CHAPTER V

The dominance of predatory nematodes at the high water level in an Ecuadorian sandy beach

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ABSTRACT

Free-living marine nematodes were sampled monthly from June 2000 to July 2001 at an exposed sandy beach. Samples were taken in dry and rainy season at high tide level on the beach, in order to study the nematode assemblage composition, temporal distribution and their relationship with the environmental factors. Also a comparison with the nematode species at the lower tide level (previous chapter) was analysed. Forty nematode species belonging to 30 genera and 15 families were found. Total nematode densities ranged from 183±28 ind./10 cm² (December 2000) to 1488±100 ind./10 cm2 (June 2000), no significant differences between dry (April-December) and rainy season (January-March) were detected. Predators were the most abundant feeding type at the nematode community (47%), although with fluctuating dominance (20-80%). The predatory nematode Enoplolaimus sp. 1 (14%) and Metachromadora sp. 1 (13%) co-dominated, showing density fluctuations over the sampling period (8-311 ind./10 cm² and 1-302 ind./10 cm² respectively), but with the highest densities in June 2000 and July 2001. Two temporal nematode species associations were observed: nematodes collected from May to September and those collected from October-April. The k-dominance curves showed highest diversity in June 2001 and lowest diversity in December 2000. Sea Surface Temperature was positively correlated, while salinity was negatively correlated with the total nematode densities. The taxonomic distinctness analysis showed that nematode species registered at the upper and at the lower station on the beach were closely related to each other (except those species from June 2000, November 2000 and May 2001 at the lower station). Nevertheless cross-shore differences were detected, explained by the highest abundances of Enoplolaimus sp. 1, Viscosia sp. 2 and Metachromadora sp. 1 at the upper station, and the highest abundances of Ceramonema sp. 1 and Ceramonema sp. 2 at the lower station. These observations illustrate the importance of predators in the interstitial food web of the upper station along an Ecuadorian beach.

KEYWORDS: free-living marine nematodes, Ecuador, predators, diversity, taxonomic distinctness.

INTRODUCTION

Predators (mainly nematodes and turbellarians) can be extremely dominant in sandy beach meiofaunal assemblages (GHESKIERE *et al.*, 2002). Predation is considered as an important structuring and regulating factor in the population dynamics of many organisms in coastal sediments (AMBROSE, 1984; WILSON, 1991). On cold-temperate, highly dynamic intermediate shores with high wave energy and subject to erosion, the "small food web" (meiofauna) are dominant (MENN, 2002). Meiofaunal organisms are agile and quickly exploit fresh organic material. Larger organisms and nematodes dominate in dissipative and accreting shore conditions, where some food materials may accumulate and zoomass builds up to support numerous visitors (shrimps, crabs, fish, and shorebirds) from higher trophic levels (MENN, 2002). Predator/prey dynamics can help to understand the ecological importance of temporal changes in monitoring populations (THRUSH, 1999).

At the meiofauna level debate exists about the impact of meiofaunal predation on the interstitial biodiversity and assemblage structure. Meiofaunal predators, particularly turbellarians, were identified as potential predators on settling infauna (WATZIN, 1983). As a taxon, nematodes consume a variety of food sources, including detritus, bacteria, diatoms and other microalgae, cyanophytes, ciliates, and other meiofauna (by predation and scavenging). Observations on the nematode feeding behaviour showed that Adoncholaimus fuscus (facultative predator) is an active nematode, which was observed to scavenge on dead or weakened Foraminifera, inserting its head and anterior part of the body in the foraminiferal test via the aperture; Enoploides longispiculosus (predator) regularly had considerable numbers of pennate diatoms in the intestine (MOENS et al., 1999), but a closer look at its feeding behaviour and prey range strongly suggests that these were derived from the intestinal contents of prey oligochaetes or nematodes. Adoncholaimus sp. often attacked a prey specimen in small groups (two or three predators) (MOENS et al., 1999, 2000; HAMELS et al., 2001 and GALLUCCI et al., 2005). However, the importance of dominant marine predatory nematodes in sandy beaches remains insufficiently documented.

This present study describe the biodiversity of the free-living marine nematodes (at species level), their densities, assemblages and trophic structure at the high tide level in San Pedro de Manglaralto (an exposed sandy beach) over a monthly sampling from June 2000 until July 2001. Three climate seasons were monitored: two dry periods

(June-December 2000 and April-July 2001) and one rainy period (January-March 2001). The 'dry' and the rainy' season were defined according the data set of the sampling campaigns. A comparison in diversity and taxonomic distinctness between the nematode species from highest (this study) and lower tide level (Chapter IV) was established to detect a zonation pattern across the Ecuadorian beach.

The study period had undergone a strong La Niña phase, after El Niño 1997-1998 (MCPHADEN, 1999).

MATERIAL AND METHODS

Study site

The beach studied was San Pedro de Manglaralto, an exposed beach on the Ecuadorian Pacific Coast (1°56′30″S, 80°43′30″W) (See map at Chapter 3, Figure 3.1). The samples were taken in front to Centro Nacional de Acuicultura e Investigaciones Marinas (CENAIM). The beach is classified as intermediate beach (Ω =1.2) but near to the reflective characteristics. The wide of the intertidal zone have about 120 m with a Relative Tide Range of 4.2 m.

Sampling strategy

Sampling was done monthly from June 2000 until July 2001 during the spring tides (full moon) at high tide level. Three replicates were collected and two analysed. Samples were obtained by forcing a hand core (sampling surface area 10 cm²), to 20 cm depth in the sediment. The samples (except those for sedimentological analyses) were fixed with 4% buffered formaldehyde water solution at 60 °C. Hot formaldehyde prevents curling of the nematodes (HEIP *et al.*, 1985; VINCX, 1996).

Temperature Sea Surface Temperature (SST) and salinity data were referred to the nearby 'El Pelado' Oceanographic station (01° 55′ 53″ S, 80° 46′ 55″ W), and pluviosity data from the CENAIM-ESPOL (Escuela Superior Politécnica del Litoral) foundation. At each sampling location the beach profile was measured as the difference in elevation every 5 meters along the transect using a leveller from a fixed reference point (0) localized in front of CENAIM. The distance is used as a proxy for elevation.

Sediment particle-size distribution was determined using Coulter LS 100[®] particle size analysis equipment. The sediment fractions were defined according to the Wentworth scale (BUCHANAN, 1984).

Extraction and Nematoda identification

In the laboratory, samples were rinsed with a gentle jet of tapwater over a 1 mm sieve to exclude macrofauna, decanted ten times over a 38 µm sieve, centrifuged three times

with Ludox[®] HS 40 (specific density 1.18) and stained with Rose Bengal. From each sample 200 nematodes (or all nematodes when less than 200 individuals were present in the examinated sample) were randomly picked out. They were subsequently mounted onto slides using the formalin-ethanol-glycerol technique (VINCX, 1996), and identified up to genus level, using the pictorial keys of PLATT AND WARWICK (1983, 1988) and WARWICK *et al.* (1988). The identification up to species level was done using the nematotheek descriptions from the Marine Biology Section of Ghent University. Systematics was based mainly on LORENZEN (1994).

