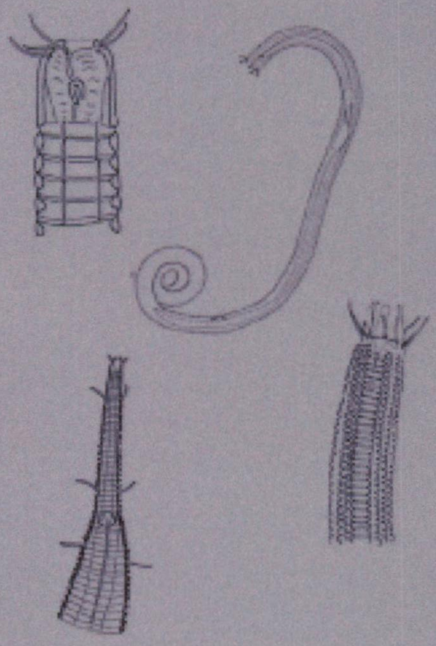
UNIVERSITEIT
GENT

FACULTEIT WETENSCHAPPEN

Mariene Biologie
Vakgroep Biologie

SPATIAL AND TEMPORAL PATTERNS OF MEIOFAUNA ALONG ECUADORIAN SANDY BEACHES, WITH A FOCUS ON NEMATODE BIODIVERSITY



Alba Katherine Calles Procel

Promotor: Prof. Dr. Magda Vincx
Co-promotor: Dr. Maria del Pilar Cornejo

Academic Year: 2006-2007
Thesis submitted in partial fulfilment of the requirements for the degree of
Doctor in Sciences (Biology)

FACULTEIT WETENSCHAPPEN

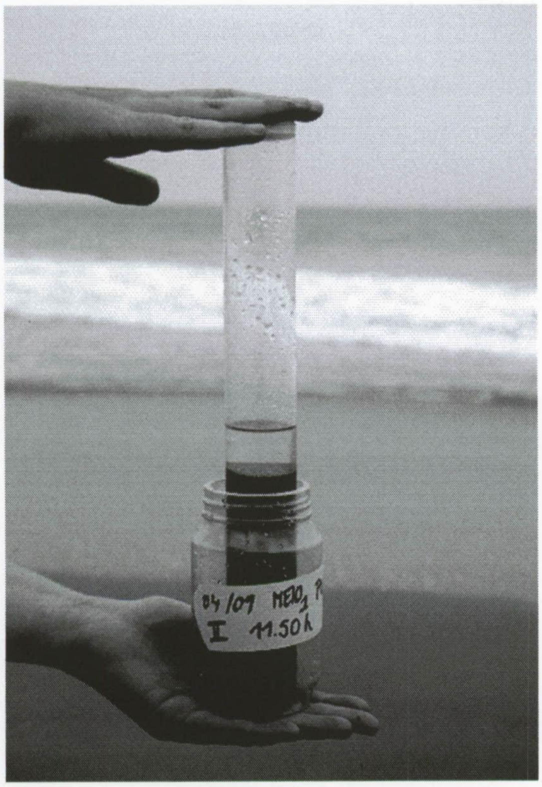
UNIVERSITEIT GENT

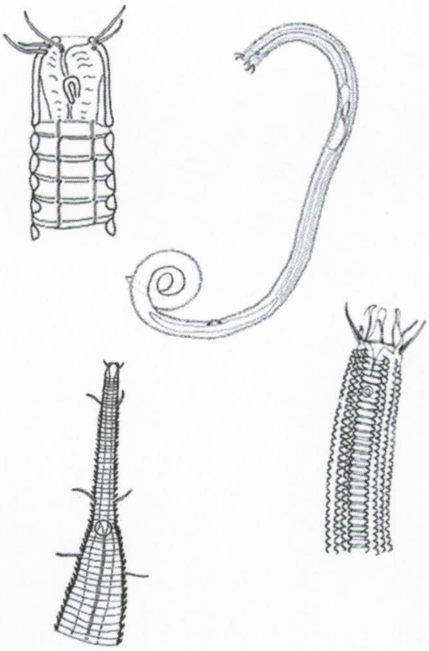
Mariene Biologie
Vakgroep Biologie

ESPOL 1958
ESCUELA SUPERIOR POLITÉCNICA DEL LITORAL
GUAYAQUIL ECUADOR

SPATIAL AND TEMPORAL PATTERNS OF MEIOFAUNA ALONG ECUADORIAN SANDY BEACHES, WITH A FOCUS ON NEMATODE BIODIVERSITY

(Patrones Espaciales y Temporales de la Meiofauna en playas arenosas ecuatorianas, con un enfoque sobre Biodiversidad de Nemátodos)





Alba Katherine Calles Procel

Promotor: Prof. Dr. Magda Vincx

Co-promotor: Dr. María del Pilar Cornejo

Academic Year: 2006-2007

Thesis submitted in partial fulfilment of the requirements for the degree of

MEMBERS OF THE READING COMMITTEE

Prof. Dr. MAGDA VINCX, PROMOTOR (UGENT, BE)

Dr. MARÍA DEL PILAR CORNEJO, CO-PROMOTOR (ESPOL, EC)

Dr. FERNANDO ARCOS (ESPOL, EC)

Dr. STEVEN DEGRAER (UGENT, BE)

