



Walking with worms: coral-associated epifaunal nematodes

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ABSTRACT

Aims To study the community structure and habitat preferences of the Epsilonematidae and Draconematidae in coral degradation zones. To assess the contribution of different localities and microhabitats to meiobenthic diversity in such ecosystems. To discuss dispersive capacities and the occurrence of cryptic species in meiobenthic organisms.

Location Porcupine Seabight (north-east Atlantic Ocean; continental slope) and a transect along the Kenyan coast (Indian Ocean; shallow lagoon).

Methods In the north-east Atlantic, dead coral fragments, sponge skeletons and sediment were collected with a boxcorer. Along the Kenyan coast, dead coral fragments and coral gravel were collected during snorkelling and skin diving. Only nematodes belonging to the families Epsilonematidae and Draconematidae were considered. Community structure was analysed using multivariate techniques. Biodiversity was represented via rarefaction curves. Additive partitioning of species diversity was conducted. Turnover between microhabitats within locations and between locations within microhabitats were compared in a ternary plot.

Results Twelve epsilonematid and five draconematid species were found in the Porcupine Seabight. In Kenya, 39 epsilonematid and 20 draconematid species were distinguished. Three species were found at both sampling locations. A table with the known distribution of all currently described species encountered in our study area is provided. At both sampling locations, the communities on coral fragments were significantly different from those in the other microhabitats, and were most diverse. In Kenya, species richness was mainly determined by local diversity and by turnover between localities. The contribution of β -diversity decreased when abundance data were analysed. Turnover between microhabitats and between coral samples from different localities was higher than turnover between locations for gravel samples.

Main conclusions Coral fragments were recognized as favourable substrata for typically epifaunal nematodes. Species-specific habitat preferences were explained by finely tuned morphological adaptations. Our results suggest that cosmopolitan species could well be cryptic species, and this explanation for the existence of morphologically identical nematodes in geographically distant areas is weighed up against other plausible explanations. Coral degradation zones are an important source for new species of Epsilonematidae and Draconematidae. The addition of sampling locations contributed to the total number of species, although the added species were generally rare.

Keywords

Biodiversity, biogeography, Draconematidae, East African coast, Epsilonematidae, habitat preferences, north-east Atlantic.

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INTRODUCTION

Marine, free-living nematodes are typically known as fine and slender worms that slide through the interstia of the sediment with undulations of their body. Aberrant body shapes occur in a number of families, for example the short, stout Desmoscolicidae and the epsilon- or s-shaped Epsilonematidae and Draconematidae, which usually have pronounced enlargements at the level of the pharynx and posterior body region. Nematodes belonging to either of the two latter families are also characterized by the presence of unique locomotory structures: Epsilonematidae have so-called ambulatory setae on the ventral side of their posterior body, and Draconematidae have both cephalic and posterior adhesion tubes. Together with the caudal glands, these structures enable the nematodes to attach themselves to a large substratum and/or crawl over its surface in a fashion that is most comparable with that of a geometrid caterpillar (Stauffer, 1924; Lorenzen, 1973). As a result of these adaptations, Epsilonematidae and Draconematidae are found almost exclusively in coarse sand and on larger substrata such as seagrass leaves and coral fragments. Hereafter, they are referred to as 'typically epifaunal nematodes'.

The species within both families are characterized by a wide spectrum of body shapes and sizes, as well as differences in other morphological features, such as cuticular ornamentation and cuticular appendages (Verschelde & Vincx, 1994).

Two recent studies on the ecology of the nematofauna in cold-water coral (Porcupine Seabight; Raes & Vanreusel, 2006) and tropical coral (Kenyan coast; Raes *et al.*, 2007) degradation zones have indicated that Epsilonematidae and Draconematidae have a pronounced preference for dead coral fragments. Comparisons between coral fragments and underlying sediment in both environments have revealed that the presence of these typically epifaunal nematodes on coral fragments is very important in explaining the differences between the nematode assemblages in both microhabitats. Furthermore, these nematodes make up a considerable proportion of the total nematode community on coral fragments. Consequently, a substantial number of epsilonematid and draconematid species may be collected from coral environments.

Epsilonematidae and Draconematidae are abundant in both deep-water and shallow coral-associated environments. Therefore, the communities from these very different environments can be compared. The current study focuses on the microhabitat preferences, biogeography and diversity of the typically epifaunal nematode communities in coral degradation zones. In this study, only a subset of the nematode community consisting of Epsilonematidae and Draconematidae is considered, which can be justified by the relatively high number of specimens and species found in both environments. Such a selection enables an evaluation of the finely tuned microhabitat preferences of the species within these two families. Our study also provides new data on the biogeography of marine, free-living nematodes.

A final part of this study focuses on biodiversity: the diversity of communities associated with different microha-

bitats is compared. Meiofauna samples from coral fragments and coral gravel were collected from seven locations along a north-to-south transect on the south coast of Kenya. This provided us with the opportunity to compare the turnover between the communities from different microhabitat types and between those from different locations. The contribution of both α -diversity (sample diversity) and β -diversity (turnover) to the total (γ) diversity (additive partitioning) is discussed.

MATERIALS AND METHODS

Sampling sites, microhabitats and laboratory analyses

For meiofaunal organisms, conditions within the sediment are different from those on a complex elevated structure on the sea floor, in terms of food availability as well as physical disturbance by (strong) bottom currents. Next to this primary distinction between large biogenic substrata and the underlying sediment as a habitat, small-scale differences in microhabitat structure can also influence meiofaunal community composition. In this respect, the rough surface of dead coral branches, sometimes covered by a fine layer of bryozoan colonies or small algae, is different from, for example, the complex three-dimensional build-up of spicules in a glass sponge skeleton.

Biological samples were collected from a cold-water coral degradation zone in the Porcupine Seabight and a tropical coral degradation zone along the coast of Kenya (Fig. 1).

The Porcupine Seabight is a large embayment of the European continental slope, located south-west of Ireland (north-east Atlantic). Material was obtained by means of Netherlands Institute for Sea Research boxcorers (cylindrical, diameter 32 cm) on 17 June 2000 (two boxcores: box IV 2000 and box V 2000) and 7 May 2001 (one boxcore: box IV 2001) (Table 1). The distance between box IV 2000 and box IV 2001 was 659 m. Sampling depth ranged between 972 and 1005 m. A detailed description of the sampling location and governing environmental conditions is given by Raes & Vanreusel (2005). The surface of the sediment in each boxcore was partly or entirely covered by fragments of dead corals [*Lophelia pertusa* (Linnaeus, 1758); Fig. 2a] and dead sponge skeletons [*Aphrocallistes bocagei* Schultze, 1886; Fig. 2b]. Recolonization of the debris by small colonies of living coral was observed, although only to a small extent. The larger coral (11) and sponge (seven) fragments were collected separately. After removal of these structures, three cores (10 cm²) were pushed into the sediment of each boxcore. This sediment consisted of poorly sorted, fine-to-medium sand (median 194.9 μ m) with a small fine silt fraction, a high amount of globigerine forams and littered with small sponge and coral fragments, mollusc shells and echinoid spines (Fig. 2c).

