal depths (Danovaro et al., 2002). Deposit feeders (as selective-1A-plus not selective-1B-deposit feeders) accounted together for more than 50% of the nematode assemblage at all stations. Their relevance is also consistent with the presence of large amounts of "fresh" organic detritus. According to previous deep-sea studies (Jensen, 1988; Tietjen, 1984, 1989) also in the Atacama Trench, predator/scavengers accounted for a minor fraction of total nematode density (ca. 1%). Tietjen (1989) suggested that the negligible contribution of this feeding type could indicate the absence of freshly dead organisms. Since predators are generally characterised by a large size, the low density of the group 2B might also have contributed to the low nematode individual biomass.

4.3. Nematode biodiversity

The biodiversity reported in the Atacama Trench follows the general pattern seen for deep-sea nematode biodiversity. Shannon diversity, genus and species richness and rarefaction curves provided the lowest values at the deepest site and this pattern was more evident at genus than at species level (Table 3; Fig. 4) indicating that the number of species per genus was higher in hadal than in bathyal sediments. Boucher and Lambshead (1995) and Lambshead et al. (2000, 2001a, b) reported that there was no difference between bathyal and abyssal nematode diversity, but Trench sediments (i.e. Puerto Rico Trench; Tietjen, 1989) are known to display a lower diversity when compared to bathyal and abyssal sites. This applies also to Atacama Trench, where biodiversity at hadal depths, consistently for all indices utilised (H', ITD, Taxonomic diversity and distinctness), was lower, thought not significantly, than at bathyal depths. This pattern was confirmed by the rarefaction statistics (Fig. 4), as curves calculated for nematodes at bathyal depths (Atacama Slope) were clearly above the one derived from nematodes in Trench sediments (and differences were significant for both genera and species: ANOVA $p<0.01$ and $p<0.05$, respectively).

Previous studies carried out in Venezuela basin and Puerto Rico Trench reported that the Shannon diversity followed the reduction of the concentrations of food sources in the sediments and the homogeneity of the grain size (silt-clay composition; Tietjen, 1984, 1989). In the Atacama Trench, silt-clay sediments dominated by >90%, whereas a more heterogeneous grain size structure was observed at bathyal depths. According to Tietjen (1984) more heterogeneous substrates are responsible for a higher number of microhabitats and this might result in an increase to the species richness (in our case for ca. 50%) and, to a lesser extent of the evenness.

The sediments of the Atacama Trench were characterised by a strong organic matter content. Rex (1983) and Rex et al. (1993) reported that also a high nutrient loading could be responsible of the reduction of diversity through several mechanisms, which include the acceleration and destabilisation of inter-specific interactions and the alteration of the nature and scale of habitat heterogeneity (Etter and Grassle, 1992). This condition is likely to occur in the Atacama Trench for at least two reasons. The first is that we observed a strong reduction of the index trophic diversity in hadal samples. The second is that we found opportunist genera (colonisers) becoming more dominant in the Trench sediments. Both these factors might have contributed to the reduction of the nematode diversity.

All parameters of nematode diversity, calculated both at species and genus level in the Atacama Trench, were significantly lower than those reported from other sites at similar depths worldwide ($p<0.05$ for bathyal and $p<0.01$ for hadal stations; Table 5). In Atacama Trench, also the rarefaction statistics, estimated in a sample of 51 individuals, were lower than data reported from other deep-sea sites (Table 5). The results of this study also indicated that, contrary to what is reported by Tietjen (1984, 1989), nematode species in the Atacama Trench were less evenly distributed (one species/genus accounting for >24% of individuals at 7800-m depth). The major difference we found by comparing our deep-sea system to all other deep-sea environments (in which nematode diversity has been investigated) is that the Atacama system, being located underneath a highly productive upwelling system, was characterised by organic matter concentrations up to two orders of magnitude higher than in typical oligotrophic equally deep sediments. Therefore, it is likely that organic enrichment affected overall deep-sea biodiversity, but to a different extent at bathyal and hadal depths.

Since the Atacama Trench displays the highest nematode densities ever recorded in the deep sea, it is not unreasonable to assume that this reflects the high productivity of the area (as also confirmed by the large accumulation of organic matter). Given that previous studies have shown nematode diversity to be positively associated with productivity, this could mean that when productivity is so high that it is more like a coastal site, then diversity could fall again (Boucher and Lambshead, 1995). However, other factors might also have contributed to the observed differences in nematode diversity. One possibility is that, being local biodiversity related to regional diversity (Boucher and Lambshead, 1995), the low diversity values observed in the Atacama Trench reflect the low regional diversity, but little information is available in this regard. Another possibility is that the low trench diversity is the result of physical sediment disturbance (Lambshead et al., 2001b), possibly due to the instability of the trench slopes.