MEMBERS OF THE EXAMINATION COMMITTEE

Prof. Dr. WIM VYVERMAN, CHAIRMAN (UGENT, BE)

Prof. Dr. MAGDA VINCX, PROMOTOR (UGENT, BE)

Dr. MARÍA DEL PILAR CORNEJO, CO-PROMOTOR (ESPOL, EC)

Dr. FERNANDO ARCOS (ESPOL, EC)

Dr. STEVEN DEGRAER (UGENT, BE)

Dr. NANCY FOCKEDEY (VLAAMS INSTITUUT VOOR DE ZEE, BE)

Prof. Dr. ANN VANREUSEL (UGENT, BE)

Prof. Dr. TOM MOENS (UGENT, BE)

TABLE OF CONTENTS

PAGE

Chapter I. General introduction, Aims and Thesis Outline

Chapter II. Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches

Chapter III. Tropical sandy beach meiofauna: a case study on the temporal patterns of a high and low water station in Ecuador

Chapter IV. Temporal variability in the composition and biodiversity of free-living marine nematodes in a tropical beach (Ecuador)

Chapter V. The dominance of predatory nematodes at the high water level in Ecuadorian sandy beaches

Chapter VI. Taxonomic description of some dominant nematode species from San Pedro de Manglaralto beach (Ecuador)

Chapter VII. General discussion and conclusions

Annexes

Figures List

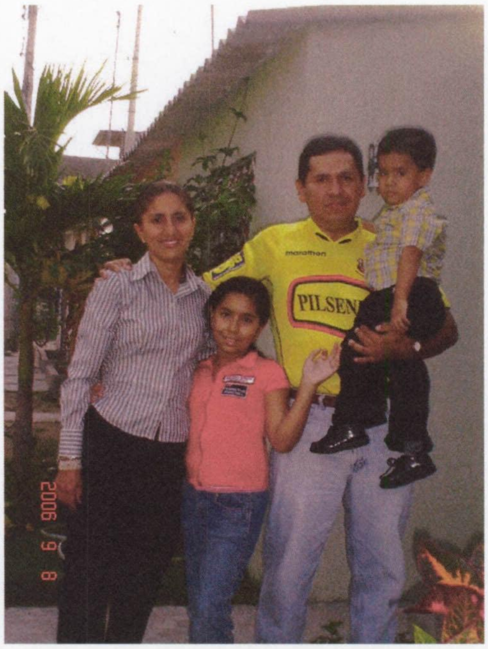
Tables List

Oh Jehová Dios de los ejércitos, ¿quién es vigoroso como tú, oh Jah?
Y tu fidelidad está todo en derredor tuyo.
Tú estás gobernando sobre la hinchazón del mar;
cuando levanta sus olas, tú mismo las calmas.

(SALMOS 89:8-9)

Dedicatoria

A mi amado esposo Ronald Cordero quien con paciencia y cariño tomaba cuidado de nuestros hijos mientras Yo dedicaba tiempo a realizar esta investigación. Momentos gratos con Adrianita en Ghent y Ronital que estudiaba conmigo estando en mi vientre al inicio de este doctorado.



Acknowledgements

I wish to convey my gratitude to Prof. Magda Vincx, my promotor, for her technique guidance during the development of this thesis, for her scientific teaching and the most important her appreciated friendship.

My sincere thanks to VLIR-ESPOL (Escuela Superior Politécnica del Litoral) Program for their technique, logistic and economic support.

It is my pleasure to express my personal gratitude to Dr. Ma. Pilar Cornejo for their valuable co-operation in all the aspects.

I am very thankful to all the staff of the Marine Biology Section, to the scientific group of benthos which discussed with me the results provided in this research.

I will always appreciate the assistance that Rita Van Driessche give me in the preparing of slides and take the scanning pictures for the new species found.

In my mind and my heart I have engraving unforgettable moments of all persons that help me in any occasion, specially my family for all the love and support to conclude my dreams 'improve in the scientific field'. My parents Vicente Calles, Alba María Procel, Rosario López, Ramiro Cordero. I want to say thank you so much to Dirk Vander Haeghen and Doriane Conrieri because they were my family in Belgium. To Leonor and Ronny, the Spanish Congregation of Ghent, Carmen and Judith, who were really my spiritual sisters and brothers.

Summary

The interstitial fauna of marine beaches has been studied at different latitudes and localities (e.g. HEIP *et al.*, 1985 for an overview; COULL, 1988) but not so much along cross-shore and temporal gradients in tropical areas (GOURBAULT *et al.*, 1998). From the South-eastern Pacific region no data on interstitial meiofauna are available for sandy beaches. Although nematodes are among the most abundant metazoans in marine sediments, only few papers, apart from purely taxonomic ones, have described the nematode species composition at intertidal sandy beaches (GOURBAULT *et al.*, 1995; GHESKIERE *et al.,* 2002; 2004, 2005 and URBAN-MALINGA *et al.*, 2004) and their seasonal variability (SHARMA AND WEBSTER, 1983; GOURBAULT, 1998; NICHOLAS AND HODDA, 1999; and NICHOLAS, 2001). This is probably due to the time-consuming species identification process and the overall high species diversities of the nematode assemblages.