Eight sites were selected on the Kenyan coast, from Watamu in the north to Kisite in the south (Fig. 1; Table 1). The distance between Watamu and Kisite was 162.5 km. Sampling depth varied between 0.3 and 6 m. At each location, large

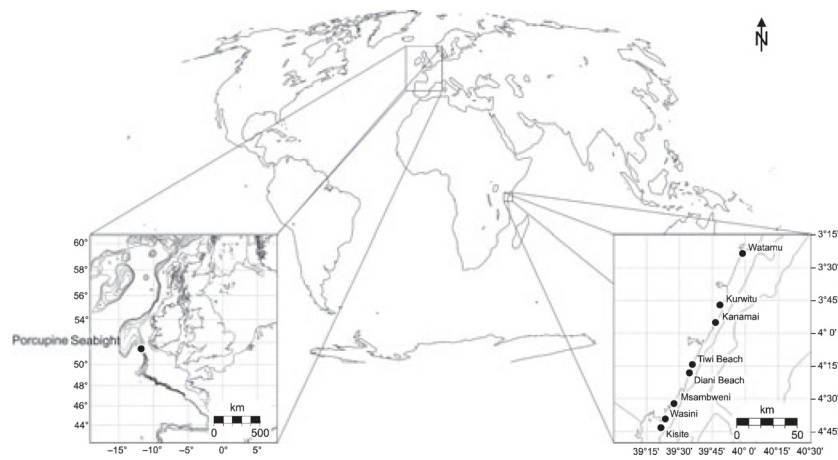


Figure 1 Geographical positions of sampling locations with details of the two regions of interest (world map, Mollweide projection).

Table 1 Coordinates and depth of sampling locations.

	Area	Latitude	Longitude	Depth (m)
Box IV 2000	Porcupine Seabight	51°24'48.2" N	11°45'55.4" W	1005
Box V 2000	Porcupine Seabight	51°24'49.4" N	11°45'55.9" W	1000
Box IV 2001	Porcupine Seabight	51°25'7.7" N	11°46'9.3" W	972
Watamu	Kenya	3°23'32" S	39°59'21" E	2–3
Kurwitu	Kenya	3°47' S	39°49' E	1
Kanamai	Kenya	3°55' S	39°47' E	0.5
Tiwi Beach	Kenya	4°14'10" S	39°36'25" E	1
Diani Beach	Kenya	4°18' S	39°35' E	0.3–2
Msambweni	Kenya	4°32' S	3°28' E	2–3
Wasini	Kenya	4°39' S	39°24' E	3–4
Kisite	Kenya	4°43' S	39°22' E	3–6

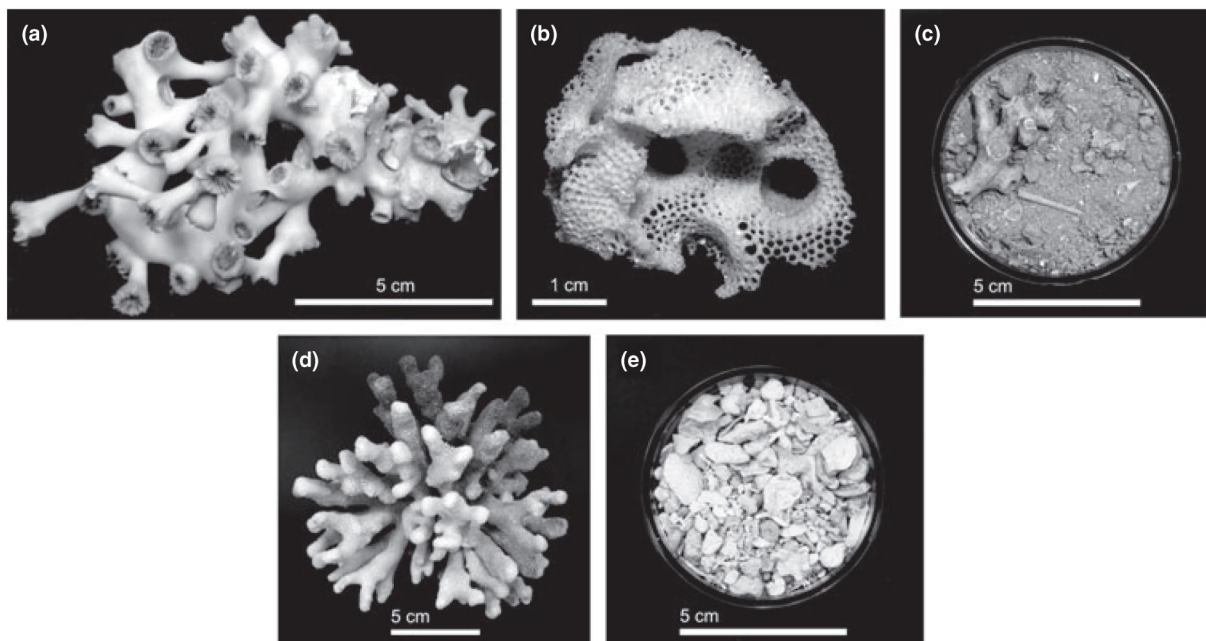


Figure 2 Microhabitat types. Porcupine Seabight: (a) dead fragment of the coral *Lophelia pertusa*; (b) skeleton of the glass sponge *Aphrocallistes bocagei*; (c) sediment. Kenya: (d) dead coral fragment (*i.e.* *Stylophora*); (e) coral gravel.

amounts of coral gravel were scooped out with a small shovel and coral fragments were removed by hand during either snorkelling or skin diving. Material was carefully collected in large plastic bags while underwater. Coral gravel is characterized by the presence of small pieces of coral that can still be recognized (in contrast to coralline sediment) (Fig. 2e). The coral fragments were compact or branched, fresh (but always dead) or eroded (Fig. 2d). Different morphotypes were distinguished, some of which could be identified to genus level: *Fungia*, *Stylophora*, *Lobophyllia*, *Porites*, *Pocillopora*, *Tubipora*. These morphotypes differed in robustness, branching complexity and surface microstructure.

All material was fixed with 4% buffered formalin. Each coral and sponge fragment was rinsed thoroughly with filtered seawater over sieves with a mesh size of 1 mm and 32 μ m, to separate macrofauna and meiofauna. Coral gravel samples were decanted with filtered seawater over the same sieves prior to centrifugation. Meiofauna was extracted from the sediment or residue by density gradient centrifugation, using Ludox HS-40 (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was stained with Rose Bengal. All Epsilonematidae and Draconematidae were picked out from each sample, up to a maximum of 1000 individuals, mounted on slides using the formalin–ethanol–glycerol technique of Seinhorst (1959) and Vincx (1996), and identified up to species level using original descriptions.

Statistical analyses

Only samples with more than three individuals were selected for analysis. For the Kenyan samples, only adults were considered, due to the impossibility of identifying the juveniles of some of the most abundant species. Bray–Curtis (dis)similarities between samples were calculated using the PRIMER ver. 5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001). All data were standardized (relative data were used) and $\log(x + 1)$ transformed prior to the analysis. Samples were grouped together using the factors ‘microhabitat’ (either coral fragments, sponge fragments and sediment, Porcupine Seabight; or coral fragments and coral gravel, Kenya) and ‘differentiated microhabitat’ (with indication of different coral morphotypes, only for Kenyan samples). The similarity matrix obtained was used to produce a non-metric multidimensional scaling two-dimensional plot (NMDS). The stress value gives a measure for goodness-of-fit of the NMDS ordination: a stress value < 0.2 gives a potentially useful two-dimensional picture (Clarke & Warwick, 2001). A cluster analysis (furthest neighbour) was carried out to confirm the NMDS results. One-way analysis of similarities (ANOSIM) was carried out to test for significant differences in community structure between the different groups, and similarity of percentages (SIMPER) was performed to verify which genera were responsible for these differences.

Parametric (one-way ANOVA) and nonparametric (Kruskal–Wallis ANOVA by ranks) ANOVA was performed using the

STATISTICA6 software (StatSoft Inc., Tulsa, OK, USA). Cochran’s *C*, Hartley’s *F* and Bartlett’s χ^2 -tests were used to verify the homogeneity of variances prior to analysis.