The feeding types suggested by WIESER (1953), distinguishing selective (1A) and non-selective deposit feeders (1B), epistratum feeders (2A) and predators/omnivores (2B), linked to buccal cavity morphology, were used to investigate the trophic structure of the assemblage.

Data analysis

The analysis were applied on the nematode densities (ind./10 cm2) of two replicates per sampling location. The univariate analysis was performed using Statistica 6.0 (STATSOFT, 2001). The multivariate analyses were applied on square-root transformed nematode data using the PRIMER v.5.2.9 software package (CLARKE AND GORLEY, 2001). Non-parametric Mann-Whitney U test (Z statistic Mann-Whitney Test; p<0.001*** - very highly significant; p<0.01** - highly significant; p<0.05* - significant) was applied to analyse the existence of significant differences between the dry and rainy season. Spearman's rank correlation was tested to examine the relationship between the nematode species density and environmental factors.

Nematode species densities were ordinated by non-metric Multi-Dimentional Scaling (nMDS) (KRUSKAL, 1964). Diversity expressed as the number of species per sample (S), the expected number of species present in a population of 100 individuals ES (100), Pielou's evenness (J'), Simpson Index (1- λ ') and Hill's diversity numbers N₁, N_{inf} (HILL, 1973) were calculated. Diversity patterns were visualized by *k*-dominance curves (LAMBSHEAD *et al.*, 1983).

Calculations of average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) (WARWICK AND CLARKE, 1995) from simulated sub-samples of different numbers of species from the nematode list were used to produce a probability funnel

against which distinctness and variation of distinctness values for the zones (upper and lower) at the beach were checked and formally addressed the question whether these zones have a 'lower than expected' taxonomic spread. Δ^+ is a measure of the average degree to which individuals in an assemblage are related to each other and Δ^+ is the variance of these pairwise path lengths and reflects the unevenness of the taxonomic tree (CLARKE AND WARWICK, 2001). Six taxonomic levels were used (species, genus, family, order, subclass and class).

Additionally, the nematode species density data at the lower tide level provided from the same sampling period (CALLES *et al.*, submitted) were used to compare the assemblage structure across the beach. One-way ANOSIM was applied to assess the significant differences between beach stations (upper and lower) and the similarity percentages programme (SIMPER) was applied to identify the species primarily providing the discrimination between the beach stations.

Results

Environmental factors

Median grain size ranged between 215 and 283 μ m (July 2000 and May 2001 respectively), corresponding to fine-medium sand. The SST varied from 21.9 °C (July 2000) to 27.5 °C (March 2001). The salinity of the water ranged between 32.5 (February 2001) and 34 (July 2000). The pluviosity registered the maximum values in January 2001 (150.9 mm) and March 2001 (113.8 mm). Samples were taken between 37-43 metres from the reference point 'zero' (indicated in the Figure 5.1).

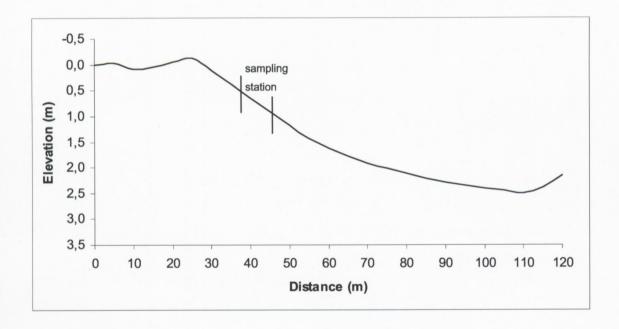


Figure 5.1 Average beach profile at San Pedro de Manglaralto. The indication lines refer to the sampling distance over which the actual samples were taken during the one-year period (June 2000-June 2001). The vertical scale is exaggerated in relationship to the horizontal. The origin (0) is named reference point through the thesis.

Nematode community

Densities and composition

ind./10 cm² (December 2000) to 1488±100 ind./10 cm² (June 2000). The overall average density was 662±91 ind./10 cm². Nevertheless, not significant differences between dry (April-December) and rainy (January-March) season were detected. In total 40 nematode species belonging to 30 genera and 15 families were found at the upper station (Table 5.1), based on the analysis of 5098 specimens. Thoracostomopsidae (17%) and Desmodoridae (17%) were the most dominant families, followed by Xyalidae (14%), Cyatholaimidae (13%), Oncholaimidae (13%), Trypiloididae (8%), Axonolaimidae (7%), Chromadoridae (4%); while, Ironidae, Ceramonematidae, Anticomidae, Microlaimidae, Leptolaimidae, Linhomoeidae and Oxystominidae represented less than 1%.

Total nematode densities (mean±standard error of the mean) varied from 183±28

Dominant nematode species

The list of the species at the upper station, their percentage of occurrence and densities (mean±standard error of the mean) over the sampling period are given in Table 5.2. Eighteen species had dominance higher than 1%, comprising 97% of the total nematode population.

Figure 5.2 shows the temporal variations of the 10 dominant nematode species. Significant differences between dry and rainy season, concerning nematode species densities were detected: *Metachromadora* sp. 1 (Z= 2.6; p<0.01**) and *Rhynchonema* cf. *hirsutum* (Z= 2.5; p<0.05*).

Most of the dominant nematode species registered the highest densities between June-Septmeber.

Enoplolaimus sp. 1 represented 14% of the nematode community, with the highest densities registered in June 2000 (377 ind./10 cm²) and July 2000 (322 ind./10 cm²), followed by a decline until November 2000 (55 ind./10 cm²), after which an slightly increase was observed between December 2000 and February 2001 (91-105 ind./10

cm²). Over the sampling period lowest densities occurred in March 2001 (4-12 ind./10 cm²). The juveniles and females being always present through the year, with the highest densities in June 2000 and July 2000 respectively, coincided with the peak of the total density. The males were absent in March 2000, nevertheless the highest densities were observed in July 2000.

Paracyatholaimus sp. 1 (13%) showed density fluctuations over the sampling period, a peak in May 2001 (374 ind./ 10 cm²) and an other one in July 2001 (255 ind./10 cm²) were observed. Over the sampling year the densities remain lower, between 0-113 ind./10 cm² in June 2000 and February 2001 respectively. The distribution of the age structure was similar along the year, the highest number of juveniles, females and males were registered between May and July 2001.

