Interregional variation of free-living nematode assemblages in tropical coral sands

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Abstract: Nematode assemblages were studied in tropical lagoonal carbonate sands at four regions in the Pacific Ocean. This material was compared to other described nematode assemblages originating from ecologically similar sites. Data were aggregated to a range of hierarchical taxonomic levels. The contribution of different environmental variables to the variability of nematode assemblages was estimated at local, regional (four studied regions) and global scales (this study plus other available data). All nematode assemblages were significantly different at species and generic levels between different study regions. At higher taxonomic levels (family and order) most regions were not distinguishable and the assemblages were dominated by Desmodoridae, Chromadoridae and Xyalidae. Multivariate analysis showed that mean grain size, silt content and depth contributed mostly to the variability of nematode assemblages at the local scale whereas geographical co-ordinates were most important at regional and global scale. However, the weak relationship between sediment characteristics, co-ordinates and biota suggests that other variables are important in structuring nematode assemblages at a global scale.

Résumé : *Variations spatiales des assemblages de Nématodes libres marins dans les sables coralliens tropicaux.* Des associations de Nématodes ont été étudiées dans des sables carbonatés prélevés en quatre régions du Pacifique. Ce matériel est comparé aux autres associations précédemment décrites dans des sites tropicaux similaires. Les données faunistiques ont été traitées à différents niveaux de hiérarchie taxonomique. La contribution des divers paramètres environnementaux à la variabilité des assemblages de Nématodes est estimée aux différentes échelles locale, régionale et globale (cette étude plus les données disponibles dans la littérature). Tous les assemblages considérés apparaissent significativement différents au niveau spécifique et générique. Aux niveaux hiérarchiques plus élevés (famille et ordre), les régions ne peuvent plus être identifiées et tous les assemblages sont alors dominés par les Desmodoridae, Chromadoridae et Xyalidae. Des analyses multivariées montrent que la médiane granulométrique, la teneur en pélites et la profondeur des sédiments prélevés contribuent pour l'essentiel à la variabilité des assemblages de Nématodes entre les régions alors que la position géographique se revèle plus importante à l'échelle régionale et globale. Cependant, la faible relation entre les caractéristiques du sédiment, la position de prélèvement et les caractéristiques des biotopes suggère que d'autres variables sont importantes pour la structuration des assemblages à l'échelle globale.

Keywords : Marine nematodes, carbonate sand, tropical, Pacific Ocean, scales, taxonomic hierarchy.

Introduction

The structure of nematode communities of tropical sublittoral lagoons is known from only a limited number of

ecological studies on carbonate sediments off the high islands and continental coastlines (e.g. Hopper & Meyers, 1967 in Florida; Grelet, 1984 in the Red Sea; Boucher & Gourbault, 1990 in the West Indies; Tietjen, 1991 in the Great Barrier Reef; Boucher, 1997 in New Caledonia) or on some semi-enclosed atoll lagoons (Alongi, 1986; Gourbault & Renaud-Mornant, 1990 a, b; Netto et al., 1999 in NW Brazil). These data sets give some basic idea of the taxonomic composition and diversity of nematode communities in tropical sediments but more work is required before a 'typical' species assemblage for coral sands could be defined (Alongi, 1989; Boucher, 1990; Boucher & Lambshead, 1995).

The proportion of undescribed nematode species is high in tropical assemblages (Boucher & Gourbault, 1990; Tietjen, 1991) whereas the genera they belong to are more or less ubiquitous (Tietjen, 1991). It is, therefore, more sensible to compare different data sets at the generic rather than at the species level.

It has been demonstrated that the usual methods of data analysis are sufficiently robust to detect the pattern of diversity at different taxonomic levels (Ferraro & Cole, 1990; Heip et al., 1988; Herman & Heip, 1988; Warwick, 1988a, 1988b; Warwick et al., 1990) and surprisingly little information is lost even when the specimens are identified at the level of genera or family. Revisiting the subject,

Somerfield & Clarke (1995) confirmed that nematode community patterns are similar up to generic level but further aggregation (at the family level or trophic structure) alters the perceived pattern of environmental factors (Somerfield et al., 1994).

The aim of this study was to analyse the structure of nematode assemblages at four locations in the Pacific Ocean: Miyako (Ryukyu Archipelago, Japan , this study), New Caledonia (Boucher, 1997), Fiji (Boucher & Kotta, 1996) and Moorea (French Polynesia, this study). This material was compared to other described nematode assemblages originating from ecologically similar sites. Data were aggregated at a variety of hierarchical taxonomic levels. The contribution of different environmental variables to the variability of nematode assemblages was estimated at regional, basin (four studied regions) and global scales (this study plus other available tropical data).

Material and methods

Study area
Nematode assemblages from lagoonal carbonate sands (fringing or barrier reef) were investigated in four regions in the Western and Central Pacific Ocean (Table 1). Samples were collected in the SW lagoon of New Caledonia

Table 1. Position, sediment characteristics and depth at the stations of this study and other comparable regions where nematode assemblages has been previously investigated (Central Great Barrier Reef by Tietjen, 1991; Davies Reef by Alongi, 1986; Guadaloupe by Boucher & Gourbault, 1990; Western Indian Ocean by Muthumbi, 1998 and Red Sea by Grelet, 1984). St1: Code of the stations in the present study; St2: Code of the stations in Boucher & Clavier (1990), Boucher & Gourbault (1990), Clavier et al. (1990), Boucher & Kotta (1996), Boucher (1997).

Region= location; depth in meters; grain size (GS) of the sediment according Wentworth scale, Grain size= GS (VFS - very fine sand, FS - fine sand, MS - medium sand, CS - coarse sand, VCS - very coarse sand, GR - gravel); Silt = silt content (%); Bottom= bottom types according Chardy et al. (1988), GS - grey-sand bottoms (seagrass beds), WS - white-sand bottoms (back reef coral sands).