All indexes of functional diversity followed the patterns observed for the structural diversity indexes. The index of trophic diversity increased

Table 5
Species diversity, evenness and mean and standard deviation of ES(51) rarefaction statistics of nematode assemblages in deep-sea sediments from different locations

Location	Depth (m)	Number of species	Diversity H′	Evenness J	ES(51)	Authors
Mediterranean Sea	1200	100	6.0	n.a	n.a	Soertaert et al. (1991)
Norwegian Sea	1245	40	5.0	0.94	n.a	Jensen (1989)
Norwegian Sea	1255	20	3.9	0.90	n.a	Jensen (1989)
Norwegian Sea	1426	28	4.5	0.95	n.a	Jensen (1989)
Puerto Rico Trench	2217	70	4.0	0.89	26.8±1.1a	Tietjen (1989)
Atacama slope	1050	63	3.1	0.88	25.0±0.4	Present study
Atacama slope	1140	65	3.2	0.87	26.7±0.1	Present study
Atacama slope	1355	60	3.2	0.89	26.0±0.1	Present study
Norwegian Sea	3062	42	4.4	0.88	n.a	Jensen (1989)
Norwegian Sea	3294	23	3.8	0.85	n.a	Jensen (1989)
Venezuela Basin	3858	53	3.4	0.93	27.2±2.0[a]	Tietjen (1984)
Venezuela Basin	3517	85	4.0	0.95	32.1±1.0[a]	Tietjen (1984)
Venezuela Basin	5054	75	3.6	0.85	31.8±2.2[a]	Tietjen (1984)
Hatteras Plain	5411	116	4.1	0.87	30.0±1.1[a]	Tietjen (1989)
Puerto Rico Trench	7460	82	3.6	0.87	25.4±1.0[a]	Tietjen (1989)
Puerto Rico Trench	8189	67	3.6	0.92	22.4±0.5[a]	Tietjen (1989)
Puerto Rico Trench	8380	62	3.3	0.86	21.6±4.0[a]	Tietjen (1989)
Atacama Trench	7800	37	2.7	0.81	18.4±0.2	Present study

[a] Data from Lambshead et al. (2000).
n.a.: not available.

with depth, suggesting the reduction of feeding type diversity at hadal depths. The index of trophic diversity and the maturity index showed an opposite pattern, confirming the large dominance of trophically homogeneous coloniser species, able to exploit the large amounts of food available, in the Trench sediments.

In the Atacama Trench the relative importance of the feeding type 1A decreased according to the decrease of bacterial abundance and biomass (Danovaro et al., 2002), whereas the relative percentage of the feeding groups 1B and 2A increased.

According to Warwick and Clarke (1998), nematodes belonging to trophic guild 1A are characterised by the highest taxonomic distinctness and group 1B by the lowest values. Therefore, changes in taxonomic distinctness are due to changes in the trophic structure of nematode assemblages.

Finally, the reduction of taxonomic diversity and distinctness in the Atacama Trench, coupled with the presence of a significantly lower number of species, genera and families (as previously reported also in Puerto Rico Trench), leads to the hypothesis that only a limited number of species may be barotolerant or adapted to extreme pressure conditions, and that this might be reflected also at genus and family level.

Acknowledgements

This work was carried out within the framework of the programme ATIE financially supported by University of Genoa. Prof. N. Della Croce, Project Co-ordinator, is acknowledged for making possible our participation in ATIE's activities. The authors are grateful to two anonymous reviewers for precious comments and suggestions and indebted to Capt. Nuñez and the crew of the RV *Vidal Gormaz* for the precious collaboration during the cruise. Thanks are also due to S. Ceradini and H. Sievers, G. Albertelli, A. Covazzi and R. Cattaneo-Vietti (Genoa) and J.I Cañete (Valparaiso) for stimulating discussions and help during sampling.

References

Ahumada, R., 1989. Producción y destino de la biomasa fitoplanctónica en un sistema de bahìas en Chile central: una hipótesis. Biologia Pesquerra, Chile 18, 53–66.

Angel, M.V., 1982. Ocean Trench Conservation. International Union for Conservation of Nature and Natural Resources. The Environmentalist 2, 17.

Bett, B., Vanreusel, A., Vincx, M., Soltwedel, T., Pfannkuche, O., Lambshead, P.J.D., Gooday, A.J., Ferrero, T., Dinet, A., 1994. Sampler bias in the quantitative study of deep-sea meiobenthos. Marine Ecology Progress Series 104, 197–203.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends in Ecology & Evolution 14, 224–228.

Bongers, T., Alkemade, R., Yeates, G.W., 1991. Interpretation of disturbance induced maturity decrease in marine nematode assemblages by means of the Maturity Index. Marine Ecology Progress Series 76, 135–1472.