Family	% of total	Number of genera	Number of species
Thoracostomopsidae	17.41	1	3
Desmodoridae	16.80	2	3
Xyalidae	13.59	8	10
Cyatholaimidae	13.28	1	3
Oncholaimidae	12.69	1	3
Tripyloididae	7.75	1	1
Axonolaimidae	6.54	2	2
Chromadoridae	4.32	2	2
Ironidae	1.98	2	2
Ceramonematidae	1.90	1	2
Anticomidae	1.35	1	1
Microlaimidae	1.21	1	1
Leptolaimidae	0.65	2	2
Linhomoeidae	0.38	3	3
Oxystominidae	0.13	2	2
TOTAL	100	30	40

Table 5.1 Overall relative abundance (%) of the nematode families collected at San Pedro de Manglaralto beach, listed in descending order of dominance, with indication of the number genera and species found.

Nematode species:			Jun-	00	Ju	I	Aug	Sep	Oct	Nov	Dec	Jan-01	Feb	Mar	Apr	May	Jun
	type	%	Av	SE	Av	SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE
Axonolaimus sp. 1	1B	6,53	223 ±	74	3 ±	3	81 ± 15	26 ± 3	24 ± 7	17 ± 3	13 ± 2	11 ± 0	19 ± 9	36 ± 0	15 ± 4	16 ± 10	119 ± 59
Bathylaimus sp. 1	1B	7,75	84 ±	76	137 ±	66	24 ± 19	34 ± 9	14 ± 0	15 ± 2	3 ± 3	11 ± 1	23 ± 2	10 ± 5	10 ± 3	109 ± 19	122 ± 0
Camacolaimus sp.	2A	0,02	0 ±	0	0 ±	0	0 ± 0	1 ± 1	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0				
Ceramonema sp. 1	1A	1,85	12 ±	4	11 ±	2	3 ± 3	1 ± 1	0 ± 0	20 ± 4	4 ± 2	2 ± 2	1 ± 1	0 ± 0	2 ± 0	48 ± 3	4 ± 4
Ceramonema sp. 2	1A	0,06	0 ±	0	0 ±	0	0 ± 0	4 ± 2	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0				
Daptonema sp.	1B	0,01	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0				
Daptonema sp. 1	1B	5,13	49 ±	17	49 ±	10	158 ± 15	22 ± 9	9 ± 6	30 ± 5	22 ± 4	20 ± 9	19 ± 6	16 ± 6	18 ± 8	48 ± 3	3 ± 3
Daptonem a sp. 2	1B	0,06	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	5 ± 4	0 ± 0	0 ± 0	0 ± 0				
Dichromadora sp.	2A	0,03	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Elzalia sp.	1B	0,01	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Enoplolaimus sp. 1	2B	14,31	311 ±	66	288 ±	34	109 ± 8	101 ± 10	33 ± 1	48 ± 6	78 ± 13	51 ± 13	84 ± 21	8 ± 4	58 ± 42	16 ± 10	31 ± 8
Enoplolaimus sp. 2	2B	3,06	56 ±	56	210 ±	27	7 ± 2	0 ± 0	9 ± 9	1 ± 1	1 ± 1	0 ± 0	0 ± 0				
Enoplolaimus sp. 3	2B	0,04	0 ±	0	0 ±	0	0 ± 0	3 ± 3	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Eumorpholaimus sp.	1B	0,35	0 ±	0	0 ±	0	0 ± 0	3 ± 3	0 ± 0	3 ± 3	16 ± 3	6 ± 6					
Gonionchus ecuadoriensis	2A	1,70	7 ±	7	71 ±	6	15 ± 5	37 ± 0	1 ± 1	3 ± 1	0 ± 0	0 ± 0	1 ± 1	1 ± 1	1 ± 1	6 ± 0	0 ± 0
Halalaimus sp.	1A	0,09	0 ±	0	0 ±	0	5 ± 5	0 ± 0	0 ± 0	4 ± 1							
Leptolaimus sp.	1A	0,63	0 ±	0	0 ±	0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	1 ± 1	4 ± 1	12 ± 7	4 ± 2	1 ± 1	19 ± 13	8 ± 4
Linhomoeus sp.	2A	0,02	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	1 ± 1	0 ± 0	0 ± 0
Metachromadora cf. gerlachi	2B	1,66	48 ±	48	17 ±	17	0 ± 0	1 ± 1	0 ± 0	10 ± 3	4 ± 0	3 ± 3	1 ± 1	1 ± 1	2 ± 0	61 ± 54	0 ± 0
Metachromadora sp. 1	2B	12,98	119 ±	15	155 ±	6	107 ± 1	50 ± 16	2 ± 2	11 ± 4	1 ± 1	2 ± 2	2 ± 0	4 ± 0	26 ± 20	302 ± 27	82 ± 5
Metadesmolaimus sp. 1	1B	0,12	4 ±	4	3 ±	3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	1 ± 1	0 ± 0	0 ± 0	2 ± 0	0 ± 0	0 ± 0
Metalinhomoeus sp.	1B	0,02	0 ±	0	0 ±	0	0 ± 0	0 ± 0	1 ± 1	1 ± 1	0 ± 0	0 ± 0	0 ± 0				
Microlaimus sp.	2A	1,21	0 ±	0	8 ±	8	0 ± 0	1 ± 1	6 ± 2	2 ± 0	0 ± 0	26 ± 4	5 ± 1	18 ± 5	2 ± 2	26 ± 19	12 ± 6
Molgolaimus sp.	1A	2,16	12 ±	12	0 ±	0	10 ± 0	0 ± 0	6 ± 6	55 ± 22	105 ± 25						
Neochromadora sp.	2A	4,29	28 ±	20	21 ±	12	10 ± 5	1 ± 1	7 ± 1	5 ± 2	23 ± 9	13 ± 8	52 ± 10	11 ± 4	31 ± 2	145 ± 3	18 ± 4
Odontanticoma sp. 1	2A	1,35	0 ±	0	62 ±	3	17 ± 7	20 ± 6	2 ± 2	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	6 ± 6	0 ± 0
Omicronema sp. 1	1B	0,04	0 ±	0	0 ±	0	3 ± 3	1 ± 1	0 ± 0	0 ± 0	0 ± 0						
Paracyatholaimus sp. 1	2A	13,10	16 ±	16	27 ±	7	40 ± 16	17 ± 3	79 ± 5	107 ± 3	23 ± 8	71 ± 2	85 ± 28	67 ± 11	13 ± 8	321 ± 53	104 ± 10
Paracyatholaimus sp. 2	2A	0,16	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	5 ± 1	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	9 ± 0
Paracyatholaimus sp. 3	2A	0,02	0 ±	0	0 ±	0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Paramonohystera sp.	1B	0,65	4 ±	4	10 ±	10	8 ± 8	14 ± 2	4 ± 3	1 ± 1	5 ± 3	1 ± 1	0 ± 0	9 ± 9	3 ± 3	3 ± 3	0 ± 0
Parodontophora sp. 1	1B	0,01	0 ±	0	0 ±	0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0				
Pseudosteineria sp.	1B	0,74	0 ±	0	43 ±	9	25 ± 9	1 ± 1	0 ± 0	0 ± 0	0 ± 0						
Rhynchonema cf. hirsutum	1B	5,13	75 ±	45	57 ±	44	213 ± 14	104 ± 21	1 ± 1	8 ± 5	4 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	10 ± 3	3 ± 3
Syringolaimus sp.	2B	0,01	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Trissonchulus sp.	2B	1,97	0 ±	0	0 ±	0	0 ± 0	0 ± 0	3 ± 1	2 ± 0	1 ± 1	27 ± 4	38 ± 9	38 ± 12	2 ± 0	3 ± 3	66 ± 17
Viscosia sp. 1	2B	1,73	60 ±	44	7 ±	1	10 ± 5	31 ± 20	1 ± 0	15 ± 3	0 ± 0	0 ± 0	3 ± 3	4 ± 2	3 ± 0	10 ± 3	0 ± 0
Viscosia sp. 2	2B	10,93	380 ±	132	174 ±	4	198 ± 63	77 ± 14	4 ± 2	17 ± 6	2 ± 0	3 ± 3	15 ± 2	16 ± 0	29 ± 5	48 ± 3	8 ± 5
Viscosia sp. 3	2B	0,03	0 ±	0	0 ±		0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Wieseria sp.	1A	0,04	0 ±	0	0 ±	0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Table 5. 2 Nematode densities (ind./ 10 cm²) at the upper station, San Pedro de Manglaralto beach.