Tableau 1. Position, caractéristiques granulométriques et profondeur des stations étudiées et préalablement publiées dans la littérature dans des sites tropicaux comparables (Grande Barrière de Corail par Tietjen, 1991 ; Davies reef par Alongi, 1986 ; Guadeloupe par Boucher & Gourbault, 1990 ; Ouest Océan Indien par Muthumbi, 1998 et Mer Rouge par Grelet, 1984). St1 : Code des stations utilisé dans la présente étude ; St2 : Code des stations utilisé par Boucher & Clavier (1990), Boucher & Gourbault (1990), Clavier et al. (1990), Boucher & Kotta (1996), Boucher (1997).

Region = site; depth = profondeur en mètres ; GS = granulométrie du sédiment selon l'échelle de Wentworth soit VFS-sable très fin, FS-sable fin, MS- sable moyen, CS-sable grossier, VCS-sable très grossier, GR-Gravelles) ; Silt = teneur en pélites (%) ; Bottom = types de fonds selon la classification de Chardy et al. (1998) soit GS-fonds de sables gris (herbiers), WS-fonds de sables blancs (arrière récif).

REGION	St1	St2	Longitude	Latitude	Depth	GS	Silt	Bottom
New Caledonia	NC1	1	166° 26' E	22° 19' S	10	FS	8.4	GS
	NC2	2	166° 22' E	22° 19' S	10	FS	5.9	GS
	NC3	3	166° 14' E	22° 20' S	6	MS	1.4	WS
	NC4	7	166° 21' E	22° 19' S	13	FS	3.9	GS
	NC5	9	166° 21' E	22° 23' S	11	MS	4.2	WS
	NC6	10	166° 18' E	22° 24' S	16	VFS	5.2	WS
	NC7	11	166° 20' E	22° 19' S	15	FS	4.8	GS
Fiji	FI1	29	178° 30' E	18° 50' S	8	MS	-	GS
	FI2	28	178° 31' E	18° 46' S	24	MS	-	?

	FI3	26	178° 32' E	18° 48' S	9	MS	-	WS
	FI4	9	178° 32' E	18° 47' S	31	CS	-	WS
	FI5	4	178° 29' E	18° 45' S	40	CS	-	WS
	FI6	13	178° 34' E	18° 48' S	38	CS	-	WS
	FI7	30	178° 29' E	18° 46' S	31	VFS	-	WS
Moorea	MO1	1	149° 54' W	17° 29' S	0.8	FS	3.0	WS
	MO2	2	149° 54' W	17° 29' S	0.8	FS	3.1	WS
	MO3	3	149° 54' W	17° 29' S	2.5	FS	1.7	WS
	MO4	4	149° 54' W	17° 29' S	1.5	MS	1.6	WS
	MO5	5	149° 54' W	17° 29' S	1.5	MS	2.1	WS
	MO6	6	149° 54' W	17° 29' S	1.7	CS	1.9	WS
	MO7	7	125° 30 E	17° 29' S	1.6	CS	1.8	WS
Miyako	JA1	-	125° 30 E	24° 50' N	2.5	GR	0.0	WS
	JA2	-	125° 30 E	24° 50' N	3.5	VCS	0.0	WS
	JA3	-	125° 30 E	24° 50' N	4.0	VCS	0.2	WS
	JA4	-	125° 30 E	24° 50' N	3.5	CS	0.2	WS
	JA5	-		24° 50' N	3.1	CS	0.1	-
Central Great Barrier Reef	IS5	-	146°E	18°S	15.0	-	34.0	-
	MS1	-	146°E	18°S	26.0	-	15.0	-
	MS2	-	146°E	18°S	33.0	-	15.0	-
	OS3	-	146°E	18°S	42.0	-	15.0	-
	OS4	-	146°E	18°S	46.0	-	28.0	-
Davies Reef	C	-	147°E	18°S	12.0	-	3.0	-
	D	-	147°E	18°S	2.0	-	2.0	-
	E	-	147°E	18°S	2.0	-	2.0	-
	F	-	147°E	18°S	3.0	-	3.0	-
	G	-	147°E	18°S	3.0	-	3.0	-
	H	-	147°E	18°S	6.0	-	14.0	-
	I	-	147°E	18°S	16.0	-	20.0	-
Guadaloupe	A	-	61°W	16°N	4.0	-	0.4	-
	B	-	61°W	16°N	2.0	-	0.5	-
	C	-	61°W	16°N	3.0	-	0.5	-
	D	-	61°W	16°N	1.5	-	1.4	-
	G	-	61°W	16°N	3.0	-	18.2	-
	H	-	61°W	16°N	0.7	-	0.5	-
Indian Ocean	108E	-	40°E	3°S	18.0	-	16.0	-
	127	-	41°E	2°S	24.0	-	16.0	-
	128	-	41°E	2°S	55.0	-	60.7	-
Red Sea	BH2	-	35°E	29°N	25.0	-	16.0	-
	BH5	-	35°E	29°N	5.0	-	2.0	-
	BR2	-	35°E	29°N	25.0	-	3.0	-
	BR5	-	35°E	29°N	5.0	-	1.0	-
	S142	-	35°E	29°N	26.0	-	1.0	-
	S145	-	35°E	29°N	3.0	-	2.0	-

(Boucher & Clavier, 1990; Clavier et al., 1990; Boucher, 1997), in the Great Astrolabe lagoon, South of Suva and North of Ono, Fiji (Boucher & Kotta, 1996), on a transect from the fringing reef to the barrier reef in Moorea, Tiahura, French Polynesia (Boucher et al., 1998) and on the transect from the coast (JA1) to the barrier reef (JA5) in Bora Bay, Miyako Island, Japan. Seven stations were sampled in each region except for Miyako where only five stations were sampled. Average distance between stations were 10 km in New Caledonia, 4 km in Fiji, 0.2 km both in Moorea and Miyako.