Free-living marine nematodes do have several favourable features for using them as bio-indicators of environmental conditions (BONGERS AND FERRIS, 1999; and SCHRATZBERGER AND WARWICK, 1999) and it is known from experiments that they are ecologically very heterogeneous and occupy different positions in benthic food webs (AARNIO, 2001). Geographically located in the equatorial tropical climate region, the Ecuadorian coast is strongly influenced by the anomalous El Niño and La Niña events every 2-8 years (SANTOS, 2006). This causes fluctuating climatic conditions, which can have an effect on several sensitive marine living organisms.

At the Ecuadorian coast two different sandy beaches situated in the Guayas province were investigated: ‘Salinas’ a sheltered beach with fine grain sand and ‘San Pedro de Manglaralto’ an exposed beach with fine to medium grain sand. The Ecuadorian coastal climate is characterized by two seasons: a dry-cool (May-December) and a wet-warm (January-April) (CORNEJO, 1999). Nevertheless, The dry season (April-December) and the rainy season (January-March) mentioned here corresponded to the data set of the environmental sampling campaigns of the present study. The sampling campaigns were conducted within the VLIR-ESPOL Program; project 4 “Environmental Management System in Agriculture and Aquaculture” in the frame of the Modelling and Population Dynamics of Bio-indicators in the coastal zone of Ecuador with emphasis on the benthic component research. The sampling

campaigns included short-term period (fortnightly) from June 2000 until July 2001, and long-term period (quarterly) from August 1999 until February 2001, during the strong La Niña, after the 1997-1998 El Niño (McPHADEN, 1999).

The present study provides the first scientific contribution to the study of the structure of the meiofauna communities, especially on the most dominant taxon Nematoda (at species level), their distribution at the intertidal zone (high tide level and low tide level) in the Ecuadorian sandy beach and their relationship with the environmental factors (pluviosity, Sea Surface Temperature, salinity, chlorophyll *a*, organic matter and median grain size).

Comparisons were made between tourist and non-tourist ('pristine') beaches situated in a sheltered and in an exposed site respectively. The temporal and spatial patterns of meiofauna (especially nematodes) from these two sites showed that densities ranged between 461±101.5 to 1848±7 ind./10 cm^2 at the sheltered beach and between 376±21.5 to 2388±161.5 ind./10 cm^2 at the exposed beach. Nematodes represented between 21-81% of the total meiofauna at the sheltered beach and 76-95% at the exposed beach, followed by turbellarians and gastrotrichs. A total of 40 genera belonging to 19 families were identified. *Neochromadora*, *Daptonema, Metadesmolaimus* and *Omicronema* were the dominant genera at the sheltered beach, while *Metachromadora*, *Rhynchonema, Paracyatholaimus, Ceramonema* and *Gonionchus* were more dominant at the exposed site. At both beaches lowest diversity occurred in August 1999 (influenced by a "La Niña" event) and highest diversity was detected in the rainy season (January-March). Non-selective deposit feeders were dominant (42%) followed by predators/omnivores (26%) and epistrate feeders (24%). Seasonal groups were detected on the basis of meiofauna composition: three groups at the sheltered beach: August 1999; May 2000, February 2001 (most touristic month) characterized by the highest turbellarians density; and the periods November 1999-February 2000 and August-November 2000. At San Pedro de Manglaralto two seasonal groups were detected: August 1999 - February 2000; May 2000 - February 2001, corresponding to the sampling sequence and characterized by highest nematodes and gastrotrichs densities in August 1999 (**CHAPTER II**).

In **CHAPTER III**, the meiofauna on a cross-shore gradient (comparison of a high and low water station) at the San Pedro de Manglaralto beach (classified as an intermediate-reflective beach), with a median grain size ranging between 215 and 290 µm at the high tide level (upper station) and 191-301 µm (corresponding to fine-medium sand) at the low tide level (lower station) were fortnightly studied between June 200 and July 2001. The average meiofauna densities decreased slightly from high water level (963±167 ind./10 cm^{2}) to low water level (890±69 ind./10 cm^{2}). Ordination showed clear cross-shore differences caused by highest densities of copepods at the upper station (275±86 ind./10 cm^{2}) and highest densities of nematodes at the lower station (738±64 ind./10 cm^{2}). The environmental factors were characterized by a Sea Surface Temperature between 21.4 and 27.5 °C; pluviosity was mainly restricted between January 2001 (151 mm) and March 2001 (114 mm) and a salinity ranging between 32 and 34 PSU. No correlation between meiofauna densities and the above mentioned environmental factors was found at the upper station, while at the lower station the total meiofauna and nematode densities showed a significant correlation with the pluviosity; the densities decreased towards the subtidal level.