Metachromadora sp. 1 represented 13% of the total nematode density. The nematode densities appear to be restricted to June-September 2000 and April-July 2001. The highest number of females was observed between April and July 2001. While at the period June-September 2000, an opposite trend was observed: the number of juveniles decreased and the females and males increased.

Viscosia sp. 2 was the forth dominant species on the nematode community (11%), showed that the highest densities were present from June 2000 until September 2000, and followed by a sharp density decline over the sampling year. Nevertheless, *Viscosia* sp. 2 registered the most highest densities (512 ind./10 cm²) compared to the other species recorded at the high tide level. Although the juveniles were present through the year, the highest number of males was observed between June-September 2000, with the maximum in June 2000.

Bathylaimus sp. 1 (8%) and Axonolaimus sp. 1 (7%) showed a clear trend, with highest densities from June to September 2000, followed by a sharp density decline. Bathylaimus sp. 1 had continuous reproduction and juveniles dominated between June-August 2000. While in Axonolaimus sp. 1 the juveniles dominated through the year.

Rhynchonema cf. hirsutum (5%) showed highest densities from June to September, followed by a sharp density decline (similar trend as *Viscosia* sp. 2). A very obvious absent of juveniles was observed over the sampling period, except between June-September 2000, but always with low densities, while the females and males dominated.

Daptonema sp. 1 and Neochromadora sp. represented 5 and 4% of the total nematode density respectively. Both species showed density fluctuations over the sampling period, the highest densities were in August (173 ind./10 cm²) and May (147 ind./10 cm²) respectively. Daptonema sp. 1 had continuous reproduction, the juveniles and females dominated through the year. While in Neochromadora sp. the females and males were dominant, but the highest numbers of females in May 2000 coincided with the peak of density of Neochromadora sp.

Enoplolaimus sp. 2, represented 3% of the total nematode density. The densities were restricted only to June-August and February-March with the highest densities in July 2000 (237 ind./ 10 cm²). The juveniles were dominant.

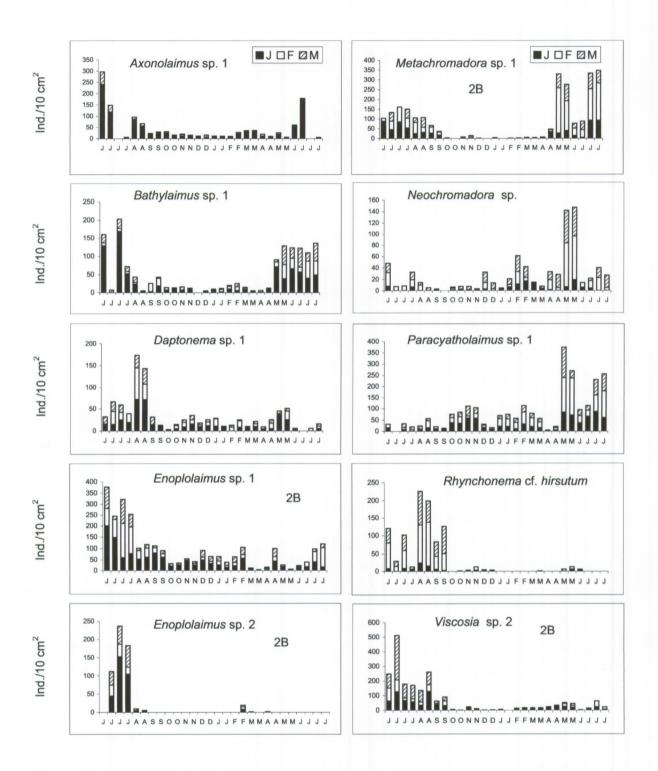


Figure 5.2 Distribution of the ten dominant species at the upper station, San Pedro de Manglaralto beach, from June 2000 until July 2001. Legend on the figure: J= juveniles, F= females, M= males. 2B= nematode predator/omnivore.

Species diversity

The species richness concerning the number of species (S) showed significant differences (p<0.05) between dry and rainy season. The highest diversity was registered in November (21 species) and the lowest diversity in December (13 species) and January (13 species) (Table 3). The *k*-dominance curves per month (Figure 5.3) showed the results based on the relative abundance of nematode species over the sampling period. The curve at the lowest position (June 2001) of the figure indicating the most diverse month over the sampling period and December (upper position) the less diverse.