These data were compared to data from other described nematode assemblages in tropical sublittoral carbonate sand: stations A, B, C, D, G, H in Guadaloupe (Boucher & Gourbault, 1990); 127, 128, 108E in the Western Indian Ocean (Muthumbi, 1998); C, D, E, F, G, H, I in Davies Reef

(Alongi, 1986); MS1, MS2, IS5, OS3, OS4 in the Central Great Barrier Reef (Tietjen, 1991) and BH2, BH5, BR2, BR5, S142, S145 in the Red Sea (Grelet, 1984).

Sampling and analyses

One core sample (10 cm²) was collected at each station by a scuba diver. The top five centimetres of sediment from each core was preserved in 4% buffered formaline solution. On a second core, sediment granulometry was determined by sieving dried samples of the top five centimetres. Median grain size and silt content of sediment were determined using cumulative weight-percentage histograms.

Meiofauna was extracted by Ludox TM centrifugation in the laboratory and sorted by hand after dilution (1/2 to 1/8) in a Motoda box splitter in order to obtain at least 150 nematodes per sample. In each sample, the abundance of different meiobenthic taxa was estimated. A hundred nematodes were randomly selected and identified to the species level. Supplementary taxonomic information (genera, family and order), based on the classification of Platt & Warwick (1988), were added into the database. The feeding types of nematodes (Wieser, 1953) were determined.

Several diversity indices were calculated. Margalef (1958) species richness: $SR = (S-1)/Log_e(n)$; Shannon-Wiener index: $H' = -\sum p_i(log_2 p_i)$; Evenness: $J' = H'/H max$ (Pielou, 1975).

The effect of region on nematode abundance and diversity indices was estimated by one way analysis of variance (ANOVA or Kruskal-Wallis test when the data did not conform to requirements of normality and homogeneity) and multiple range testing using least significant differences (LSD) at p<0.05. Univariate parametric correlation coefficients were computed between the numeric environmental parameters, the abundance of meiobenthic taxa and different diversity indices.

Multivariate data analyses were performed by the statistical program "PRIMER" (Clarke & Warwick, 1994). MDS analysis on double-square-root transformed data of nematode abundance was used to quantify the dissimilarities between nematode communities. The Bray-Curtis similarity measure (Bray & Curtis, 1957) was used to construct the similarity matrices of nematode abundance data and Euclidean distance was used to construct the similarity matrix for environmental data. The statistical differences in nematode assemblages between study regions were calculated by ANOSIM permutation test (Clarke, 1993). The contribution of different taxa to the analysis was calculated by the SIMPER procedure (Clarke, 1993). A Spearman rank correlation (ρ_W) was computed between the similarity matrices of nematode abundance and environmental data to examine the ecological significance of environmental variables on nematode assemblages

(Clarke & Ainsworth, 1993). A permutation procedure is essential here because classical statistical approaches to significance testing are not valid for typical community matrices.

Results

Major meiobenthic taxa

There was a considerable variation in the structure of meiofaunal taxa between the four study areas. Almost all regions were significantly different in terms of meiobenthic assemblages (ANOSIM P<0.001). The assemblages in Fiji and Moorea were relatively uniform (ANOSIM P=0.53) (Fig. 1). Nematodes were dominant at Fiji, Moorea and New Caledonia sites whereas copepods were dominant in Japan. Polychaetes were the third dominant taxon in all the regions. Kinorhynchs were relatively abundant in New Caledonia and tardigrades and gastrotrichs were more abundant in Miyako.
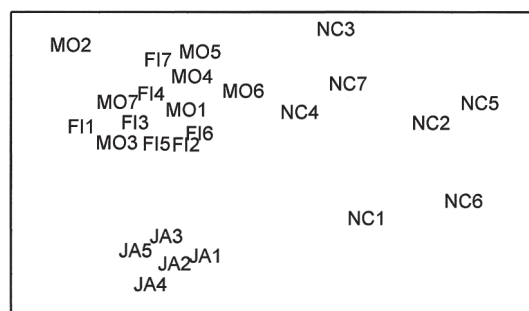
Figure 1. MDS ordination of meiofauna taxa from Miyako (JA1 to JA5), New Caledonia (NC1 to NC7), Fiji (FI1 to FI7) and Moorea (MO1 to MO7).

Figure 1. Ordination selon la méthode MDS des taxa de la méiofaune à Miyako (JA1 à JA5), en Nouvelle-Calédonie (NC1 à NC7)), aux Fidji (FI1 à FI7) et à Moorea (MO1 à MO7).

Depending on the region, either mean grain size, silt content of sediment, depth or geographical position was most important in explaining the structure of meiobenthic assemblages. The abundance of nematodes was negatively correlated with mean grain size (r=-0.53, P=0.006). In contrast, copepods had a highest abundance in coarser sediments (r=0.71, P<0.001). The abundance of tardigrades and priapulids were correlated with silt content. The former preferred coarser (r=-0.41, P=0.04) and the latter more silty sediments (r=0.50, P=0.01). At the basin scale, the effect of latitude was stronger than all other measured variables (Table 2).

Table 2. Spearman rank correlations between similarity matrices of fourth-root transformed meiobenthos data and abiotic variables (p<0.05). Additionally, the combination of environmental variables that results in highest correlation value (*Best variables*) are presented.