Community structure, diversity and temporal distribution of free-living marine nematodes from the low water level at San Pedro de Manglaralto beach (exposed, intermediate-reflective beach) were described in **Chapter IV**. A total of 37 nematode species belonging to 30 genera and 17 families were recorded. Xyalidae was the most dominant family (43%), it was comparable with the dominance of Xyalidae (21%) in the Australian beaches (Nicholas and Hodda, 1999) and Gheskiere *et al.* (2004) (30%) in the Belgian beaches. The total nematode densities ranged from 359±11 ind./10 cm^{2} (April 2001) to 1170±119 ind./10 cm^{2} (June 2000). The non-selective deposit feeders were the most abundant feeding group at the nematode community (43%), although with fluctuating dominance (4-90%). Based on species composition analysis, nematode sample groups were detected reflecting the following temporal pattern: (I) June-December, (II) January and (III) February-May. Dissimilarities (71%) were found between the species of the group II and III, explained principally by highest densities of *Daptonema* sp. 1 (490±197 ind./10 cm^{2}) and *Rhynchonema* cf. *hirsutum* (163±18 ind./10 cm^{2}) at the group II; *Ceramonema* sp. 1 (208±50 ind./10 cm^{2}) and *Ceramonema* sp. 2 (75±15 ind./10 cm^{2}) at group III. The *k*-dominance curves indicated lowest diversity and highest dominance in January 2001 versus lowest dominance and highest diversity between June-December 2000. The evenness and dominance (Simpson index) diversity revealed significant differences between seasons, with lowest values in January 2001 (0.63 and 0.70 respectively). *Daptonema* sp. 1 a dominant nematode species showed density fluctuations related with the pluviosity.

The study described in **CHAPTER V** showed the importance of predators in the interstitial food web of the high water level along an Ecuadorian beach. This study mainly aimed to investigate the biodiversity of the free-living marine nematodes (at species level), their densities, assemblages, age and trophic structure at the high tide level in San Pedro de Manglaralto beach. Also a comparison in diversity and taxonomic distinctness between the nematode species from high water level and lower water level (studied in CHAPTER IV) was established to detect a zonation pattern across the Ecuadorian beach. In total 40 nematode species belonging 30 genera and 15 families were found at the high water level. Thoracostomopsidae and Desmodoridae families represented 34% of the total nematode species composition. Total nematode densities ranged from 183±28 ind./10 cm^2 (December 2000) to 1488±100 ind./10 cm^2 (June 2000), no significant differences between dry (April-December) and rainy season (January-March) were detected. The proportion of the four feeding types, varied in a large range along the sampling year: from 0% to 18% for selective deposit feeders, 12-56% for non-selective deposit feeders, 2-53% for epistrate feeders and 20-80% for predators/omnivores. The juveniles were present throughout the sampling period, and the highest densities (654±156 ind./ 10 cm^2) were coupled with peak densities of the nematode populations (1488±100 ind./10 cm^2) in June 2000. 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 cm^2 and 1-302 ind./10 cm^2 respectively), but with the highest densities in June 2000 and July 2001 respectively. Two temporal nematode species associations were observed: May-September and October-April; the separation is explained for the highest abundances of *Axonolaimus* sp. (223±74 ind./10 cm^2) *Bathylaimus* sp. 1 (137±66 ind./10 cm^2), *Metachromadora* sp. 1 (155±6 ind./10 cm^2), *Rhynchonema* cf. *hirsutum* (213±14 ind./10 cm^2) and *Viscosia* sp. 2 (380±132 ind./10 cm^2) found between June and September, followed by a subsequently density decline. 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 nematode species richness was more or less similar at the upper an at the lower station on the beach, and varying between 12 to 21 species per month at the upper station and between 15 and 21 species per month at the lower station. The average taxonomic distinctness showed that the species were taxonomically closely related to each other (except those species from June 2000, November 2000 and May 2001 at 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 high water level, and the highest abundances of *Ceramonema* sp. 1 and *Ceramonema* sp. 2 at the low water level.

During the ecological surveys, many nematode species could not be named and will be probably new to science. We have described 3 new species in the **CHAPTER VI** from San Pedro de Manglaralto, collected at low water level.

Ceramonema adrianae sp. n. (named *Ceramonema* sp. 1 in the former chapters) is characterized by the following sexual dimorphism: amphid in the males is longer than the females (10 µm vs. 7 µm) and dorsally wound in the males; the presence of one pair of terminal setae on the distal cone of the mail tail and the position of the outer labial setae (situated at a 'posterior' circle) very close (1-2 µm) to the cephalic setae. The new species is closely related to *Ceramonema algoensis* Furstenberg & Vincx, 1993 because of the absence of a subcuticular vacuolization and no elongated annule in the cloacal region. It differs from *C. algoensis* in having a lower number of annules (153-209 vs. 300-315), no elevated lip region and shorter spicules length (21-27 µm vs. 28-32 µm). A dichotomic identificacion key for the sixteen species of *Ceramonema* is provided.

Rhynchonema ronaldi sp. n. is closely related to *Rhynchonema hirsutum* Hopper, 1961; because both species have symmetrical spicules which are curved and with the distal end pointed, the gubernaculum is a plate-like structure with a dorsal apophysis, amphids at the level of the base of the stoma but differs from *R. hirsutum* by the absence of supplementary copulatory organs (this new species has been named *Rhynchonema* cf. *hirsutum* in the ecological chapters).

Gonionchus ecuadoriensis sp. n. is characterized by the longitudinal ornamentations starting at the cervical region and continuing throughout the body to the tip tail, an unarmed buccal cavity, equal spicules and the gubernaculum with a small dorsal apophysis. *Gonionchus ecuadoriensis* sp. n. closely resembles *Gonionchus longicaudatus* (Ward, 1972). *Gonionchus ecuadoriensis* sp. n.; however has a smaller amphid diameter (2-3 vs. 9 µm) in the males and in the females (3-4 vs. 7 µm); a shorter tail length (77-104 µm) in the males compared to *G. longicaudatus* (179 µm). A dichotomic identification key of the genus *Gonionchus* is provided to

separate the thirteen species into two groups, principally on the presence or absence of longitudinal ornamentations.