Rarefaction curves were constructed from values of the expected number of species $ES(n)$ (Hurlbert, 1971). The additive partitioning of species diversity along the Kenyan coast into measures of α - and β -diversity (Veech *et al.*, 2002; Crist *et al.*, 2003) was conducted with the PARTITION software (Veech & Crist, 2007). A ternary plot was constructed to measure and compare turnover between microhabitats within locations and between neighbouring locations within microhabitats, as recommended by Koleff *et al.* (2003). The values of a' , b' and c' (the percentage of shared species a , of species exclusively present in the neighbouring sample b and of species exclusively present in the focal sample c) were plotted against a background of β_{sim} -values (Lennon *et al.*, 2001). The darkest areas on the plot represent highest turnover.

RESULTS

For our analyses, a total of 811 epsilonematids and draconematids were collected from the Porcupine Seabight, while in Kenya 4293 adult specimens were assembled. Seventeen species from the Porcupine Seabight were included in the analyses (12 Epsilonematidae, five Draconematidae), belonging to eight genera (five Epsilonematidae, three Draconematidae). At the time of sampling (2001), 70.6% (12) of these species were new to science. Since then, five species have been newly described: four from our sampling area (Raes *et al.*, 2003, 2006) and one from Korea (Rho & Kim, 2004). At present, the percentage of undescribed species is 41.2% (seven). Fifty-eight species (39 Epsilonematidae, 19 Draconematidae) from Kenya, belonging to 12 genera (eight Epsilonematidae, four Draconematidae), were used in our analyses; 62.1% (36) of these species are new to science.

Three species were found at both sampling locations: *Dracograllus demani* Allen & Noffsinger, 1978; *Epsilonema margaritatum* Decraemer & Gourbault, 1987 and *Trieptilonema tripapillata* Decraemer, 1982. A list of all 30 currently described species encountered in our study area (including *Apenodraconema chlidosis* Allen & Noffsinger, 1978, which was not used in our analyses as only juveniles of this species were found), and their known distribution, are provided in Table 2. These species have been found in a multitude of microhabitats, such as fine, medium and coarse sand (either coralline, shelly or otherwise), coralline, green and other algae, coral fragments, sponges, sponge spicule mats, bryozoan debris, polychaete tubes, diverse macro-epifauna, crabs and bottom debris. Some of the species we found in the Porcupine Seabight have also been recorded in the North Sea, on the Iberian Margin, on the Great Meteor Seamount, in the Mediterranean Sea, North Pacific Ocean, South Pacific Ocean, Indian Ocean, Caribbean and in Antarctica. The Porcupine Seabight has most of its Epsilonematidae and Draconematidae in common with the Iberian Margin (three species), Kenyan (three species) and Papua New Guinea coasts (three species). There is considerable

Table 2 Distribution of currently described species found in this study.

	Species	Locality	Reference	Habitat	Microhabitat
Shared species	<i>Dracograllus demani</i> Allen & Noffsinger, 1978	Marseille (France)	Allen & Noffsinger (1978)	Sublittoral	
		Laing Island; Duangit Reef (Papua New Guinea)	Decraemer (1988)	Reef flat; littoral; sublittoral	Polychaete tubes; coralline algae; green algae; coarse coralline sand; dead coral fragments
		Watamu (Kenya)	Vershelde & Vincx (1993a)	Littoral	Coarse coralline sand
		Porcupine Seabight	New data	Cold-water coral degradation zone (continental margin)	Sponge skeletons
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Wasini; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	<i>Epsilonema margaritatum</i> Decraemer & Gourbault, 1987	Guadeloupe; Jamaica (Caribbean)	Decraemer & Gourbault (1987)	Littoral/lagoon	Medium coralline sand
		Papua New Guinea	Decraemer <i>et al.</i> (2001)	Littoral/lagoon	Coarse sand
		English Channel	Decraemer <i>et al.</i> (2001)	Sublittoral	Coarse sand
		Marseille (France)	Decraemer <i>et al.</i> (2001)	Sublittoral	Coarse sand
		Porcupine Seabight	Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Sponge skeletons
	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments	
<i>Trieptilonema tripaillata</i> Decraemer, 1982	Laing Island (Papua New Guinea)	Decraemer (1982)	Lagoon	Associated with <i>Halimeda</i>	
	Porcupine Seabight	Raes <i>et al.</i> (2006)	Cold-water coral degradation zone	Fine-to-medium sand; coral fragments; sponge skeletons	
	Kurwitu (Kenya)	Raes <i>et al.</i> (2006)	Tropical coral degradation zone (sublittoral)	Coral fragments	
Porcupine Seabight	<i>Akanthepsilonema sinicornibus</i> Raes, Decraemer & Vanreusel, 2006	Porcupine Seabight	Raes <i>et al.</i> (2006)	Cold-water coral degradation zone (continental margin)	Fine-to-medium sand; coral fragments
		Porcupine Seabight	Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Fine-to-medium sand; coral fragments; sponge skeletons
		Off San Ciprian (Iberian Margin)	New data	Cold-water coral degradation zone (continental margin)	Coral fragments
	<i>Bathypsilonema spongiosum</i> Clasing, 1986	Quellon Viejo; Talcan Island; Huelmo (Chile)	Clasing (1986)	Littoral	Coarse sand
		Porcupine Seabight	Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Coral fragments; sponge skeletons
	<i>Epsilonema cygnoides</i> (Metschnikoff, 1867) Gerlach & Riemann, 1931	Salerno; Naples; Ischia (Italy); Rovinj (Croatia)	several authors in Decraemer <i>et al.</i> (2001)	Sublittoral	Algae
Kiel Bay (Germany); Bergen; Barents Sea (Norway)		several authors in Decraemer <i>et al.</i> (2001)	Sublittoral	Algae	
Porcupine Seabight		Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Coral fragments	
<i>Epsilonema multispiralum</i> Raes, Vanreusel & Decraemer, 2003	Porcupine Seabight	Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Fine-to-medium sand; coral fragments; sponge skeletons	