Tableau 2. Corrélations de rang de Spearman entre les matrices de similarité établies sur les racines quadratriques des abondances du méiobenthos et des variables abiotiques (p<0.05). La combinaison de variables environnementales fournissant la meilleure valeur de corrélation (*Best variables*) est indiquée.

Variable	Miyako	New Caledonia	Fiji	Moorea	Pacific regions
1. Longitude	-	0.338	-0.136	-	0.250
2. Latitude	-	0.177	0.109	-	0.510
3. Depth	0.135	0.077	0.100	0.003	0.013
4. Median	0.309	-0.034	-0.065	0.240	0.106
5. Silt	-0.215	0.364	-	0.265	0.108
6. Distance	-	-	-	-	0.433
Best					
variables	*0,579*	*0,462*	*0,457*	*0,353*	*0.510*
	(3,4)	*(1,5)*	*(1,2,3)*	*(4,5)*	*(2)*

Regional and basin scales

A total of 305 nematode species were recorded. Species number and all the diversity indices were significantly different between the four regions (ANOVA, *P*<0.001). Nematode species diversity was higher in Fiji and New Caledonia than in Moorea and Miyako (Table 3). The equitability index (J') showed less pronounced differences than the other indices.

Table 3. The mean and standard error of the mean for four diversity indices in four study area (N= number of samples; S=species number; SR= species richness; H'= Shannon index; J'= evenness).

Tableau 3. Moyenne et erreur standard de quatre indices de diversité calculés dans les quatre sites étudiés (N = nombre d'échantillons ; S = nombre d'espèces ; SR = richesse en espèces ; H' = indice de Shannon ; J' = équitabilité).

	N	S	SR	H'	J'
Miyako	5	22.2±2.5	4.60±.0.53	3.44±0.23	0.77±0.03
New Caledonia	7	33.4±2.1	7.04±0.45	4.43±0.20	0.88±0.03
Fiji	7	31.6±2.1	6.64±0.45	4.28±0.20	0.86±0.03
Moorea	7	16.0±2.1	3.26±0.45	2.88±0.20	0.73±0.03

Positive correlation were found between sediment silt content and species number (r=0.66 *P*=0.002), Margalef species richness (r=0.66 *P*=0.002), Shannon-Wiener index (r= 0.63 *P*=0.003) and Pielou evenness (r=0.52 *P*=0.019). All diversity indices increased with depth (r_S=0.52 P_S=0.018, r_{SR}=0.52 P_{SR}=0.018, $r_{H'}$=0.50 $P_{H'}$=0.026,

$r_{J'}$=0.37 $P_{J'}$=0.09) and decreased with mean grain size (r_N= -0.48 P_N=0.034, r_{SR}=-0.48 P_{SR}=0.034, $r_{H'}$=-0.58 $P_{H'}$=0.007, $r_{J'}$=-0.58 $P_{J'}$=0.008).

The degree of heterogeneity of nematode assemblages within a region (equivalent to beta diversity) is related to the average distance between sampling stations because the stations were located in similar biotopes i.e. shallow sublittoral coral sands. Beta diversity increased with increasing distance between the stations. However, the effect was detectable only at specific and generic level (Fig. 2). Sample or alpha diversity (S, SR, H', J'), being related to the volume of sample, is not affected as the sample size was the same at each station. Interregional distances were two orders of magnitude higher than those between the stations of a particular region. Therefore, we conclude that the effect of different sampling scales has little impact on the interpretation of interregional differences of nematode assemblages.
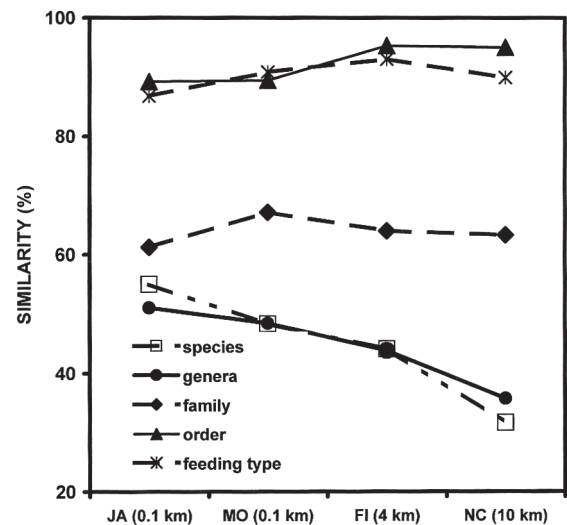
Figure 2. Average similarity of nematode assemblages at a range of taxonomic aggregation within each studied site. For Miyako (JA) and Moorea (MO), the mean distance between stations is about 0.1 km; for Fidji (FI), 4 km; for New Caledonia (NC), 10 km.

Figure 2. Similarité moyenne des assemblages de Nématodes en fonction du niveau d'agrégation taxonomique dans les différents sites. Pour Miyako (JA) et Moorea (MO), la distance moyenne entre stations est de l'ordre de 0,1 km ; pour Fidji (FI), elle est de 4 km ; pour la Nouvelle-Calédonie (NC), elle est de 10 km.

Each region was characterized by several nematode species (Table 4). *Paradesmodora sp1* comprized an average 8.3% of nematode abundance in four studied areas. This species was dominant in Moorea (27.2%) and abundant in Fiji (5.6%) but missing in New Caledonia and Miyako. It

Table 4. List of dominant species ordered taxonomically whose grand mean is GM> 0.5% in the four studied regions (numbers are percentage of abundance in the 100 selected nematode specimens).

Tableau 4. Liste des espèces dominantes présentées par famille dont la dominance générale moyenne est GM>0.5% dans les quatre sites étudiés. Les chiffres sont les pourcentages de dominance pour les 100 specimens sélectionnés au hasard.