Boucher, G., Lambshead, P.J.D., 1995. Ecological biodiversity of marine nematodes in samples from temperature, tropical and deep-sea regions. Conservation Biology 9, 1594–1604.

Clarke, K.R., 1993. Non parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35, 523–531.

Danovaro, R., 1999. Organic matter composition and bacterial activity in the sediments of the Atacama Trench. Atacama Trench International Expedition (ATIE) Agor 60 Vidal Gormaz. II, University of Genoa Press, pp. 1–88.

Danovaro, R., Della Croce, N., Petrillo, M., 1999a. ATIE (Atacama Trench International Expedition): evidence for extremely rich active benthic communities. Deep-Sea Newsletter 28, 14–15.

Danovaro, R., Dinet, A., Duineveld, G., Tselepides, A., 1999b. Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions-Catalan Sea (western Mediterranean) and the Cretan Sea (eastern Mediterranean). Progress in Oceanography 44, 287–312.

Danovaro, R., Gambi, C., Della Croce, N., 2002. Meiofauna hotspot in the Atacama Trench (Southern Pacific Ocean). Deep-Sea Research I 49, 843–857.

Della Croce, N., Albertelli, G., Danovaro, R., Petrillo, M., Ceradini, S., Covazzi, A., Curzi, P.V., 1998. Atacama Trench International Expedition (ATIE) Agor 60 Vidal Gormaz. I Report, University of Genoa Press, pp. 1–24.

Dinet, A., Vivier, M.H., 1979. Le meiobenthos abyssal du Golfe de Gascogne. II. Les peuplements de Nematodes et Leur divesite specifique. Cahiers de Biologie Marine 20, 109–123.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep-sea as a function of sediment particle size diversity. Nature 360, 576–578.

Fossing, H., Gallardo, V.A., Jørgensen, B.B., Hüttel, M., Nielsen, L.P, Schulz, H., Candfield, D., Forster, S., Glud, R.N., Gundersen, J.K., Ramsing, N.B., Teske, A., Thamdup, B., Ulloa, O., 1995. Concentration and transport of nitrate by mat-forming sulphur bacterium Thioploca. Nature 374, 713–715.

Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. Oceanography and Marine Biology Annual Review 23, 399–489.

Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Jensen, P., 1987. Feeding ecology of free-living aquatic nematodes. Marine Ecology Progress Series 35, 187–196.

Jensen, P., 1988. Nematode assemblages in the deep-sea benthos of Norwegian Sea. Deep-Sea Research I 35, 1173–1184.

Lambshead, P.J.D., Platt, H.M., Shaw, K.M., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. Journal of Natural History 17, 859–874.

Lambshead, P.J.D., Elce, B.J., Thistle, D., Eckman, J.E., Barnett, P.R.O., 1994. A comparison of the biodiversity of deep-sea marine nematodes from three in the Rockall Trough, Northeast Atlantic and one stations in the San Diego Trough, Northeast Pacific. Biodiversity Letters 2, 95–107.

Lambshead, P.J.D., Tietjen, J., Ferrero, T., Jensen, P., 2000. Latitudinal diversity gradients in the deep-sea with special reference to North Atlantic nematodes. Marine Ecology Progress Series 194, 159–167.

Lambshead, P.J.D., Tietjen, J., Moncrieff, C.B., Ferrero, T., 2001a. North Atlantic latitudinal diversity patterns in deep-sea marine nematode data: reply to Rex et al. Marine Ecology Progress Series 210, 299–301.

Lambshead, P.J.D., Tietjen, J., Glover, A., Ferrero, T., Thistle, D., Gooday, A., 2001b. The impact of large-scale natural physical disturbance on the diversity of deep-sea North Atlantic nematodes. Marine Ecology Progress Series 214, 121–126.

Margalef, R., 1958. Information theory in ecology. General Systems 3, 36–71.

Moens, T., Vincx, M., 1997. Observations on the feeding ecology of estuarine nematodes. Journal of Marine Biology Association UK 77, 211–227.

Moens, T., Verbeeck, L., Vincx, M., 1999. Feeding biology of predatory and facultatively predatory nematode (*Enoploides longispiculosus* and *Adoncholaimus fucus*). Marine Biology 134, 585–593.

Pfannkuche, O., 1985. The deep-sea meiofauna of the Porcupine Seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stocks. Oceanologica Acta 8, 343–353.

Pielou, E.C., 1975. Ecological Diversity. Wiley, New York, p. 165.

Platt, H.M., Warwick, R.M., 1983. A Synopsis of the Freeliving Marine Nematodes. Part I: British Enoplids. Cambridge University press, Cambridge, p. 307.