	N	S	J'	ES (100)	1-λ'	N ₁	N _{inf}
J	1488 ± 100	14 ± 2	0.79 ± 0.024	11.20 ± 1.41	0.83 ± 0.031	7.81 ± 1.16	3.46 ± 0.75
J	1354 ± 188	17 ± 1	0.83 ± 0.008	13.98 ± 0.39	0.88 ± 0.002	10.33 ± 0.02	4.69 ± 0.10
Α	1041 ± 11	17 ± 1	0.79 ± 0.036	13.47 ± 0.42	0.86 ± 0.010	9.42 ± 0.53	4.30 ± 0.26
S	557 ± 16	18 ± 1	0.82 ± 0.036	14.91 ± 0.14	0.88 ± 0.012	10.82 ± 0.64	4.71 ± 0.42
0	192 ± 7	16 ± 1	0.69 ± 0.002	12.68 ± 0.02	0.77 ± 0.001	6.67 ± 0.19	2.42 ± 0.07
N	328 ± 11	21 ± 1	0.76 ± 0.009	16.82 ± 0.43	0.85 ± 0.001	10.15 ± 0.08	3.05 ± 0.00
D	183 ± 28	13 ± 1	0.72 ± 0.004	11.27 ± 1.02	0.77 ± 0.008	6.19 ± 0.25	2.35 ± 0.04
J	246 ± 23	13 ± 3	0.81 ± 0.047	11.14 ± 1.24	0.83 ± 0.006	7.62 ± 0.35	3.46 ± 0.44
F	372 ± 66	15 ± 1	0.79 ± 0.023	12.30 ± 0.08	0.85 ± 0.003	8.55 ± 0.08	4.37 ± 0.52
M	245 ± 19	15 ± 2	0.82 ± 0.007	12.92 ± 0.81	0.86 ± 0.014	9.00 ± 0.60	3.69 ± 0.33
Α	231 ± 83	18 ± 1	0.81 ± 0.032	15.98 ± 1.36	0.87 ± 0.023	10.23 ± 1.17	3.80 ± 0.67
M	1269 ± 18	19 ± 1	0.76 ± 0.043	14.11 ± 0.10	0.84 ± 0.027	9.17 ± 0.96	4.01 ± 0.66
J	703 ± 130	15 ± 1	0.82 ± 0.007	12.63 ± 0.81	0.87 ± 0.002	9.12 ± 0.32	4.67 ± 0.01
J	1057 ± 34	17 ± 1	0.72 ± 0.004	12.67 ± 0.39	0.81 ± 0.003	7.55 ± 0.25	3.10 ± 0.04

Table 5.3 Species number (N), species richness (S), Eveness (J'), expected number of species present in 100 individuals ES (100), Shannon diversity (H'), Simpson Index (1-λ') and Hill's number (N_{inf}) from each sample. Data are represented as means (n= 2) and standard errors (SE).

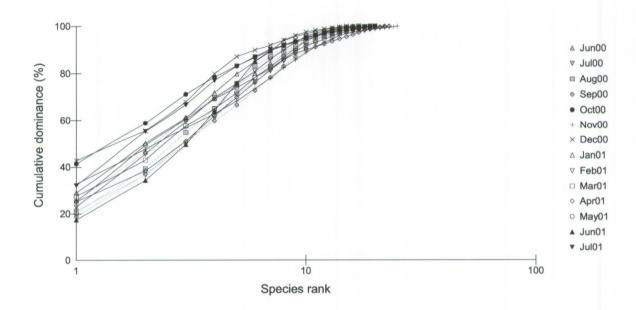


Figure 5.3 K-dominance curves per month at upper station, San Pedro de Manglaralto beach.

Trophic composition

Predators were the most dominant feeding group at the nematode community (47%). The proportion of the four feeding types (Figure 5.4), varied in a large range along the sampling year: from 0% to 18% for selective deposit feeders (1A), 12-56% for non-selective deposit feeders (1B), 2-53% for epistrate feeders (2A) and 20-80% for predators/omnivores. Significant differences (p<0.05) between dry (April-December) and rainy season (January-March) were found, explained by the highest dominance of the predators/omnivores in June 2000 (53-80%) and July 2000 (61-65%) and highest dominance of non-selective deposit feeders in August 2000 (43-56%). Also it is observed that during the rainy months the epistrate feeders were the most abundant feeding group representing between 37% and 53%.

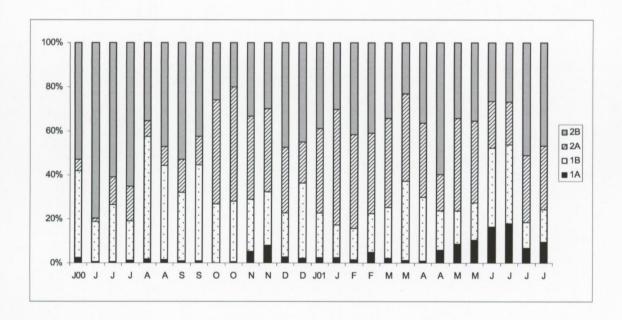


Figure 5.4 Trophic composition of the nematode community at upper station, San Pedro de Manglaralto beach.

Nematode age structure

The reproduction was continuous, the juveniles were present throughout the sampling period, and the highest densities (654±156 ind./ 10 cm²) were coupled with peak densities of the nematode populations (1488±100 ind./10 cm²). The juveniles ranged between 26% (July 2001) and 56% (March 2001), whereas the females ranged between 20% (November 2000) and 50% (July 2000) and for males between 17% (March 2001) and 42% (June 2000) (Figure 5.5).

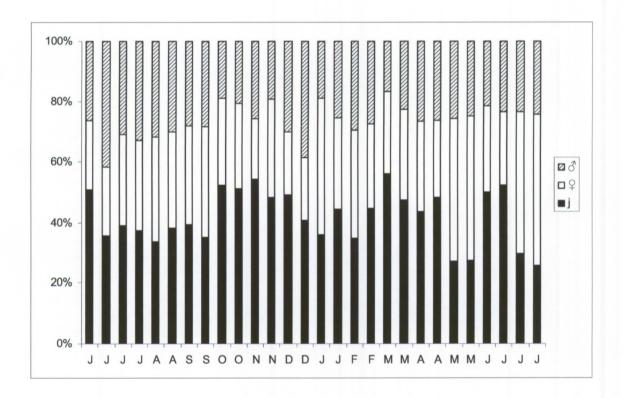


Figure 5.5 Nematode age structure at San Pedro de Manglaralto beach.

Assemblage structure

The cluster analysis (Figure 5.6) and MDS-ordination (Figure 5.7) showed two associations of the nematode species at the upper station: (1) nematodes collected from June (2000 and 2001) to September 2000 and May 2001 and (2) those collected from October 2000 to April 2001; this separation could be explained for the seasonal pattern of the dominant species *Axonolaimus* sp., *Bathylaimus* sp. 1, *Metachromadora* sp. 1, *Rhynchonema* cf. *hirsutum* and *Viscosia* sp. 2, with the highest densities found between June and September, followed by a subsequent density decline (See Figure 5.2).