Families	Genera	Species	Miyako	New Caledonia	Fiji	Moorea
Anticomidae	*Paranticoma*	*sp. 1*	-	1.3	2.1	0.1
Oncholaimidae	*Viscosia*	*sp. 1*	2.6	-	0.6	-
Chromadoridae	*Atrochromadora*	*sp. 1*	-	1.9	-	-
	Chromadorina	*sp. 1*	-	3.1	-	-
	Chromadorita	*sp. 2*	1.8	-	-	-
	Chromadorita	*sp. 3*	25.7	0.4	-	-
	Parapinnanema	*sp. 1*	5.8	-	-	-
	Prochromadorella	*sp. 1*	-	-	4.4	6.0
	Ptycholaimellus	*sp. 1*	-	-	4.9	1.1
	Ptycholaimellus	*sp. 2*	-	3.7	-	-
	Spilophorella	*sp. 1*	2.6	-	-	-
	Spilophorella	*sp. 3*	-	1.9	-	-
	Trochamus	*sp. 1*	6.2	-	-	-
	Trochamus	*sp. 2*	1.8	-	-	-
Comesomatidae	*Dorylaimopsis*	*sp. 1*	-	-	2.7	-
	Laimella	*sp. 1*	-	-	1.9	-
	Sabatieria	*sp. 1*	0.2	-	0.4	2.0
	Sabatieria	*sp. 2*	-	-	4.7	2.7
Ethmolaimidae	*Gomphionema*	*sp. 1*	-	-	0.6	5.4
Cyatholaimidae	*Marylynnia*	*annae* Wieser & Hopper, 1967	14.8	-	-	-
	Marylynnia	*sp. 1*	-	-	2.6	-
	Marylynnia	*sp. 2*	-	-	3.0	5.6
	Marylynnia	*sp. 4*	-	1.3	1.4	-
	Metacyatholaimus	*sp. 1*	-	0.1	2.0	0.1
	Metadesmolaimus	*sp. 1*	-	-	-	17.4
	Nannolaimoides	*sp. 1*	-	1.0	0.1	3.6
	Nannolaimoides	*sp. 2*	-	2.4	-	-
	Nannolaimus	*phaleratus* Wieser & Hopper, 1966	-	0.1	4.9	0.4
Selachinematidae	*Laxus*	*cosmopolitus* Ott et al., 1995	-	15.0	10.3	0.1
	Laxus	*sp. 2*	3.4	-	-	-
	Leptonemella	*sp. 1*	-	-	1.4	0.9
Desmodoridae	*Bolbonema*	*sp. 2*	-	2.3	-	-
	Chromaspirina	*sp. 1*	-	1.0	1.1	-
	Onyx	*sp. 2*	-	2.3	-	-
	Paradesmodora	*sp. 1*	-	-	5.7	27.3
	Pseudodesmodora	*sp. 1*	2.0	-	-	-
Microlaimidae	*Aponchium*	*cylindricolle* Cobb, 1920	-	1.0	0.9	-
	Calomicrolaimus	*sp. 1*	0.2	-	-	3.0
	Microlaimus	*sp. 3*	-	2.6	-	-
	Molgolaimus	*sp. 3*	-	-	3.3	0.4
Monoposthiidae	*Monoposthia*	*sp. 1*	-	2.1	-	-
Leptolaimidae	*Manunema*	*sp. 1*	1.8	-	-	-
Desmoscolecidae	*Desmoscolex*	*sp. 1*	1.0	-	1.0	-
	Dracograllus	*sp. 1*	4.2	-	-	-
	Leptepsilonema	*sp. 1*	2.8	-	-	-
	Perepsilonema	*papulosum* Lorenzen, 1973	2.6	-	-	-
Xyalidae	*Cobbia*	*sp. 1*	-	0.1	4.7	0.4
	Elzalia	*sp. 1*	-	1.3	1.4	-
	Paramonohystera	*sp. 1*	-	1.9	-	-
	Promonhystera	*sp. 1*	0.8	-	1.3	1.3
	Rhynchonema	*sp. 1*	2.0	-	-	5.6
	Stylotheristus	*sp. 3*	-	-	-	3.7
Linhomoeidae	*Terschellingia*	*sp. 1*	-	-	1.3	0.6
Axonolaimidae	*Axonolaimus*	*sp. 1*	-	-	1.0	0.9
	Parodontophora	*sp. 1*	-	-	0.6	2.0

was followed by *Chromadorita sp3* (grand mean GM= 6.5%) being very abundant in Japan (25.6%) and occurring at low densities in New Caledonia (0.4%). The third dominant was *Laxus cosmopolitus* Ott et al., 1995 (GM 6.4%.) occurring only in Fiji (10.4%) and New Caledonia (15.2%). *Marylynnia annae* was very common in Japan (14.8%, GM 3.7%).

The most common families were Desmodoridae (GM 22.9%), Chromadoridae (GM 20.8%), Xyalidae (GM 14.1) and Cyatholaimidae (GM 10.8%). The assemblages were numerically dominated by Chromadoridae in Miyako (46.0%) and Desmodoridae in New Caledonia (27.4%), Fiji (26.1%) and Moorea (28.7%). In Moorea, the proportion of Xyalidae (28.6%) was almost as high as that of Desmodoridae.

MDS ordination of nematode abundance data showed that the regions were clearly distinguished from each other at specific and generic levels (ANOSIM *P*<0.001) but not at the family and order levels. When nematode feeding types were taken into account, only some replicates at Moorea were distinct from other regions (ANOSIM *P*<0.001) (Fig. 3). This was mostly due to the higher proportion of non-selective deposit feeders (ANOVA *P*<0.001) and the lower proportion of selective deposit feeders. ANOVA showed significant differences only between Moorea, Fiji and Miyako at *P*<0.05) and carnivore-omnivores (ANOVA non-significant) in Moorea as compared to the three other regions. The ratio of non-selective deposit feeders to epigrowth feeders was not significantly different between the four study areas.