The ecological survey of the meiofauna of Ecuadorian sandy beaches, with emphasis on the species distribution of free-living marine nematodes, revealed the fact that the Ecuadorian beaches are not extremely rich in density nor in diversity of meiofauna. Interesting correlations are detected between rainfall and nematode species composition, in such a way that *Daptonema* sp.1 can be considered as a bio-indicator for excess in rainfall (although not very much reflected in a decrease of salinity of the overlying sea water). The nematode species community along the Ecuadorian beach resembles more an 'estuarine' community (with dominance of *Daptonema* and *Metachromadora*) than a real marine community. More detailed investigations on the chemistry of the interstitial environment could possibly help in understanding better the dynamics in the sandy beaches in Ecuador. The obtained results within this doctorate study form an important baseline study for future meiofauna investigations (focusing on the monitoring aspects as well as on new experimental approaches regarding environmental preferences).

Resumen

La fauna intersticial marina se ha estudiado en las diversas latitudes y lugares (e.g. HEIP *et al.*, 1985 overview; COULL, 1988) pero pocos estudios sobre zonación y variabilidad temporal en áreas tropicales (GOURBAULT *et al.*, 1998). De la región Sureste del Pacífico no existen datos sobre meiofauna intersticial disponibles para las playas arenosas. Aunque los nemátodos están entre los metazoarios más abundantes de sedimentos marinos, sólo pocas publicaciones, excepto aquellas taxonómicas, han descrito la composición de las especies de nemátodos de vida libre en la zona intermareal de las playas arenosas (GOURBAULT *et al.*, 1995; GHESKIERE *et al.*, 2002; 2004, 2005 and URBAN-MALINGA *et al.*, 2004) y su variabilidad estacional (SHARMA AND WEBSTER, 1983; GOURBAULT, 1998; NICHOLAS AND HODDA, 1999; and NICHOLAS, 2001). Esto es probablemente debido al consumo de tiempo en el proceso de identificación de las especies y a las altas diversidades totales de las especies de las comunidades de nemátodos.

Los nemátodos marinos de vida libre tienen varias características favorables para usarlas como bio-indicadores de condiciones ambientales (BONGERS AND FERRIS, 1999; and SCHRATZBERGER AND WARWICK, 1999) y también es conocido a través de experimentos que los nemátodos son ecológicamente muy heterogéneos y ocupan diversas posiciones en las cadenas alimenticias bénticas (AARNIO, 2001). Geográficamente localizado en la región tropical ecuatorial, el clima de la costa de Ecuador es influenciado fuertemente por los fenómenos de anomalía climática 'El Niño' y la 'Niña' que ocurren cada 2-8 años (SANTOS, 2006). Esto causa que las condiciones climáticas tengan grandes fluctuaciones, que pueden tener un efecto sobre la fauna marina.

En playas arenosas de la costa ecuatoriana, dos playas arenosas situadas en la provincia de Guayas fueron investigadas: una playa protegida 'Salinas' con tamaño medio de arena de medianos a finos y 'San Pedro de Manglaralto' una playa expuesta con el tamaño medio de arena gruesa. El clima de la costa ecuatoriana is caracterizado por tener dos estaciones: una estación seca (May-December) y una estación lluviosa (January-April) (CORNEJO, 1999). Sin embargo, los períodos de estación seca y lluviosa mencionados en este estudio correponden a los datos ambientales de las campañas de muestreo. Las campañas del muestreo fueron conducidas dentro del programa VILR-ESPOL, proyecto 4 "Sistema de Manejo Ambiental en Agricultura y Acuacultura" en el marco de Modelaje y Dinámica

Poblacional de Bio-indicadores de la zona costera de Ecuador con énfasis sobre la investigación de la componente béntica. Las campañas de muestreo incluyeron un período corto (quincenalmente) desde Junio 2000 hasta Julio 2001 y un período largo (trimestralmente) desde Agosto 1999 hasta Febrero 2001, durante una fuerte fase de La Niña ocurrida después de El Niño 1997-1998 (McPHADEN, 1999).

El presente estudio es la primera contribución científica al estudio de la estructura de las comunidades de la meiofauna, especialmente en el taxón dominante Nematoda (a nivel de especies), su distribución en la zona intermareal (desde la pleamar hasta la bajamar) en las playas arenosas ecuatorianas y su relación con los factores ambientales (pluviosidad, Temperatura Superficial del Mar, salinidad, clorofila *a,* materia orgánica y tamaño mediano de grano de arena).