Table 2 Continued

Species	Locality	Reference	Habitat	Microhabitat
	Off San Ciprian (Iberian Margin)	New data	Cold-water coral degradation zone (continental margin)	Coral fragments
<i>Glochinema trispinatum</i> Raes, Vanreusel & Decraemer, 2003	Porcupine Seabight	Raes <i>et al.</i> (2003)	Cold-water coral degradation zone (continental margin)	Fine-to-medium sand; coral fragments; sponge skeletons
	Kapp Norvegia (Antarctica)	New data	Bryozoan and sponge spicule mats	Sponges; sponge spicules; bryozoan debris; diverse macro-epifauna
	Off San Ciprian (Iberian Margin)	New data	Cold-water coral degradation zone (continental margin)	Coral fragments
<i>Temuidraconema koreensis</i> Rho & Kim, 2004	Namae (South Korea)	Rho & Kim (2004)	Shelf (150–250 m)	Coarse sediment; crabs; sponges; bryozoans
	Porcupine Seabight	Raes <i>et al.</i> (in press)	Cold-water coral degradation zone (continental margin)	Fine-to-medium sand; coral fragments; sponge skeletons
	Great Meteor Seamount	G. Gad (pers. comm.)	Seamount	Biogenic coarse sand (with coral fragments)
Kenya <i>Apenodraconema chlidosis</i> Allen & Noffsinger, 1978	Tahiti (Society Islands)	Allen & Noffsinger (1978)	Sublittoral	Red coralline algae; algae
	Fangataufa Atoll (Polynesia)	Gourbault & Decraemer (1992)	Sublittoral	Coarse sand
	Watamu; Tiwi beach; Diani Beach (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Bathypelsonema compactum</i> Clasing, 1984	Galapagos Islands	Clasing (1984)	Littoral	Medium to coarse sand
	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Dracognomus annae</i> Verschelde & Vincx, 1993	Gazi (Kenya)	Verschelde & Vincx (1993a)	Mangrove	Sediment
	Watamu; Kurwitu; Tiwi beach; Diani Beach; Msambweni (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Dracognomus dermatoglyphus</i> Verschelde & Vincx, 1993	Gazi (Kenya)	Verschelde & Vincx (1993a)	Mangrove	Sediment
	Watamu; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel
<i>Dracograllus eira</i> (Inglis, 1968) Allen & Noffsinger, 1978	St Vincent's bay (New Caledonia)	Inglis (1968)	Littoral	
	Laing Island; Talia Point (Papua New Guinea)	Decraemer (1988)	Reef flat; littoral; sublittoral	Polychaete tubes; coarse coral sand; dead coral fragments
	Watamu (Kenya)	Verschelde & Vincx (1993a)	Littoral	Coarse coralline sand
	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Dracograllus laingensis</i> Decraemer, 1988	Laing Island (Papua New Guinea)	Decraemer (1988)	Reef flat; littoral; sublittoral	Polychaete tubes; coarse coral sand; dead coral fragments
	Watamu; Kurwitu; Kanamai; Tiwi beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Dracograllus papuensis</i> Decraemer, 1988	Laing Island (Papua New Guinea)	Decraemer (1988)	Reef flat; sublittoral	Polychaete tubes; green algae; dead coral fragments
	Kurwitu; Kanamai; Tiwi beach; Msambweni; Wasini; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Draconema claparedii</i> (Metschnikoff, 1867) Filipjev, 1918	Salerno (Italy)	Metschnikoff (1867)	Sublittoral	
	Marseille (France)	Allen & Noffsinger (1978)		
	Naples (Italy)	Schepotieff (1907, 1908)		
	English Channel	Allen & Noffsinger (1978)		
	Roscoff (France)	Giard & Barrois (1874)		

Table 2 Continued

Species	Locality	Reference	Habitat	Microhabitat
<i>Draconema haswelli</i> (Irwin-Smith, 1918) Kreis, 1938	Clare Island (Ireland)	Southern (1914)	Sublittoral	Shelly sand
	Norway	Schepotieff (1907, 1908)		
	Menorca (Spain)	Palacin (1985); Masalles (1985)	Littoral	Algae
	Watamu; Tiwi beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral fragments
	Port Jackson (Australia)	Irwin-Smith (1918)	Sublittoral	Associated with bottom debris
<i>Epsilonema parvospina</i> Decraemer, 1982	Broken Bay (Australia)	Allen & Noffsinger (1978)		
	Red Sea	Allen & Noffsinger (1978)		
	Indonesia	Kreis (1938)		
<i>Leptepsilonema richardi</i> Verschelde & Vincx, 1992	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	Laing Island (Papua New Guinea)	Decraemer (1982)	Lagoon; reef flat	Associated with <i>Halimeda</i>
	Watamu (Kenya)	Verschelde & Vincx (1994)	Littoral	Coarse coralline sand
<i>Metepsilonema chilotum</i> Clasing, 1986	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Wasini; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	Quellon Viejo; Quinchao Island (Chile)	Clasing (1986)	Littoral	Coarse sand
	Watamu; Kurwitu; Kanamai (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel
<i>Metepsilonema hardyi</i> Decraemer & Gourbault, 1990	Guadeloupe; La Désirade (Caribbean)	Decraemer & Gourbault (1990b)	Littoral	Medium coralline sand
	Tiwi beach; Diani Beach; Msambweni (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel
<i>Metepsilonema striatulum</i> Decraemer & Gourbault, 1990	Guadeloupe; Iles des Saintes; La Désirade (Caribbean)	Decraemer & Gourbault (1990a)	Littoral	Medium to coarse coralline sand
	Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Paradraconema floridense</i> Allen & Noffsinger, 1978	Coral Key; Bear Cut (Florida, USA)	Allen & Noffsinger (1978)	Sublittoral	Associated with <i>Halimeda</i>
	Port Jackson (Australia)	Allen & Noffsinger (1978)		
	Solano (Colombia)	Allen & Noffsinger (1978)		
	Ibusuki; Shimoda (Japan)	Allen & Noffsinger (1978)		
	Galeta Beach; Panama City (Panama)	Allen & Noffsinger (1978)		
	Little Santa Cruz Island; Matabungkay; Zamboanga (The Philippines)	Allen & Noffsinger (1978)		
	Samoa; Pago pago	Allen & Noffsinger (1978)		
	Tiarei; Tahiti; Uturoa; Raiatea (Society Islands)	Allen & Noffsinger (1978)		
	Laing Island (Papua New Guinea)	Decraemer (1982)	Lagoon; reef flat	Associated with <i>Halimeda</i> ; coralline sand; sand
	Watamu; Kurwitu; Diani Beach; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral fragments
<i>Perepsilonema kellyae</i> Gourbault & Decraemer, 1988	Guadeloupe; La Désirade (Caribbean)	Gourbault & Decraemer (1988)	Littoral	Fine-to-medium coralline sand
	Gazi (Kenya)	Verschelde & Vincx (1994)	Littoral	
	Thio; Amédée (New Caledonia)	Decraemer <i>et al.</i> (2001)	Littoral	Fine-to-medium sand
	Djakarta; Bali (Indonesia)	Decraemer <i>et al.</i> (2001)	Littoral	Coarse sand
	Recife (Brasil)	Decraemer <i>et al.</i> (2001)	Sublittoral	Coarse sand
	Watamu; Kanamai (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
<i>Perepsilonema moineau</i> Gourbault & Decraemer, 1992	Moorea Island; Fangataufa Atoll (Polynesia)	Gourbault & Decraemer (1992)	Littoral; sublittoral (coral reef)	Coarse sand

Table 2 Continued

Species	Locality	Reference	Habitat	Microhabitat
<i>Perepsilonema papulosum</i> Lorenzen, 1973	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	Puerto Montt (Chile)	Lorenzen (1973)	Littoral	Coarse sand
	Galapagos Islands	Clasing (1984)	Littoral	Medium to very coarse sand
	Kouaré (New Caledonia)	Decraemer et al. (2001)	Littoral	Fine-to-medium sand
	One Tree Island (Australia)	Decraemer et al. (2001)	Littoral	
<i>Polkepsilonema mombasae</i> Verschelde & Vincx, 1992	Bora Bay (Japan)	Decraemer et al. (2001)	Lagoon	Fine-to-medium sand
	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	Laing Island (Papua New Guinea)	Decraemer (1982)	Littoral	Between <i>Halimeda</i>
	Watamu (Kenya)	Verschelde & Vincx (1993b)	Littoral	Coarse coralline sand
<i>Piernepsilonema servaesae</i> Verschelde & Vincx, 1992	Diani Beach; Msambweni (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments
	Watamu (Kenya)	Verschelde & Vincx (1993b)	Littoral	Coarse coralline sand
	Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach (Kenya)	New data	Tropical coral degradation zone (sublittoral)	Coral gravel; coral fragments

variation on a bathymetric scale, as some of the species (*D. demani*, *E. margaritatum* and *Bathyepsilonema spongiosum* Clasing, 1986) occur on sandy beaches as well as in the deep sea. The species we found along the Kenyan coast were already known from other geographical areas including Indonesia, the Philippines, North Pacific Ocean, South Pacific Ocean, North Atlantic Ocean, South Atlantic Ocean, Caribbean, Gulf of Mexico, Mediterranean and Red Sea. Seventy-four per cent of these species also live in littoral zones. The community was composed mainly of species that live along the Kenyan coast (eight), but also of species from Laing Island, Papua New Guinea (nine) and from Guadeloupe (four).