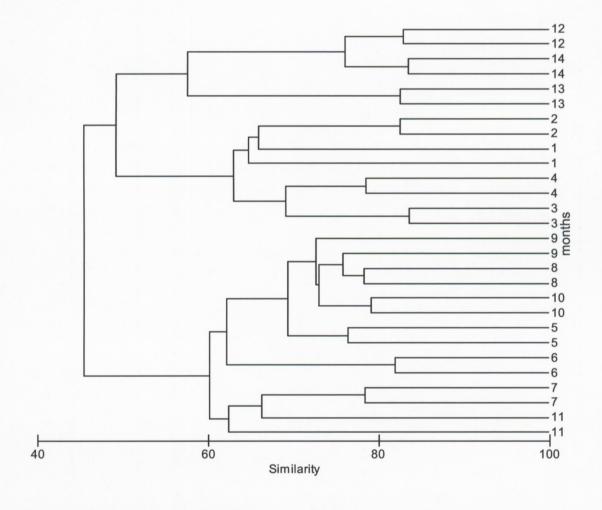


Figure 5.6 Dendogram resulting from Cluster analyses on square-root nematode species densities. Numbers indicated the monthly sampling in a chronological order from June 2000 to July 2001.

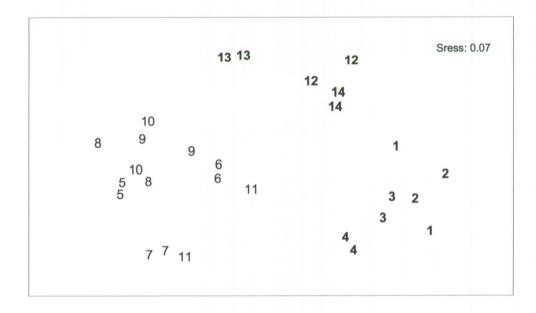


Figure 5.7 Multi-Dimensional Scaling (MDS) on square-root species abundance data at upper station. Numbers indicated the monthly sampling in a chronological order from June 2000 to July 2001. Bold numbers (Group 1: June-September) and Clear numbers (Group 2: October-April)

Relationship with environmental factors

Correlations of nematodes with SST, pluviosity, distance (as a proxy for elevation) and median grain size were analysed. The results showed significant correlations with SST and salinity principally (Table 5.4).

Species:	Median grain size	Distance (as proxy for elevation)	SST	Salinity	Pluviosity
Axonolaimus sp. 1	0,3420	0,0005 (-)***	0,4336	0,8833	0,6287
Bathylaimus sp. 1	0,5709	0,6571	0,0265 (-)*	0,0269 (+)*	0,7349
Camacolaimus sp.	0,7234	0,2953	0,1586 ns	0,1586	0,2675
Ceramonema sp. 1	0,2790	0,0944	0,0161 (-)*	0,0425 (+)*	0,0983
Ceramonema sp. 2	0,6051	0,2167	0,0897	0,0897	0,3352
Daptonema sp. 1	0,3717	0,6530	0,2720	0,3450	0,0565
Daptonem a sp. 2	0,8621	0,2174	0,1091	0,1091	0,0289 (-)*
Dichromadora sp.	0,1770	0,1770	0,1770	0,1770	0,5448
Enoplolaimus sp. 1	0,1053	0,4420	0,0019 (-)**	0,0209 (+)*	0,4007
Enoplolaimus sp. 2	0,0162 (-)**	0,5942	0,5121	0,3993	0,7515
Eumorpholaimus sp.	0,0159 (+)**	0,2657	0,7264	0,7874	0,9245
Gonionchus ecuadoriensis sp. n.	0,7881	0,0191 (+)*	0,0007 (-)***	0,0003 (+)***	0,1537
Halalaimus sp.	0,5979	0,0462 (-)*	0,4182	0,4182	0,1551
Leptolaimus sp.	0,0044 (+)**	0,5931	0,0034 (+)**	0,0056 (-)**	0,0216 (+)*
Linhomoeus sp.	0,8136	0,3548	0,0744	0,0297 (-)*	0,1117
Metachromadora cf. gerlachi	0,1181	0,0566	0,4775	0,6541	0,3716
Metachromadora sp. 1	0,9558	0,1272	0,0037 (-)**	0,0017 (+)**	0,2410
Metadesmolaimus sp. 1	0,0163 (-)*	0,2709	0,6399	0,3264	0,5650
Microlaimus sp.	0,2520	0,9661	0,0567	0,1414	0,0255 (+)*
Molgolaimus sp.	0,6203	0,2389	0,8885	0,9521	0,3702
Neochromadora sp.	0,1335	0,7902	0,0653	0,0376 (-)*	0,2332
Odontanticoma sp. 1	0,4818	0,0182 (+)*	0,0003 (-)***	0,0004 (+)***	0,1405
Omicronema sp. 1	0,8427	0,9753	0,2953	0,2953	0,3676
Paracyatholaimus sp. 1	0,0015 (+)**	0,7647	0,8724	0,9823	0,7099
Paramonohystera sp.	0,5190	0,9693	0,7422	0,5585	0,2718
Parodontophora sp. 1	0,3954	0,1080	0,9040	0,9040	0,9039
Pseudosteineria sp.	0,0293 (-)*	0,3942	0,0055 (-)**	0,0055 (+)**	0,0413 (-)*
Rhynchonema cf. hirsutum	0,2568	0,5093	0,0094 (-)**	0,0066 (+)**	0,0004 (-)***
Syringolaimus sp.	0,9040	0,3954	0,2723	0,2723	0,1390
Trissonchulus sp.	0,2469	0,4208	0,0045 (+)**	0,0153 (-)*	0,0102 (+)**
Viscosia sp. 1	0,8714	0,0563	0,0062 (-)**	0,0018 (+)**	0,3986
Viscosia sp. 2	0,2204	0,1562	0,0393 (-)*	0,0209 (+)*	0,4567
Wieseria sp.	0,2779	0,1062	0,0722	0,0722	0,5774
Total	0,8811	0,7435	0,0079 (-)**	0,0076 (+)**	0,2590

⁽⁺⁾ Positive correlation; (-) Negative correlation

Table 5.4 Spearman rank correlation coefficient p-levels between nematode species and environmental factors.

^{*}significant; **highly significant; *** very highly significant

Nematode species comparison across the beach: diversity and taxonomic distinctness

Differences in species list exist among the upper and lower station (see lower station data in Calles *et al.*, submitted) with an average Bray-Curtis dissimilarity of 73% (R= 0.966, p<0.001). The ten main discriminating nematode species for each station, their dissimilarity relative abundance and their corresponding Wieser feeding type (1953) are listed in Table 5.5.

The species richness was more or less similar at both stations over the sampling period, except in December and January with lowest values at the upper station (Figure 5.8).

Beach zone	Species list	%	type
Upper station	Enoplolaimus sp. 1	15	2B
	Paracyatholaimus sp. 1	14	2A
	Daptonema sp. 1	9	1B
	Bathylaimus sp. 1	9	1B
	Axonolaimus sp. 1	9	1B
	Viscosia sp. 2	8	2B
	Neochromadora sp.	8	2A
	Metachromadora sp. 1	7	2B
	Viscosia sp. 1	3	2B
	Trissonchulus sp.	3	2B
Lower station	Ceramonema sp. 1	15	1A
	Ceramonema sp. 2	9	1A
	Metachromadora cf. gerlachi	9	2B
	Rhynchonema cf. scutatum	9	1B
	Daptonema sp. 1	8	1B
	Parodontophora sp. 1	8	1B
	Paracyatholaimus sp. 1	7	2A
	Metadesmolaimus sp. 1	6	1B
	Microlaimus sp.	4	2A
	Omicronema sp. 1	4	1B

Table 5.5 Top ten discriminating species at the upper and the lower station, their dissimilarity relative abundance and feeding type. (1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epistratum feeders and 2B: omnivores/predators).