Se compararon playas turísticas y no turísticas ('pristinas") situadas en un sitio protegido al oleaje y otro expuesto respectivamente. Los patrones temporales y espaciales de la meiofauna (especialmente nemátodos) de estos dos sitios demostraron que las densidades varían entre 461±101.5 ind./10 cm^2 y 1848±7 ind./10 cm^2 en la playa protegida y entre 376±21.5 ind./10 cm^2 y 2388±161.5 ind./10 cm^2 en la playa expuesta. El phylum Nematoda representó entre 21-81% de la meiofauna total en la playa protegida y 76-95% en la playa expuesta, seguido por los turbelarios y los gastrotrichos. Un total de 40 géneros que pertenecen a 19 familias fueron identificados. *Neochromadora*, *Daptonema*, *Metadesmolaimus* y *Omicronema* fueron los géneros dominantes en la playa protegida, mientras que *Metachromadora*, *Rhynchonema*, *Paracyatholaimus*, *Ceramonema* y *Gonionchus* fueron dominantes en la playa expuesta. En ambas playas la diversidad más baja ocurrió en Agosto 1999 (influenciado por el fenómeno de la Niña) y la diversidad más alta fue detectada en la estación de lluvia (Enero-Marzo). Los nemátodos alimentadores de depósitos no selectivos fueron dominantes (42%) seguidos por predadores/omnivoros (26%) y los alimentadores de epiestratos (24%). Grupos estacionales fueron detectados en base a la composición de meiofauna: tres grupos en la playa expuesta: Agosto 1999; Mayo 2000, Febrero 2001 (mes altamente turístico) caracterizado por la densidad más alta de turbelarios y los períodos Noviembre 1999-Febrero 2000 y Agosto-Noviembre 2000. En San Pedro (playa expuesta) se detectaron dos grupos estacionales: Agosto 1999 - Febrero 2000; Mayo 2000-Febrero 2001, correspondiendo a la secuencia del muestreo y caracterizado por la densidad más alta de nemátodos y gastrotrichos en Agosto de 1999 (**CAPÍTULO II**).

En el **CAPÍTULO III**, la meiofauna sobre el gradiente de playa (zonación) en la playa de San Pedro de Manglaralto (clasificada como playa intermedia-reflexiva), con un tamaño medio de grano de arena entre 215 y 290 µm en pleamar y 191-301 µm en bajamar (que corresponde a la arena fina-mediana) fue estudiada quincenalmente desde Juneio 2000 hasta Julio 2001. Las densidades de la meiofauna decrecieron desde la pleamar (963±167 ind./10 cm^2) hasta la bajamar (890±69 ind./10 cm^2). Mediante el análisis multivariado de ordenación se demostró claramente un patrón de zonación entre pleamar y bajamar, las diferencias de meiofauna fueron causadas por las densidades más altas de copépodos harpacticoideos en pleamar (275±86 ind./10 cm^2) y por las densidades más altas de nemátodos en bajamar (738±64 ind./10 cm^2). Los factores ambientales fueron caracterizados por una Temperatura Superficial del Mar entre 21.4 y el 27.5 °C, una alta pluviosidad registrada entre Enero de 2001 (151 mm) y Marzo de 2001 (114 mm) y una salinidad entre 32 y 34 PSU. No se encontró ninguna correlación entre las densidades de la meiofauna y los factores ambientales (mencionados antes) en pleamar; mientras que en bajamar las densidades totales de la meiofauna y de nemátodos demostraron que existe una correlación significativa con la pluviosidad; las densidades disminuyeron hacia el nivel submareal.

La estructura de la comunidad, la diversidad y la distribución temporal de los nemátodos marinos de vida libre en bajamar en la playa de San Pedro de Manglaralto (playa expuesta, intermedia-reflectiva) fueron descritas en el **CAPÍTULO IV**. Se registraron un total de 37 especies de nemátodos que pertenecen a 30 géneros y a 17 familias. Xyalidae fue la familia más dominante (43%), esta dominancia de Xyalidae es comparable con las playas australianas (NICHOLAS Y HODDA, 1999) (21%) y GHESKIERE *et al.* (2004) (el 30%) en Bélgica. Las densidades totales de los nemátodos fueron entre 359±11 ind./10 cm^2 (Abril 2001) y 1170±119 ind./10 cm^2 (Junio 2000). Los nemátodos alimentadores de depósitos no selectivos fueron el grupo de alimentación más abundante en la comunidad (43%), aunque con fluctuaciones en la dominancia (4-90%). De acuerdo con análisis de la composición de la especie, se detectaron grupos de muestras que reflejaron el siguiente patrón temporal: (I) Junio-Diciembre, (II) Enero y (III) Febrero-Mayo. Las diferencias (71%) fueron encontradas entre las especies del grupo II y III, explicada principalmente por las densidades más altas de la especie *Daptonema.* sp. 1 (490±197 ind./10 cm^2) y *Rhynchonema* cf. *hirsutum* (163±18 ind./10 cm^2) en el grupo II; *Ceramonema* sp. 1 (208±50 ind./10 cm^2) y *Ceramonema* sp. 2 (75±15 ind./10 cm^2) en el grupo III. La curva de dominancia (*k*-

dominancia curva) mostró baja diversidad y alta dominancia en Enero 2001, mientras que entre Junio-Deciembre 2000 se encontró la dominancia más baja y la diversidad más alta. Los índices de diversidad de uniformidad y de dominancia de especies revelaron diferencias significativas entre las estaciones, con los valores más bajos en Enero 2001 (0.63 y 0.70 respectivamente). *Daptonema* sp. 1 una especie dominante de nemátodo demostró las fluctuaciones de la densidad relacionadas con la pluviosidad.