Porcupine Seabight

Both the cluster dendrogram (Fig. 3a) and NMDS graph (Fig. 3b) showed that the coral samples were relatively well separated from the other microhabitats. There were only three mismatched samples (one sediment sample and two sponge samples in the coral fragments cluster) in the cluster dendrogram. This clear-cut distinction was confirmed by the significant dissimilarities between the communities on coral fragments and those on sponge fragments (one-way ANOSIM: $R = 0.53$; $P = 0.001$) and between the communities on coral fragments and those in the sediment (one-way ANOSIM: $R = 0.63$; $P = 0.003$). There were no significant differences between replicates or sampling years. Average dissimilarities between the communities on coral fragments and sponge skeletons on the one hand, and between those on coral fragments and in the sediment on the other hand, were low (around 50%). *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003; *Cygnonema belgicae* sp. n. and *Triepsilonema tripapillata* Decraemer, 1982 appeared to be the most impor-

tant species in separating the communities on coral fragments from those of the other microhabitats, according to the SIMPER analysis (Table 3). *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003 explained most of the separation of the sponge communities, and *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003 was very important in the sponge and sediment communities as opposed to the coral-inhabiting communities. The latter species appeared to be abundant in all three habitats, although it was dominant only on sponges and in the sediment (Table 4). *Epsilonema multispiralum* and *T. tripapillata* were the dominant species on coral fragments. Coral fragments yielded a significantly higher Draconematidae/Epsilonematidae ratio (0.1–0.8) when compared with the other two microhabitats (Kruskal–Wallis ANOVA; $P = 0.0072$).

Rarefaction curves indicated that the communities on coral fragments were more diverse than those on sponge skeletons and in the sediment (Fig. 4a).

Kenya

The average number of individuals per sample was higher in the tropical coral degradation zone in Kenya than in the cold-water coral reef samples. Considerable differences in sample size were observed: between seven and 565 individuals (without juveniles). There was a very clear and significant (one-way ANOSIM: $R = 0.67$; $P = 0.001$) separation of the communities from coral fragments and those from coral gravel, both in the cluster dendrogram (Fig. 3c) and in the NMDS biplot (Fig. 3d). Average similarity between the communities in the gravel samples (46.8%) was higher than that between coral samples (40.2%). The average dissimilarity between the assemblages in both microhabitats was relatively high (79.0%). This was

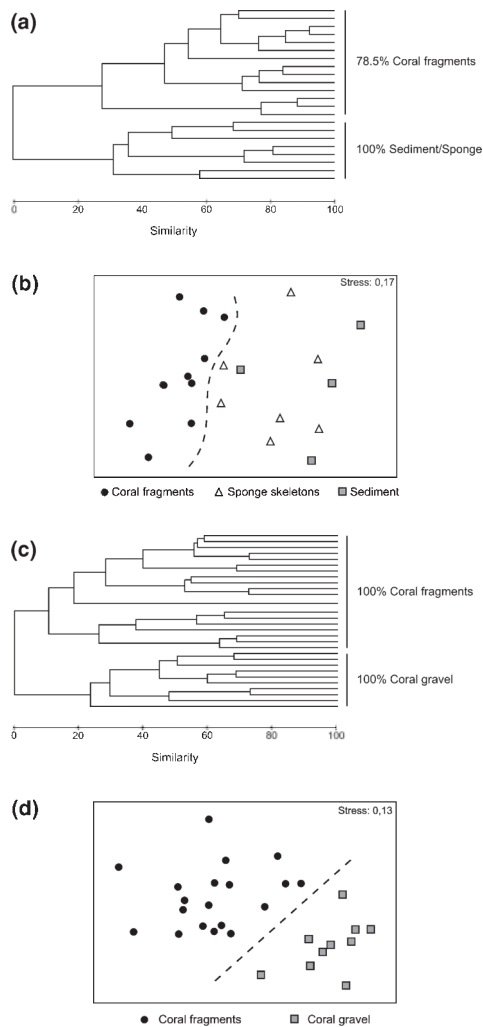


Figure 3 Multivariate analyses. Porcupine Seabight samples: (a) cluster dendrogram; (b) non-metric multidimensional scaling biplot. Kenya samples: (c) cluster dendrogram; (d) non-metric multidimensional scaling biplot. The percentage of equally classified samples in each cluster of the dendrogram is indicated.

attributed mainly to *Epsilonema parvospina* Decraemer, 1982 and *Paradraconema* sp. 4 sp. n., two species with higher relative abundances on coral fragments, and to *Perepsilonema papulosum* Lorenzen, 1973; *Dracognomus annae* Verschelde & Vincx, 1993 and *Dracognomus* sp. 2 sp. n., which were more abundant in coral gravel (Table 3). These results were confirmed by the dominance of these taxa in the respective microhabitats (Table 4). Within the gravel samples, no significant differences between sampling locations were found. Coral fragment samples from the neighbouring locations Diani Beach and Tiwi Beach were, however, significantly different from each other in terms of their community composition (one-way ANOSIM: $R = 0.52$; $P = 0.015$). There was no obvious effect of coral morphotypes on community structure as evidenced by an NMDS biplot, although some differences were found between the communities on *Porites* and on the finely branched *Pocillopora* (one-way ANOSIM; low number of actual permuta-

tions; $R = 0.764$). We found no significant difference in the Draconematidae/Epsilonematidae ratio between coral fragments and coral gravel.

Rarefaction curves indicated a higher diversity on the coral fragments, although the values for ES (50) in coral samples were not significantly higher than those in coral gravel (one-way ANOVA; $P = 0.92$) (Fig. 4b).

Total species richness of the tropical coral degradation zone in Kenya (γ) was determined mainly by local diversity (α ; 38.2%) and the turnover between localities (44.5%). The contribution of the α -component to total diversity in terms of the Shannon–Wiener index was very high (71.2%), while β -diversity contributed little (Fig. 5).

Although β_{sim} values of turnover between microhabitats on the one hand and between locations on the other hand (pairwise comparison of neighbouring locations from north to south for both microhabitats) were not significantly different (one-way ANOVA; $P = 0.15$), it can be observed on the ternary plot (Fig. 6) that turnover between microhabitats and between coral samples from different localities was higher than turnover between locations for gravel samples: most white triangles and black dots are plotted in a darker area (higher turnover) than the grey squares. The extent of turnover at different levels was, however, highly variable.

DISCUSSION

Habitat preferences

The observed habitat preferences in the Porcupine Seabight area largely agree with the results of a previous study on the total nematode community of this area, which was, however, conducted with genus-level identifications (Raes & Vanreusel, 2006). In contrast, the sponge and sediment communities in that study were also significantly dissimilar from each other. Nevertheless, even at the genus level, coral fragments were dominated by *Epsilonema* and characterized by high abundances of Epsilonematidae and Draconematidae, whereas sponge skeletons and sediment yielded much lower numbers of typically epifaunal nematodes. In the study of Raes & Vanreusel (2006), some similarities between sponge and sediment communities were attributed to the sediment-trapping capacity of the three-dimensional framework of sponge spicules. This hypothesis could explain the absence of significant differences between these microhabitats in the present study.

Epsilonematidae typically thrive in coarse sediments, which are subject to strong hydrodynamic forces (Willems *et al.*, 1982; Vanaverbeke *et al.*, 2004). In the Porcupine Seabight area, only the animals living on coral fragments are thought to be subjected to considerable physical disturbance by current activity (which is strong at the sampling location), while the other nematodes might live relatively protected in the sediment. Coral fragments can be considered a more favourable substratum for epifaunal nematodes, as these nematodes, by their special way of locomotion and their ability to attach themselves to the substratum, have a competitive

Table 3 SIMPER results for the three pairs of groups considered in this study.