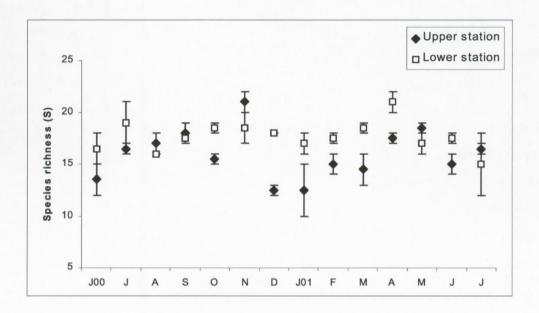


Figure 5.8 Mean nematode species richness (± standard errors of the mean) at upper and lower station, San Pedro de Manglaralto beach.

The Figure 5.9A displays the 95% funnel for the simulated distribution of average taxonomic distinctness for random subsets of fixed size m from the master nematode list (52 species). Superimposed on this plot are the true values of Δ^+ generated from species lists for each station across the beach. From this figure the lower distinctness Δ^+ was observed in June 2000, November 2000 and May 2001 at the lower station and fall outside the 95% confidence limit of simulated values from the master list, indicating that they are not taxonomically closely species. The data from April 2001 is closely to the simulated mean Δ^+ but is separated from the funnels for the highest number of species found. Figure 5.9B similarly shows the values of variation of taxonomic distinctness (Λ^+) for the same dataset.

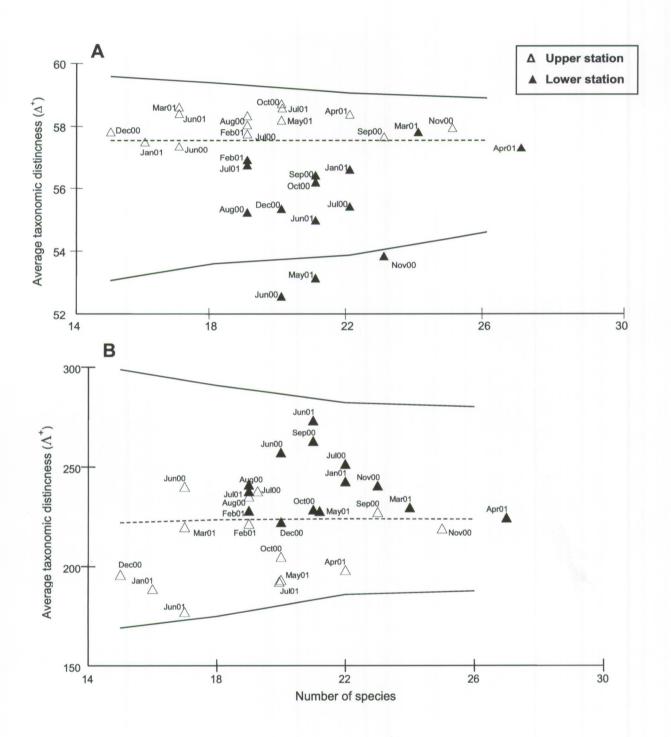


Figure 5.9 The 95% probability funnels for average taxonomic distinctness (Δ^{\dagger}) and Variation in Taxonomic distinctness (Λ^{\dagger}) plotted against the number of species on upper and lower station at San Pedro de Manglaralto beach. Dashes lines indicated the simulated mean Δ^{\dagger} and Λ^{\dagger} from 1000 random selections from the master list of 52 nematode species from this study site.

DISCUSSION

According to GHESKIERE *et al.* (2005) the upper beach possesses a set of characters defined by the interactions between the physical contrasts of the adjacent ecological systems (sea/land) and consequently an unique microhabitat is created. Therefore the upper beach was described as the transition zone where nematode species from both pure terrestrial and pure marine ecosystem co-exist.

Nematodes belonging to the terrestrial order Dorylaimida (Aporcelaimus spp., Aporcelaimellus spp., Nygolaimus sp. and Mesodorylaimus spp.) and Rhaditida (Acrobeles spp.) in low densities (less to 0.5%) were responsible for the higher average taxonomic diversity and distinctness on the upper zone at Mediterranean and Baltic beaches (GHESKIERE et al., 2005). Also GHESKIERE et al. (2004) explained that the continuous influx of freshwater from the hinterland dunes could promote terrestrial nematodes to invade the upper beaches as well. At the Ecuadorian upper beach, terrestrial nematodes were not found. In our study the nematode community at the upper beach was dominated by Thoracostomopsidae (17%), Desmodoridae (17%) and Xyalidae (14%), while at the Australian upper beaches (NICHOLAS AND HODDA, 1999) Cyatholaimidae (19%) and Desmodoridae (13%) dominated. GHESKIERE et al. (2005) found highest dominance (up to more than 50% of the total interstitial assemblage) of the nematode predators at the upper stations along an Italian beach (Aporcelaimus sp. 1, Epacanthion enoploidiforme, Trileptium subterraneum and Aporcelaimellus sp. 2) and a Polish beach (Aporcelaimus sp. 2, Tripyloides acherusius and Aporcelaimellus sp. 3). Such high dominance of predatory nematodes was extremely remarkable in marine sediments where relative abundance of predators generally do not exceed 20% (HEIP et al., 1985). Also at the Australian beaches NICHOLAS AND HODDA (1999), found that the nematode predators (20-63%) were the most abundant feeding group on the beach. At the Ecuadorian beach, the predatory nematodes represented 47% of the nematode community at the upper station versus 14% of the nematode community at the lower station. The dominant predators Enoplolaimus sp. 1 (311±66 ind./ 10 cm²) and Metachromadora sp. 1 (340±7 ind./ 10 cm²) showed highest densities in June 2000 and July 2001 respectively.

GHESKIERE et al. (2005) showed that the abundance and the diversity of marine nematode predators were higher on coarse-grained beaches than on fine-grained beaches.

Despite differences of the sampled beach type and its geographical position (Poland, Belgian, Mediterranean and Ecuadorian beaches), the nematode predators were more dominant in the upper beach.