The analysis indicates that the generic level is sufficiently robust to identify regional differences in the structure of nematode assemblages in tropical lagoonal sediments. On the other hand, the trophic composition of nematode assemblages seems to be uniform over wider areas and the lack of difference in trophic composition does not necessarily indicate a similar taxonomic composition in different study regions.

Table 5 shows the relationships between abiotic environmental variables (position, mean grain size, silt content and depth) and the pattern of nematode assemblages at regional, basin and global scale. The permutation tests were performed at species, generic, family, and order levels and the trophic composition of the assemblages was taken into account. Different environmental variables were responsible for the variability of nematode assemblages within different regions. Longitude and latitude gave the best match for nematode assemblages at the basin scale. Depending on taxonomic level, either sampling scale or mean grain size of sediment were the third most important variables.

Global scale

The nematode assemblages at Moorea, Fiji, New Caledonia and Japan were compared to those available from other tropical sublittoral sediments: Guadaloupe (Boucher & Gourbault, 1990), Red Sea (Grelet, 1984), Central Great Barrier Reef BR (Tietjen, 1991), Davies Reef (Alongi, 1986) and Indian Ocean (Muthumbi, 1998).

Generally, the measures of species richness were significantly higher in Fiji, New Caledonia and Indian Ocean as compared to other regions. Other differences were more variable. MDS ordination was performed at the generic level to assess the taxonomic coherency of the datasets (Fig. 4). All nine regions were significantly different from each other (ANOSIM p<0.008). However, two main assemblages may be distinguished: the NorthWestern Ocean and Great Barrier Reef, and the Central and SouthWestern Pacific Ocean. The average abundance of *Terschellingia* and *Theristus* were relatively high almost in all areas. Regions from the NorthWestern Pacific and Great Barrier Reef were characterized by high abundance of *Viscosia,* the Central and SouthWestern Pacific by *Marylynnia, Prochromadorella, Ptycholaimellus* and *Oncholaimellus.* The Indian Ocean, Red Sea and Guadaloupe had higher abundance of *Daptonema* and *Microlaimus.*

The highest correlation between abiotic data and similarity matrices of biotic data occurred with latitude (P_W=0.178), mean grain size (P_W=0.213) and silt content (P_W=0.090). However, the correlation coefficients had much lower values as compared to the similar analysis at regional scale.

Based on the trophic composition of the assemblages, the regional differences were not so clear. Davies Reef had higher ratio of non-selective
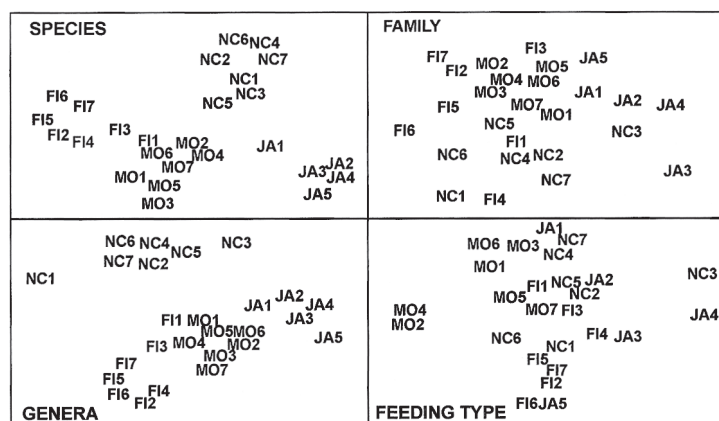
Figure 3. MDS ordination of nematode species, genera, family and trophic groups at the four study sites. For the code of station see fig. 1.

Figure 3. Ordination selon la méthode MDS des abondances des espèces, familles et groupes trophiques aux quatre sites étudiés. La signification des codes est fournie dans la figure 1.

Table 5. Spearman rank correlations between abiotic variables and similarity matrices of fourth-root transformed nematode data aggregated at a range of taxonomic levels (p<0.05). Additionally, the combination of environmental variables which results in highest correlation value (*Best variables*) are presented.

Tableau 5. Corrélation de rang de Spearman entre les variables abiotiques et les matrices de similitude établies sur les racines quadratiques des abondances de nématodes considérés à différents niveaux de hiérarchie taxonomique (p<0.05). La combinaison des variables environnementales présentant les meilleurs niveaux de corrélation (*Best variables*) sont fournies.