El estudio descrito en el **CAPÍTULO V** demostró la importancia de depredadores en la cadena alimenticia intersticial durante pleamar en una playa ecuatoriana. Este estudio tuvo como objetivo principal investigar la biodiversidad de los nemátodos marinos de vida libre (a nivel de especies), densidades, composición, edad y estructura trófica durante pleamar en la playa de San Pedro de Manglaralto. También una comparación en diversidad y distinción taxonómica entre las especies de nemátodos de pleamar y bajamar (estudiadas en el CAPÍTULO IV) fue establecida para detectar un patrón de zonación a través de la playa de Ecuador. Un total de 40 especies de nemátodos que pertenecen a 30 géneros y 15 familias fueron encontrados en pleamar. Las familias de Thoracostomopsidae y de Desmodoridae representaron el 34% de la composición total de las especies de nemátodos. Las densidades totales de nemátodos varían entre 183±28 ind./10 cm^2 (Diciembre 2000) y 1488±100 ind./10 cm^2 (Junio 2000), no diferencias entre la estación seca (Abril-Diciembre) y la estación de lluvia (Enero-Marzo) fueron detectadas. La proporción de los cuatro tipos de alimentación de nemátodos, varía a lo largo del año de muestreo: 0-18% para los alimentadores de depósito selectivo, 12-56% para los alimentadores de depósito no selectivo, 2-53% para los alimentadores del epistrato y 20-80% para predadores/omnívoros. Los juveniles fueron registrados a través de todo el período de muestreo, y las densidades más altas (654±156 ind./ 10 cm^2) fueron relacionadas con las densidades máximas de las poblaciones de nemátodos (1488±100 ind./10 cm^2) en Junio de 2000. Los nemátodos predadores *Enoplolaimus* sp. 1 (14%) y *Metachromadora* sp. 1 (13%) co-dominaron, demostrando fluctuaciones de densidad sobre el período de muestreo (8-311 ind./10 cm^2 y 1-302 ind./10 cm^2 respectivamente), pero con las densidades más altas en Junio 2000 y Julio 2001 respectivamente. Dos asociaciones temporales de la especie de nemátodos fueron observadas: Mayo-Septiembre y Octubre-Abril; la separación se explica por las abundancias más altas de *Axonolaimus* sp. 1 (223±74 ind./10 cm^2) *Bathylaimus* sp. 1 (137±66 ind./10 cm^2), *Metachromadora* sp. 1 (155±6 ind./10 cm^2), *Rhynchonema* cf. *hirsutum* (213±14 ind./10 cm^2) y *Viscosia* sp. 2 (380±132 ind./10 cm^2) encontradas entre Junio y Septiembre, seguidos por una declinación de la densidad. La curva de *k*-dominancia demostró que la diversidad más alta fue en Junio 2001 y la diversidad más baja en Diciembre 2000. La temperatura superficial del mar fue correlacionada positivamente, mientras que la salinidad fue correlacionada negativamente con las densidades totales de nemátodos.

La riqueza de las especies de nemátodos fue más o menos similar tanto en pleamar como bajamar, variando entre 12 a 21 especies por mes en pleamar y entre 15 a 21 especies por mes en bajamar. El promedio de distinción taxonómica demostró que las especies fueron relacionadas taxonómicamente (excepto las especies de Junio 2000, Noviembre 2000 y Mayo 2001 en bajamar). Sin embargo diferencias de zonación fueron detectadas, explicado por las abundancias más altas de *Enoplolaimus* sp. 1, *Viscosia* sp. 2 y *Metachromadora* sp. 1 en pleamar, y las abundancias más altas de *Ceramonema* sp. 1 y *Ceramonema* sp. 2 en bajamar.

Durante las investigaciones ecológicas, muchas especies de nemátodos no se podían nombrar y serán probablemente nuevas a la ciencia. Hemos descrito 3 nuevas especies de San Pedro de Manglaralto en el **CAPÍTULO VI**, colectados en bajamar.

La especie *Ceramonema adrianae* sp. n. (nombrada como *Ceramonema* sp. 1 en los capítulos anteriores) son caracterizados por el dimorfismo sexual siguiente: el anfid (estructura sensorial) en los machos es más largo que las hembras (10 vs. 7 µm) y dorsalmente dirigido en los machos; la presencia de un par de setas terminales en el cono distal de la cola y la posición de la seta labial externa (situados en un círculo 'posterior') muy cerca a las setas cefálicas (1-2 µm). La nueva especie se relaciona con *Ceramonema algoensis* FURSTENBERG Y VINCX, 1993 debido a la ausencia de vacuolización subcuticular y ausencia de un anulo alargado en la región cloacal. Se diferencia de *C. algoensis* en tener un menor número de piezas anulares (153-209 vs. 300-315), labios no elevados y una longitud más corta de las espículas (21-27 vs. 28-32 µm). Una clave dicotómica de identificación para las dieciseis especies de *Ceramonema* es proporcionada.

La especie *Rhynchonema ronaldi* sp. n. (esta nueva especie se ha nombrado como *Rhynchonema* cf. *hirsutum* en los capítulos ecológicos) se relaciona con *Rhynchonema hirsutum* Hopper, 1961; porque ambas especies tienen espículas simétricas, curvas y con el extremo distal punteagudo, el gubernaculum es en forma de una placa con un apofisis dorsal, el anfid al nivel de la base del estoma; pero se diferencia de *R. hirsutum* por la ausencia de órganos copulatorios suplementarios.