Highly dynamic, intermediate shores with high wave energy and subject to erosion are characterized by high fluxes of organic material through the beach, but without storage of food sources in the sediment (MENN, 2002). On the steep-profiled, coarse-grained (Sylt) shore, strong hydrodynamics resulted in erosion and high fluxes of organic material through the beach, but prevented any storage of food sources; in contrast, at the flat-profiled, fine-grained beach (Rømø) shore, with low wave energy and accretion, organic carbon accumulated from surf waters (MENN, 2002). On these shores the "small food web" (meiofauna) of agile organisms dominates, but differed in taxonomic composition and nematodes strongly dominated the assemblage at Rømø. While organic storage and the "large food web" (macrofauna, epifauna, fish and shorebirds) is important on stable, dissipative and accreting shores (Figure 5.10).

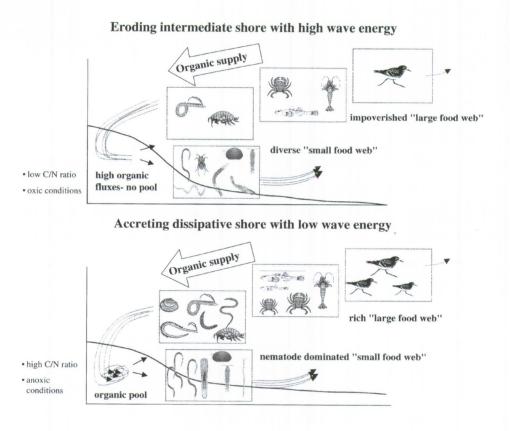


Figure 5.10 Food web structure on cold-temperate shores. Arrows indicated flow of organic and mineralized substrates (source: MENN, 2002).

Despite the median grain size in the Ecuadorian beach ranged from 215 to 283 µm at the upper station and from 191 to 260 µm at the lower station, corresponding to fine-medium sand, significant differences (p<0.001) were found at the sediment. Nematodes are also food for an array of other meiofaunal organims (KENNEDY, 1994). Most predatory infauna has a more restricted reproductive period than opportunistic species whose larvae are present in the water column for large portions of the year (DAUER *et al.*, 1982). Species which inefficiently refuge from predation, possess high reproductive potentials with extended periods of recruitment allowing their existence in environments affected by predation. The nematode reproduction at species level was continuous in the Ecuadorian beach, the juveniles were present through the sampling period, and the highest densities (654±156 ind./ 10 cm²) were coupled with peak densities of the population in June 2000.

On the Ecuadorian beach some species were found most often or restricted to a particular location on the beach (Table 5.6) (*i.e. Trissonchulus, Enoplolaimus* sp. 1 at theupper station; *Synonchiella* sp. at the lower station). It is in contrast with the Australian study by NICHOLAS AND HODDA (1999), where no definite trend in the distributions of species on the cross-shore occurred.

Factors controlling field distributions on sandy sediments were studied by GALLUCI et al. (2005). Enoploides longispiculosus is a prominent predacious nematode of the North Sea and adjacent estuaries. The densities varied strongly, even between sites with only subtle differences in sediment composition. E. longispiculosus abundances were positively correlated with grain size, proportion of fine sand and emersion period during low tides, and negatively with silt, very fine sand content and prey selectivity.

KNOX (2001) explained that a reduction in species richness is expected on the upper shore as environmental conditions were more extreme and the abundance and distribution of organisms are controlled by physical factors such as extremes of temperature and desiccation. The species from the upper shore demonstrated is able to tolerate osmotic changes and resist the effects of the associated stress more effectively than species from lower intertidal or subtidal sites (FORSTER, 1998).

The average taxonomic distinctness revealed that in both stations at the Ecuadorian beach the species are taxonomically closely related, except those species found at the lower station during June 2000, November 2000 and May 2001. GHESKIERE *et al.* (2005) found differences in the taxonomic distinctness between Mediterranean and

Baltic sandy beaches with the lowest distinctness Δ^+ in the Italian swash zone assemblage.

CONCLUSIONS

Across the Ecuadorian beach, zonation patterns in terms of meiofauna (CALLES *et al.*, submitted) and nematode assemblage structure (compared in this study) were detected, caused by: the highest densities of copepods at the upper station (275±86 ind./10 cm²) and highest densities of nematodes at the lower station (738±64 ind./10 cm²), with nearly absence of copepods near the low water level; while the predatory nematodes (*Enoplolaimus* sp. 1, *Metachromadora* sp.1, *Trissonchulus* sp., *Viscosia* sp. 1 and *Viscosia* sp. 2) were dominant (up more than 40% of the interstitial assemblage) at the upper station. Those results illustrated the importance of predators in the interstitial food web of the upper station along an Ecuadorian beach.

SPECIES I IST	BEACH STATION				
SPECIES LIST	Upper	Lower			
Anoplostoma sp.		x			
Axonolaimus sp. 1	X				
Bathylaimus sp.		X			
Bathylaimus sp. 1	X				
Camacolaimus sp.	x	X			
Ceramonema sp. 1	X	x			
Ceramonema sp. 2	x	X			
Cobbia sp.		X			
Daptonema sp.	X	x			
Daptonema sp. 1	X	×			
Daptonema sp. 2	X	x			
Daptonema sp. 3		x			
Dasynemoides sp.		X			
Dichromadora sp.	X	x			
Ditlevsenella sp.		×			
Elzalia sp.	X				
Enoplolaimus sp.		X			
Enoplolaimus sp. 1	x				
Enoplolaimus sp. 2	x				
Enoplolaimus sp. 3	x				
Eumorpholaimus sp.	X	x			
Eurystomina sp.		x			
Gonionchus ecuadoriensis sp. n.	x	x			
Halalaimus sp.	X	x			
Leptolaimus sp.	X	x			
Linhomoeus sp.	X				
Metachromadora cf. gerlachi	x	x			
Metachromadora sp. 1	×				
Metadesmolaimus sp. 1	x	X			
Metadesmolaimus sp. 1	^	X			
Metalinhomoeus sp.	x	^			
Microlaimus sp.	x	X			
Molgolaimus sp.	×	^			
Neochromadora sp.	×	x			
Odontanticoma sp. 1	×	x			
Omicronema sp. 1	x	x			
Paracyatholaimus sp. 1	×	x			
Paracyatholaimus sp. 1	×	x			
Paracyatholaimus sp. 2	×	^			
Paramonohystera sp.	×	X			
Pareurystomina sp.	^	x			
Parodontophora sp. 1	X	X			
Pomponema sp.	^	×			
Pseudosteineria sp.	x	×			
Rhynchonema cf. hirsutum	X	X			
Synonchiella sp.	^	×			
Syringolaimus sp.	X	^			
Trissonchulus sp.	X				
Viscosia sp. 1	×	x			
Viscosia sp. 1 Viscosia sp. 2	X	×			
Viscosia sp. 2 Viscosia sp. 3	X	^			
Wieseria sp. 3	^				

Table 5.6 Distribution of free-living marine nematodes at the upper and the lower station in San Pedro de Manglaralto beach. The predators in bold.