	Porcupine Seabight			
	Average dissimilarity: 52.21%		Average dissimilarity: 56.94%	
	Coral fragments	Sponge fragments	Coral fragments	Sediment
<i>Epsilonema multispiralum</i> Raes, Vanreusel & Decraemer, 2003	13.58%		17.33%	
<i>Bathyeppilonema lopheliae</i> Raes, Vanreusel & Decraemer, 2003		12.16%		
<i>Glochinema trispinatum</i> Raes, Vanreusel & Decraemer, 2003		11.66%		15.58%
<i>Cygnonema belgicae</i> sp. n.	9.81%		12.24%	
<i>Triepsilonema tripapillata</i> Decraemer, 1982	9.45%		11.41%	
		Kenya		
		Average dissimilarity: 78.95%		
		Coral fragments		Coral gravel
<i>Epsilonema parvospina</i> Decraemer, 1982		8.40%		
<i>Perepsilonema papulosum</i> Lorenzen, 1973				5.89%
<i>Dracognomus annae</i> Verschelde & Vincx, 1993				5.59%
<i>Dracognomus</i> sp. 2 sp. n.				5.45%
<i>Paradraconema</i> sp. 4 sp. n.		4.68%		

Data are for average dissimilarity between the two groups, the species most important in explaining this dissimilarity, their procentual contribution to the dissimilarity (> 9% in Porcupine Seabight; > 4% in Kenya) and their habitat preference.

advantage here. This is confirmed in the present study by the fact that, except for two species, all epsilonematid and draconematid species show a preference for coral fragments. These two species show finely tuned morphological adaptations to their environment. *Glochinema trispinatum* is a slender nematode supported by long, fine ambulatory setae, and might therefore be much more vulnerable to physical disturbance by strong currents. The preference of *B. lopheliae* for sponge skeletons may be related to the hook-shaped tip of the ambulatory setae in this species, which could be used in clinging on to the smooth substrata of the sponge spicules. On the other hand, a hook-shaped tip has also been observed in other Epsilonematidae and might not be so exceptional. This cannot be confirmed at this time, however, as SEM pictures of the distal end of ambulatory setae in Epsilonematidae remain scarce.

Sediment infill between the coral branches and the presence of coral fragments within the sediment might explain the low average dissimilarities between the microhabitats.

A distinction between the exposed nature of coral fragments and the relative protection within the coral gravel may also explain the differences in community composition between these microhabitats along the Kenyan coast. This hypothesis was proposed for the total nematode community at the genus level (Raes *et al.*, 2007). The genera *Paradraconema* (Draconematidae) and *Epsilonema* (Epsilonematidae) were recognized as indicator genera for coral fragments. The present study confirms this at the species level. The species that were

considered indicators for coral gravel by the SIMPER analysis possess morphological features that make attachment to a surface difficult. *Perepsilonema papulosum* lacks any ambulatory setae, and both *Dracognomus* species are characterized by fine and reduced adhesion tubes. The morphology of the specialized locomotory structures in both families could play an important role in explaining habitat preferences. It could therefore be expected that the more exposed coral fragments yielded significantly higher relative abundance of Draconematidae. Draconematids possess adhesion tubes associated with glands, with which they can attach themselves more strongly to a substratum than Epsilonematidae. However, a significantly higher Draconematidae/Epsilonematidae ratio on corals was found only in the Porcupine Seabight community, even when *Dracognomus* was added to the Epsilonematidae group in Kenya.

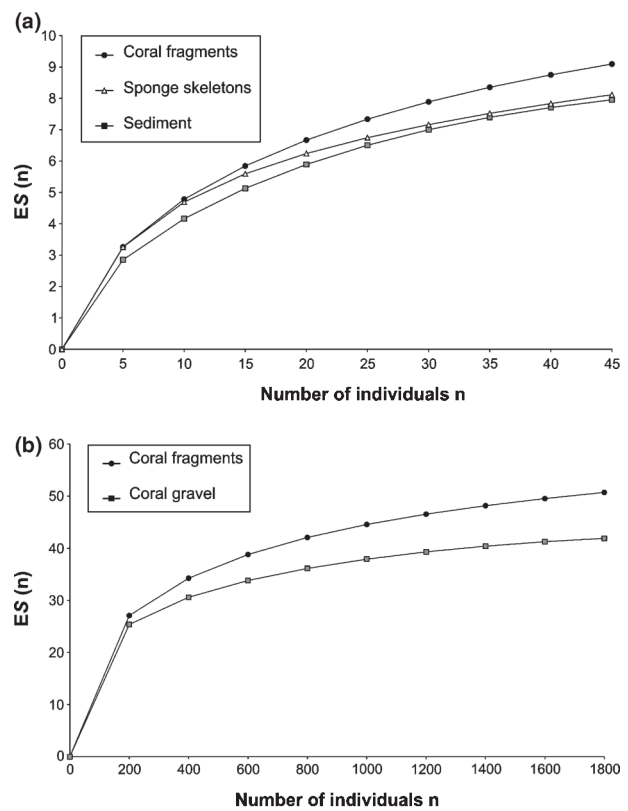
Biogeography

Decraemer *et al.* (2001) established that cosmopolitanism in Epsilonematidae is common. Our data confirm and endorse this observation, and indicate that the same is true for Draconematidae. Although our list of occurrences (Table 2) includes only those species found in the current study, the geographical and bathymetrical range over which some of these species occur is astonishing, and inspires reflection on the biogeography of marine nematodes.

Table 4 Dominant species within the Epsilonematidae and Draconematidae (relative abundance > 5%), per microhabitat in each region.

	Species	%
Porcupine Seabight		
Coral fragments	<i>Epsilonema multispiralum</i> Raes, Vanreusel & Decraemer, 2003	41.9
	<i>Triepsilonema tripapillata</i> Decraemer, 1982	22.9
	<i>Glochinema trispinatum</i> Raes, Vanreusel & Decraemer, 2003	7.3
	<i>Akanthepsilonema sinicornibus</i> Raes, Decraemer & Vanreusel, 2006	6.7
	<i>Cygnonema belgicae</i> sp. n. Rho & Kim, 2004	5.5
	<i>Tenuidraconema koreensis</i> Rho & Kim, 2004	5.0
	Sponge skeletons	<i>Glochinema trispinatum</i> Raes, Vanreusel & Decraemer, 2003
<i>Epsilonema multispiralum</i> Raes, Vanreusel & Decraemer, 2003		16.8
<i>Triepsilonema tripapillata</i> Decraemer, 1982		14.2
<i>Bathyepsilonema lopheliae</i> Raes, Vanreusel & Decraemer, 2003		11.6
Sediment		<i>Glochinema trispinatum</i> Raes, Vanreusel & Decraemer, 2003
	<i>Triepsilonema tripapillata</i> Decraemer, 1982	17.4
	<i>Epsilonema multispiralum</i> Raes, Vanreusel & Decraemer, 2003	6.5
	<i>Tenuidraconema koreensis</i> Rho & Kim, 2004	6.5
	Kenya	
Coral fragments	<i>Epsilonema parvospina</i> Decraemer, 1982	36.6
	<i>Epsilonema</i> sp. 12 sp. n.	12.6
	<i>Paradraconema</i> sp. 4 sp. n.	9.5
	<i>Epsilonema</i> sp. 10 sp. n.	7.0
Coral gravel	<i>Perepsilonema papulosum</i> Lorenzen, 1973	19.1
	<i>Dracognomus annae</i> Verschelde & Vincx, 1993	15.5
	<i>Dracognomus</i> sp. 2 sp. n.	12.9
	<i>Epsilonema</i> sp. 15 sp. n.	9.2
	<i>Epsilonema margaritatum</i> Decraemer & Goubault, 1987	6.0

Sampling effort and exploration intensity greatly influence our view on the distribution of epifaunal nematodes. The taxonomic record of Epsilonematidae and Draconematidae has grown considerably in recent years thanks to descriptions by a limited group of researchers and from a limited number of sampling locations. Descriptions of numerous new species from the Kenyan coast by Verschelde & Vincx (1992, 1993a,b, 1994), from Laing Island (Papua New Guinea) by Decraemer (1982, 1988) and from Guadeloupe by Decraemer & Goubault

**Figure 4** Rarefaction curves. (a) Porcupine Seabight; (b) Kenyan coast. Note different scales on the x- and y-axis. ES(n), expected number of species.