	Species	Genera	Family	Order	Feeding type
Miyako					
1. Depth	0.419	0.457	0.900	-0.458	-0.163
2. Median	-0.291	-0.123	-0.109	0.101	0.336
3. Silt	-0.149	-0.164	0.092	0.244	0.111
Best variables	*0.419 (1)*	*0.457 (1)*	*0.900 (1)*	*0.244 (3)*	*0.431 (2,3)*
New Caledonia					
1. Longitude	0.239	0.714	0.490	0.264	0.641
2. Latitude	0.074	0.077	0.076	0.051	0.517
3. Depth	-0.121	0.285	0.110	0.429	0.285
4. Median	0.409	0.265	0.389	0.244	0.253
5. Silt	0.376	0.462	0.306	-0.140	-0.095
Best variables	*0.475 (1,2,3,5)*	*0.738 (1,2,3,5)*	*0.604 (1,2,3)*	*0.429 (3)*	*0.740 (1,3)*
Fiji					
1. Longitude	0.312	0.280	0.243	0.039	-0.001
2. Latitude	0.049	0.014	-0.026	0.567	0.264
3. Depth	-0.068	-0.203	-0.239	-0.435	-0.371
4. Median	-0.235	-0.044	-0.100	0.031	-0.001
5. Silt	-	-	-	-	-
Best variables	*0.385 (1,2)*	*0.353 (1,2)*	*0.243 (1)*	*0.567 (2)*	*0.264 (2)*
Moorea					
1. Depth	0.314	0.133	-0.157	-0.131	-0.261
2. Median	0.297	0.207	0.051	-0.106	-0.059
3. Silt	0.074	0.078	0.105	0.299	-0.053
Best variables	*0.323 (2,3)*	*0.274 (2,3)*	*0.149 (2,3)*	*0.299 (3)*	*-0.053 (3)*
Pacific regions (n=4)					
1. Longitude	0.602	0.655	0.439	0.194	0.167
2. Latitude	0.873	0.767	0.446	0.189	0.132
3. Depth	0.108	0.103	0.075	-0.191	-0.136
4. Median	0.414	0.439	0.390	0.229	0.114
5. Silt	0.451	0.482	0.377	0.024	0.038
6. Sampling distance	0.732	0.561	0.261	-0.003	0.014
Best variables	*0.873 (2)*	*0.768 (1,2,6)*	*0.523 (1,2)*	*0,248 (1,2,4)*	*0.193 (1,2)*
All regions (n=9)					
1. Longitude	-	0.222	0.070	0.042	-0.152
2. Latitude	-	0.178	0.070	0.089	-0.095
3. Depth	-	-0.124	-0.136	-0.222	-0.135
4. Median	-	0.213	0.190	0.048	0.048
5. Silt	-	0.090	0.067	-0.036	0.062
Best variables		*0.291 (2,4,5)*	*0.203 (2,4)*	*0.127 (2,4)*	*0.121 (4,5)*

deposit feeders to epigrowth feeders compared to most other regions (Fig. 5).

Mean grain size correlated with the proportion of non-selective deposit feeders (r=-0.318 *P*=0.020) and epigrowth feeders (r=0.342 *P*=0.012), silt content (SC) and depth (D) with selective deposit feeders (r_{SC}=0.440 P_{SC}=0.001, r_D=0.467 P_D<0.001) and epigrowth feeders (r_{SC}=-0.501 P_{SC}<0.001, r_D=-0.413 P_D=0.002).
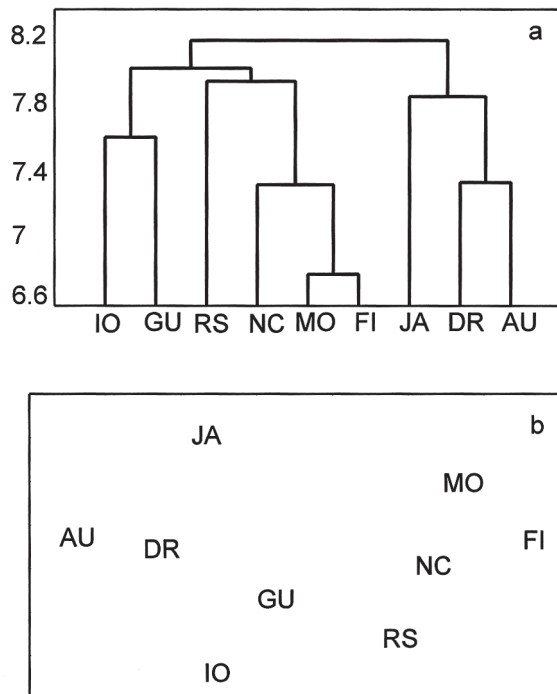
Figure 4. Cluster analysis (**a**) and MDS ordination (**b**) of nematode generic abundance at Miyako (JA), Davies Reef (DR), Central Great Barrier Reef (AU), New Caledonia (NC), Fiji (FI), Moorea (MO), Guadaloupe (GU), Indian Ocean (IO) and Red Sea (RS).

Figure 4. Classification hiérarchique (**a**) et ordination (**b**) selon la méthode MDS des abondances des genres de Nématodes recensés à Miyako (JA), Davies Reef (DR), Grande Barrière de Corail (AU), Nouvelle-Calédonie (NC), Fidji (FI), Moorea (MO), Guadeloupe (GU), Océan Indien (IO) et Mer Rouge (RS).
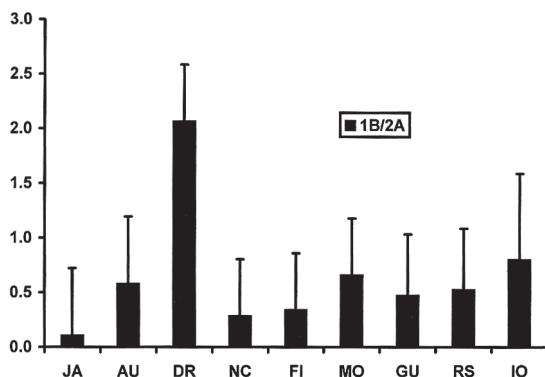
Figure 5. Average values (s.e.) of the ratio of non-selective deposit feeders (1B) to epigrowth feeders (2A) with standard error in nine tropical regions. For the code of regions, see fig. 4.

Figure 5. Valeurs moyennes et erreur standard du rapport des mangeurs de dépôts non-sélectif (1B) sur les suceurs d'épistrates (2A) dans les neuf sites tropicaux connus. Voir les codes des régions à la figure 4.

Discussion

This study is the first quantitative attempt to compare nematode assemblages in tropical carbonate sands and try to understand the main attributes of these assemblages. In contrast with a variety of studies in temperate seas (Heip et al., 1985), comparatively little is known about the composition and diversity of tropical sublittoral nematodes (e.g. Alongi, 1987; Alongi, 1990; Tietjen, 1991; Boucher & Lambshead, 1995; Boucher, 1997). Unlike temperate seas, the generalized distribution pattern of dominant/typical nematode assemblage has not yet been described.