Renaud-Mornant, J., Gourbault, N., 1990. Evaluation of abyssal meiobenthos in the eastern central Pacific (Clarion-Clipperton Fracture Zone). Progress in Oceanography 24, 317–329.

Rex, M.A., 1983. Geographical patterns of species diversity in the deep-sea benthos. In: Rowe, G. T. (Ed.), The Sea. Wiley, New York, 8: 453–472.

Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L., Wilson, G.D.F., 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365, 636–639.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. American Naturalist 102, 243–282.

Schewe, I., Soltwedel, T., 1998. Deep-sea meiobenthos of the central Arctic ocean: distribution patterns and size-structure under extreme oligotrophic conditions. Vie et Milieu 49, 79–92.

Seinhorst, J.W., 1959. A rapid method for the transfer of nematodes from fixative to unhydrous glycerine. Nematologica 4, 67–69.

Sievers, H.A., Ceradini, S., Petrillo, M., Danovaro, R., Della Croce, N., 1999. A note on the thermal structure in South Eastern Pacific waters off Antofagasta, Chile. Atacama Trench International Expedition (ATIE). Second report. Preliminary Results, 83pp.

Soetaert, K., Heip, C., 1989. The size structure of nematode assemblages along the Mediterranean deep-sea transect. Deep-Sea Research I 36, 93–102.

Soetaert, K., Heip, C., 1995. Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. Marine Ecology Progress Series 125, 171–183.

Soetaert, K., Heip, C., Vincx, M., 1991. Diversity of nematode assemblages along a Mediterranean deep-sea transect. Marine Ecology Progress Series 75, 275–282.

Soltwedel, T., Pfannkuche, O., Thiel, H., 1996. The size structure of deep-sea meiobenthos in the North-Eastern Atlantic: nematode size spectra in relation to environmental variables. Journal of Marine Biology Association UK 76, 327–344.

Thiel, H., 1975. The size structure of the deep-sea benthos. Internationale Revueder Gesamten Hydrobiologie 60, 575.

Thistle, D., Sherman, K., 1985. The nematode fauna of a deep-sea site exposed to strong near bottom currents. Deep-Sea Research I 31, 1077–1088.

Thistle, D., Lambshead, P.J.D., Sherman, K., 1995. Nematode tail-shape groups respond to environmental differences in the deep sea. Vie Milieu 45, 107–115.

Tietjen, J.H., 1976. Distribution and species diversity of the deep-sea nematodes off north Carolina. Deep-Sea Research I 23, 755–768.

Tietjen, J.H., 1984. Distribution and species diversity of deep-sea nematodes in the Venezuela basin. Deep-Sea Research I 31, 119–132.

Tietjen, J.H., 1989. Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. Deep-Sea Research I 36, 1579–1594.

Tietjen, J.H., 1992. Abundance and biomass of metazoan meiobenthos in the deep-sea. In: Rowe, G., Pariente, V. (Eds.), Deep-Sea Food Chain and the Global Carbon Cycle, Vol. 360. Kluwer Academic publishers, Dordrecht, Netherlands, pp. 45–62.

Tietjen, J.H., Deming, J.W., Rowe, G.T., Macko, S., Wilke, R.J., 1989. Meiobenthos of the Hatteras Abyssal Plain and Puerto Rico Trench: abundance, biomass and association with bacteria and particulate fluxes. Deep-Sea Research I 36, 1567–1577.

Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities on the south-eastern Weddell Sea shelf and slope (Antarctica). Marine Ecology Progress Series 181, 237–256.

Vanreusel, A., Vincx, M., Schram, D., Van Gansbeke, D., 1995. On the vertical distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic. Internationale Revueder Gesamten Hydrobiologie 80, 313–326.

Vanreusel, A., Van-den-Bossche, I., Thiermann, F., 1997. Free-living marine nematodes from hydrothermal sediments: similarities with communities from diverse reduced habitats. Marine Ecology Progress Series 157, 207–219.

Vanreusel, A., Clough, L., Jacobsen, K., Ambrose, W., Jivaluk, J., Ryheul, V., Herman, R., Vincx, M., 2000. Meiobenthos of the Central Arctic ocean with special emphasis on the nematode community structure. Deep-Sea Research I 47, 1855–1879.

Vincx, M., Bett, B.J., Dinet, A., Ferrero, T., Gooday, A.J., Lambshead, P.J.D., Pfannkuche, O., Soltwedel, T., Vanreusel, A., 1994. Meiobenthos of the deep Northeast Atlantic. Advance in Marine Biology 30, 2–88.

Warwick, R.M., Clarke, K.R., 1998. Taxonomic distinctness and environmental assessment. Journal of Applied Ecology 35, 532–543.

Wieser, W., 1953. Die beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv Fur Zoology 2 (4), 439–484.