(1987, 1990a,b) and Goubault & Decraemer (1988) have had a considerable impact on the content of Table 2. For example, the communities we studied along the Kenyan coast are composed to a great extent of species described or recorded from Papua New Guinea. Moreover, of the 175 currently described species of Epsilonematidae and Draconematidae, 11.5% (20 species) have been found in Papua New Guinea. This shows that one detailed study at a single location can have a considerable impact on our knowledge of the biogeography of Epsilonematidae and Draconematidae. It also emphasizes the importance of, and the need for, comprehensive studies in areas where suitable substrata for epifaunal nematodes are available.

The occurrence of morphologically identical meiofaunal taxa in completely divergent areas, even at lower systematic levels, has been an unsolved enigma for many years now. The solution to this 'meiofauna paradox' (Giere, 1993), adopted in this context for nematodes, should be looked for in (1) the dispersive attributes and mechanisms of nematodes, (2) the existence of cryptic species and conservative morphology of nematodes, or (3) the possibility of parallel evolution. Taking these three factors into account, we see five potential explanations for the existence of morphologically identical nematodes in geographically distant areas: (1) they belong to the same species because genetic and morphological equality is maintained by active gene flow between the populations; (2)

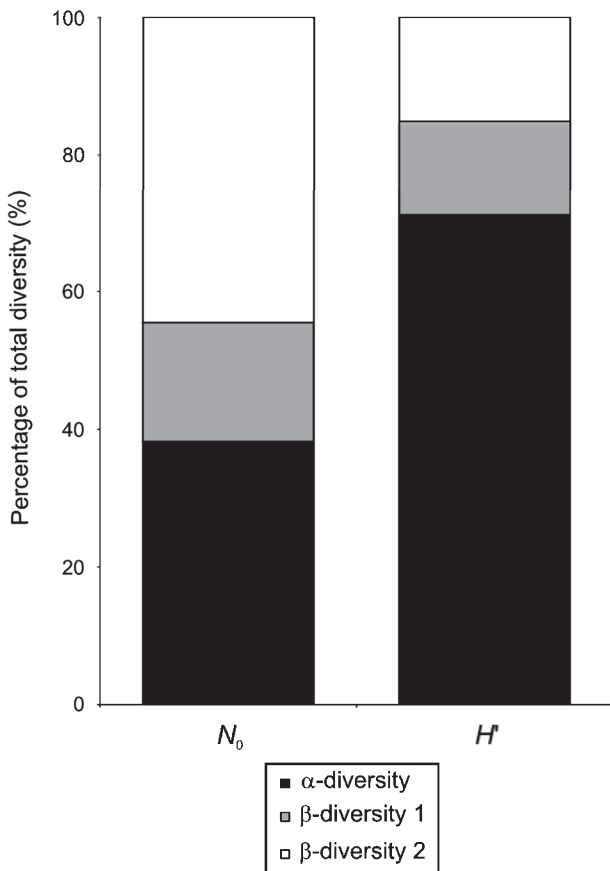


Figure 5 Additive partitioning of total diversity for the number of species N_0 and Shannon–Wiener diversity H' (Kenyan data). β -Diversity 1 is the fraction of β -diversity resulting from differences between microhabitats; β -diversity 2 is the fraction of β -diversity resulting from differences between locations.

they belong to the same species because the populations are isolated from each other but the morphology and genetic structure in both populations is conserved; (3) they belong to different cryptic species; (4) they belong to different pseudo-sibling species *sensu* Knowlton (1993); or (5) they belong to different species that have obtained the same morphology due to parallel evolution.

Several studies have reviewed the mechanisms and opportunities of meiobenthic dispersal (Gerlach, 1977; Palmer, 1988; Giere, 1993). Few meiobenthic taxa have pelagic larvae, and nematodes are especially recognized as taxa with limited mobility, poor swimming capacity (Hopper & Meyers, 1966) and a conservative reproductive method (lack of dispersive stages), characterizing them as biogeographically localized organisms (Castillo-Fernandez & Lamshead, 1990). As mentioned in the Introduction, Epsilonematidae and Draconematidae are characterized by a crawling locomotion distinctly different from the undulating movement of most other nematodes, rendering them more mobile on larger substrata (Stauffer, 1924; Lorenzen, 1973). This type of locomotion can, however, only be used to bridge short distances. Dispersal of meiobenthic organisms over larger spatial scales has to go

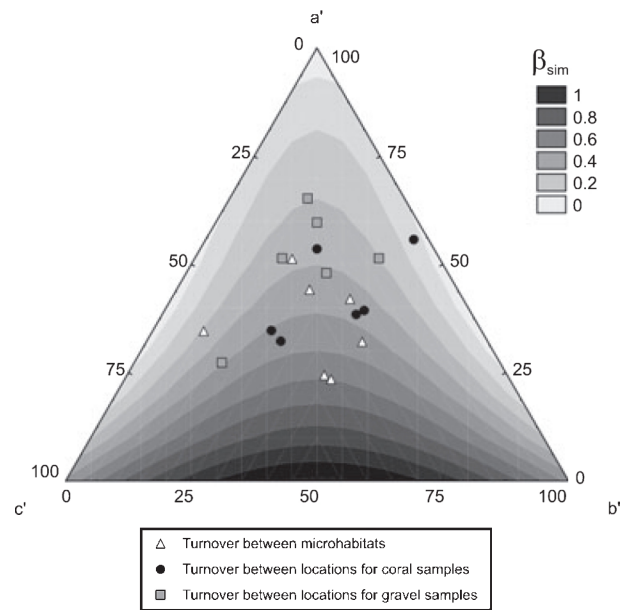


Figure 6 Ternary plot (Kenyan data) representing species turnover between microhabitats within each location and between locations for both coral and gravel samples. Shading visualizes the values of β_{sim} .

through the water column, either by rafting on drifting material, in water and sediment used as ballast for ships, or via currents (Gerlach, 1977). The latter possibility is probably the most common and most generally available route, as it is not determined by the coincidental presence of suitable transport. Meiofauna is indeed regularly found in the water column (Hagerman & Rieger, 1981). Chandler & Fleeger (1983) have experimentally proven the colonization of meiofauna through the water column. Meiofauna may leave the sediment either through active emergence or through passive erosion by hydrodynamic activity (Palmer, 1988). Organisms dwelling near the sediment surface or on substrata such as seagrasses (or corals) are more susceptible to passive erosion than infaunal animals (Palmer, 1984, 1988). Nevertheless, Hicks (1986) has shown that meiofaunal dispersal from seagrass beds is primarily an active process. The sediment surface- and seagrass-dwelling meiofauna in the aforementioned studies was mainly composed of copepods, which are relatively good swimmers. It seems, however, plausible that although epifaunal nematodes such as Epsilonematidae and Draconematidae are not good swimmers, they are able actively to let go of the substratum by releasing their ambulatory setae or adhesion tubes. In this way, they might control their own dispersal to a certain extent. All this suggests that the coral fragment-inhabiting nematodes investigated in our study could be prone to facilitated and frequent dispersive events. Yet we did not find any indication that the coral-dwelling nematodes were more widely distributed than the sediment/gravel-dwelling ones. Furthermore, most of the species listed in Table 2 live in both microhabitats.