To address this question, we used series of samples from nine sites, five of which were collected with the same techniques by the senior author (GU, NC, MO, FI, JA) i.e. 10 cm^2 hand coring (0-5 cm) by scuba diving and splitting of the sample in order to randomly obtain 100 individuals. Comparisons were however made with samples collected in different ways. The Red Sea and Davies Reef sites were similarly sampled by scuba diving on the five top centimetres but on different surface area for the second site (4.9 cm^2) and on different sample size (200 individuals, and 35 to 226 individuals respectively). Only Great Barrier Reef and Indian Ocean sites were sampled with box corers, a sampling method supposed to be the closed to scuba diving. Sample size were different (150 to 553 specimens). Previous studies have shown that, although species number increases with sample size (Boucher, 1980), no significant difference in the structure of the species assemblage could be detected for 100, 200 and 300 individual samples. More problematic is the size of the sediment column studied : 10 cm and 5 cm respectively, a difference which is known to affect the species composition due to a well know vertical zonation of the different species in the sediment column (Jensen, 1987). Difference in the taxa assemblages of the Great Barrier Reef samples (AU) have thus to be considered with some caution.

The structure of nematode assemblages was highly sensitive to the selected taxonomic level. The patterns of nematode abundance at the levels of species and genera were not different in this study. Aggregations at higher taxonomic levels resulted in a notable shift in assemblage structure. Somerfield & Clarke (1995) have reported similar findings. These results justify the use of nematode genus data for comparing assemblage structure at a global scale. Since the identification of nematodes at the species level is far more complicated and time consuming than generic identification, this conclusion have some important practical implications in poorly studied areas such as tropical biotopes or the deep sea. Focusing on the generic rather than species composition of nematode communities will allow investigation of far more sites for a given deployment of resources.

There is some evidence that, despite widespread geographical separation, nematode assemblages from sublittoral carbonate sediments of tropical seas are dominated by identical or closely related genera (Grelet, 1984; Alongi, 1986; Boucher & Gourbault, 1990; Tietjen, 1991). The present study suggests that this is also true at the family level i.e. the assemblages were dominated by Desmodoridae, Chromadoridae and Xyalidae. The proportion of the Chromadoridae was much higher in the Western Pacific Ocean - New-Caledonia (Boucher, 1997), Great Barrier Reef (Tietjen, 1991), Davies Reef (Alongi, 1986) and Japan - compared to other study areas. The distribution of *Desmodoridae* and *Xyalidae* was more variable. Genera dominant in one region could have low density or even be missing in other. However, the regions that were spatially closer had higher generic affinity. *Paradesmodora* was dominant in Fiji and Moorea but lacking elsewhere except in the Red Sea (Grelet, 1984) where it occurred in low numbers. *Theristus* or the related genera *Metadesmolaimus* were relatively abundant in all studied areas, but the former was dominant only in Davies Reef and central Great Barrier Reef (AU).

The diversity of nematode assemblages was higher in New Caledonia, Fiji and Indian Ocean compared with other study regions. Decrease in nematode diversity indices from New Caledonia to Polynesia conforms to the general trend observed for macrofauna taxa. Higher diversity was related to the finer sediment composition.

There exists no single explanation as to whether abiotic or biotic factors determine the structure and diversity of nematode assemblage (Giere, 1993). It is likely that biotic interactions are more important in physically stable environment while abiotic factors dominate in the regions where the intensity of disturbance is higher. Tropical carbonate sands are subjected to frequent disturbance (Connell, 1978) and periodic oxygen depletion (Sournia, 1976; Boucher & Gourbault, 1990) and, hence, abiotic factors might be expected to be most important in regulating the structure of nematode assemblages. Nematode species assemblages are known to be very sensitive to slight changes in sediment composition (Govaere et al., 1980). However, the diversity of these assemblages related to sediment characteristics remains rather controversial. Previous studies have shown that an increase of silt content may either decrease or increase nematode diversity (Tietjen, 1980; Boucher, 1990; Boucher & Gourbault, 1990; Boucher & Lambshead, 1995).

Various studies indicate that variability exists on a scale of a few centimetres (e.g. Heip et al., 1985). Variability on a larger scale (km scale) may have either negligible (Heip et al., 1979) or significant effect on nematode assemblages (Li et al., 1997). During this study, the sampling scale within the local sites ranked from one hundred meters in Moorea and Miyako to 10 km in New Caledonia. In the latter area, the replicate variability often exceeded the variability between sites (Boucher, 1997) indicating that the pattern of nematode distribution seems to be relatively homogeneous over tens of kilometres in tropical carbonate sands. On the other hand, significant interregional differences indicate high heterogeneity in the structure of nematode assemblages at the scale of 1000 km.

Multivariate analyses showed that grain size, silt content and depth contributed mostly to the variability of nematode assemblages at the local scale whereas geographical coordinates were most important at regional and global scales (Table 5). However, the combination of several environmental variables often gave better match than single variable indicating the complexity of the effect. Although our samples originate from sublittoral carbonate sands, the effect of sediment also was relatively strong at the global scale. Nevertheless, the values of correlation coefficient were relatively low. In contrast to the commonly held view that sediment characteristics, such as median grain size or silt content, are the prime factors in structuring benthic assemblages, some other sediment characteristics or environmental variables related to the biogeochemistry of interstitial water may be responsible for the global scale variability of nematode assemblages. On the other hand, the structure of assemblage based on the feeding types of nematodes only was always significantly related to the sediment characteristics irrespective of scales studied.

Acknowledgements

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