Although meiofauna settlement is considered a largely passive process, active habitat selection may be expected in

seagrass beds according to Palmer (1988). Ullberg & Ólafsson (2003) have shown experimentally that marine, free-living nematodes may actively choose suitable habitats. Given the clear-cut distinction between coral and gravel communities of epifaunal nematodes and the exposed nature of the coral fragments (and, to a lesser extent, the surface of the coral gravel) in the current study, we assume that a combination of passive (erosion and resuspension) and active (active emergence and active habitat inspection/selection after settlement by crawling) processes determines colonization of these microhabitats by nematodes.

It is not clear whether dispersal via the water column can sustain active gene flow between geographically distant areas such as the Porcupine Seabight and the coast of Kenya. The biogeography of a species such as *Tenuidraconema koreensis* Rho & Kim, 2004, which is found in the Porcupine Seabight and at the coast of Korea, is even more astonishing, and such populations could be isolated from each other, at least to some extent. Not only geographical distance, but also the complexity of the dispersion routes that link both populations and the difficulties associated with bridging a bathymetric boundary of 750–850 m, may hamper dispersal and gene flow between these populations. On a smaller spatial scale, the occurrence of *T. koreensis* populations in the Porcupine Seabight and on the Great Meteor Seamount could be explained by passive transport via Mediterranean Outflow Water and stepping stones, following the same trajectory as the larvae of the coral *L. pertusa* on which they occur (Raes *et al.*, in press).

From Table 2, it is clear that *T. koreensis* is not the only species with a putative cosmopolitan distribution. Populations of such species could be genetically different from each other, or even consist of different species. Morphologically similar nematodes may belong to different biological species – they could be reproductively isolated. Tests for reproductive isolation of marine nematode populations are hampered by difficulties associated with culturing these animals. Nevertheless, a comparison with mitochondrial sequence data could indicate whether these animals, which are morphologically identical, belong to the same species at the molecular level, or whether they represent different cryptic species. Recent studies have indicated that some meiobenthic ‘species’ are actually complexes of cryptic species and, as a result, that putatively cosmopolitan species have more limited geographical ranges (Schmidt & Westheide, 2000; Rocha-Olivares *et al.*, 2001; Derycke *et al.*, 2005). Such complexes are especially prominent in small invertebrates with few taxonomically diagnostic characters. The prevalence of cryptic species indicates that morphological stasis persists after speciation events, while species continue to diverge genetically in the absence of morphological differentiation. Evidence for such a decoupling of molecular and morphological evolution is summarized by Rocha-Olivares *et al.* (2001).

According to Knowlton (1993), the establishment of many sibling species has resulted from failure to recognize subtle morphological distinctions between existing species, which are therefore referred to as ‘pseudosibling species’. This problem

can arise from inadequate definition of diagnostic features, inadequate identification of homologous structures and intra-specific variability, and is especially acute in taxa with few morphological features, such as nematodes. However, a detailed assessment of intraspecific variability was made for the species treated in this paper. Based on that, diagnostic characters were carefully delineated and species were separated with caution. This exceptional caution is also the reason why only adults were considered in the Kenya samples. In our study, the possibility of inadequate morphological observation was considerably reduced in this way.

We provided some arguments against the first (same species with gene flow between populations), second (isolated populations with conserved morphology and genetic structure) and fourth (different pseudosibling species) explanations from the list of five explanations for finding morphologically identical nematodes in geographically distinct areas. The assumption that they are cryptic species appears very plausible, although molecular analysis is needed to confirm this idea. A final possibility is that they are closely related but different species, which have obtained a similar morphology as a response to similar environmental conditions (similar microhabitats). A completely independent development of an exceptional and specialized morphology, as for example in *T. tripapillata*, seems unlikely, although some functional morphological features of epsilonematids may have evolved independently in different taxa because their morphological information is enclosed in the genetic code of these animals. This could easily be the case for the three papillae on the terminal tip of the tail, each with the separate outlet of one of the three caudal glands (Raes *et al.*, 2006). Such papillae are thought to be important for improved attachment to the substratum and could therefore have arisen in response to strong hydrodynamic stress on coral fragments.

Diversity

Coral degradation zones, in both temperate deep and tropical shallow environments, are clearly an important source of new Epsilonematidae and Draconematidae species. The higher diversity on coral fragments compared with the other microhabitats confirms the statement made above that coral fragments can be considered a more favourable substratum for typically epifaunal nematodes. This suggests that these typically epifaunal nematodes are able to establish more extensive and diverse communities on coral fragments, probably due to the fact that they are morphologically and ecologically well adapted to a life in this exposed habitat, which is less suitable for most other nematodes (Raes & Vanreusel, 2006; Raes *et al.*, 2007). However, the differences between the ES(n) values for coral fragments and coral gravel were not significant in Kenya, indicating that a higher overall diversity on coral fragments may also be caused by the more considerable differences in community structure between coral samples, resulting in a high total number of species. This is confirmed by the lower average similarity values within this microhabitat. The typically epifaunal nematode

communities in Kenya are clearly more species-rich than those in the Porcupine Seabight area, although this may be due to the pronounced difference in sampling scale (three boxcores at the same location in the Porcupine Seabight area vs. a whole transect along the Kenyan coast).

Our analysis of additive partitioning indicates that sample (α) diversity is far more important in contributing to the total diversity when working with abundance data (H'). This is, however, no longer true when working with presence–absence data. Furthermore, the contribution of different locations to total diversity is high when working with species richness, but is clearly reduced when adding abundance information. This indicates that the addition of sampling locations contributes considerably to the total number of species, although the added species are generally rare. The contribution to total diversity of β -diversity related to differences between microhabitats is low for both presence–absence and abundance data. In contrast, the ternary plot indicates a generally higher turnover between microhabitats compared with turnover between gravel samples from neighbouring locations (within a microhabitat). This agrees well with the important structuring role of microhabitats for the communities, which was observed in our study. However, turnover between coral samples from neighbouring locations also appears to be generally high. This is in agreement with the more considerable differences in community structure between coral samples. In this regard, this result confirms the observation from the rarefaction curve from Kenya that coral fragments contribute more than gravel samples to the total diversity. The high contribution of α - (or sample) diversity, and hence the importance of variability between samples irrespective of their microhabitat or location, is reflected in the scattered position of the markers on the ternary graph.

CONCLUSIONS

This study investigated a subset of the meiofauna in comparable microhabitats from very different ecosystems, which are geographically and bathymetrically separated from each other. Despite these environmental differences, similar (and in some cases even identical) species were found. This emphasizes the importance of microhabitat type in structuring the nematode community, but also raises questions about the extent of genetic divergence between morphologically identical nematodes in geographically distant areas.

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the meio-epifauna associated with tropical and cold-water coral reefs'.

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BIOSKETCHES

Maarten Raes is a marine biologist who studied the taxonomy, ecology, biogeography and biodiversity of the nematofauna associated with cold-water and tropical corals. At present, his research deals with the biology of the Antarctic meiobenthos and the impact of temperature increase on this fauna.

The subjects of research and fields of interest of **Wilfrida Decraemer** are the taxonomy, morphology (light microscopy and ultrastructure), phylogeny and biogeography of free-living marine nematodes and plant-parasitic nematodes, specifically the virus-vector families.

The expertise of **Ann Vanreusel** includes several aspects of meiobenthos (smallest benthic metazoans) ecology and taxonomy. Her research focuses on free-living marine Nematoda, using multi-method approaches (molecular, morphological, ultrastructural, field or laboratory experimental, biomarkers etc.) to understand their ecology and biodiversity.

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