Las especies de *Gonionchus ecuadoriensis* sp. n. se caracterizan por los ornamentations longitudinales que comienzan en la región cervical y que continúan a través del cuerpo hasta la extremidad de la cola, cavidad bucal sin dientes, espículas iguales y el gubernaculum con un apofisis dorsal pequeño. *Gonionchus ecuadoriensis* sp. n. se asemeja a *Gonionchus longicaudatus* (Ward, 1972). Las especies de *Gonionchus ecuadoriensis* sp. n. , tienen el diámetro del anfid más pequeño, en los machos 2-3 vs. 9 µm y en las hembras 3-4 vs. 7 µm; la longitud de la cola más corta en los machos (77-104 µm) comparada con *G. longicaudatus* (179 µm). Una clave de identificación dicotómica del género *Gonionchus* se proporciona para separar las trece especies en dos grupos, principalmente en la presencia o la ausencia de ornamentaciones longitudinales.

El estudio ecológico de la meiofauna de las playas arenosas de Ecuador, con énfasis sobre la distribución de la especie de nemátodos marinos de vida libre, reveló el hecho de que las playas de Ecuador no son extremadamente ricas en densidad ni en la diversidad de la meiofauna. Las correlaciones interesantes se detectan entre la precipitación y la composición de las especies del nemátodo *Daptonema* sp. 1, de una manera tal que se puede considerar a esta especie como bio-indicadora para el exceso en la precipitación (aunque no mucho está reflejado en una disminución de la salinidad de la agua de mar). La comunidad de las especie de nemátodos a lo largo de la playa de Ecuador es parecida más una comunidad 'estuarina' (con dominancia de *Daptonema* y *Metachromadora*) que una comunidad verdaderamente marina. Investigaciones más detalladas en la química del ambiente intersticial podrían ayudar posiblemente a entender mejor la dinámica en las playas arenosas en Ecuador. Los resultados obtenidos dentro de este estudio doctoral forman un estudio importante de la línea de base para las investigaciones futuras de la meiofauna (que se centran en los aspectos de monitoreo así como también en nuevos acercamientos experimentales con respecto a preferencias ambientales).

CHAPTER I

General Introduction, Aims and Thesis Outline

INTRODUCTION

Beach characteristics and their classification

Beaches are dynamic sedimentary systems which require a number of boundary conditions and external inputs. While waves and sediment are essential for beach formation, a sub-surface boundary or base is required for the beach to rest on. The three-dimensional morphology (cross and long shore character of the beach) of this surface is critical to the formation and maintenance of the beach. During and subsequent to its formation, beaches also depend on the sediment budget, wave climate and tidal regime, together with other factors including wind regime, regional biota, water chemistry and temperature. Beaches are commonly composed of fine to medium sand at the low to mid-latitudes; they are more commonly composed of gravel at higher latitudes. Sediment size is the major contributor to beach slope, morphology and beach type. Tides contribute energy through tidal currents, which regionally and locally can transport sediment and influence beach and barrier morphology (SHORT, 1999).

Beaches are a product of waves and sediment, and are influenced by a range of additional parameters, some of which have been used to classify beach systems. Traditionally beaches have been classified by the major resources of energy, namely wave height, wave energy or the wave climate, the tidal range, the sediment size, and impacts due to the atmospheric climate. The major qualitative beach classification systems are listed in Table 1.1. Tides are a non-essential beach component (DAVIES, 1964). The contribution can range from none in tide-less seas and lakes to a dominating factor in macrotidal environments. This observation has resulted in a geographical classification of coastal environments based on the absolute tidal range. It is common to divide sandy beaches into three categories: microtidal ranges of less than 2 m, mesotidal ranges between 2 and 4 m and macrotidal ranges in excess of 4 m (DAVIES, 1964). Distinct coastal morpho-types that are characteristic for each of these tide range classes may be identified.

By definition non-tidal coasts are structured only by waves, in contrast to tidal coasts which are structured by waves as well by tides. However, while tidal range will always play a secondary role to waves in beach morphodynamics (the mutual interactions of waves with the beach topography), increasing tide range will, in combination with wave conditions, contribute substantially to beach morphology and will increasingly spread the impact of shoaling, breaking and swash wave activity.

Masselink (1993) developed an empirical model to simulate the tide-induced migration of hydrodynamic processes across beaches and found that a useful parameter to quantify tidal effects was the Relative Tide Range (RTR=MSR/Hb, where Hb is the wave height and MSR is the mean spring tide range).

Wave-dominated beaches were classified using three parameters: modal breaker height (H_b), wave period (T) and grain size (as defined by sediment fall velocity, W_s). Gourlay (1968) combined these parameters into the dimensionless fall velocity or Dean' parameter ($\Omega = H_b / W_s T$) (Short, 1999). When $\Omega < 1$ beaches tend to be reflective, when $\Omega > 6$ they tend to be dissipative and in between ($1 < \Omega < 6$) are the so-called intermediate beaches (Masselink and Short 1993).

Figure 1.1 shows the beach types. *Dissipative* beaches represent the high-energy end of the beach spectrum, are characterized by a wide, low gradient surf zones (usually flat) that extends from the foot of the dune to the low tide zone across where spilling breakers dissipate their energy, hence the name dissipative. They require fine sand (<0.2 mm), relative high waves (>2.5 m), and preferably short wave periods. For this reason they are only found on open swell coasts (T> 10s) in areas of fine to very fine sand with persistent high swell (> 2m), as in storm wave and high energy west coast swell environments. They have been reported on the coasts of southern Australia, South Africa, west coasts of Oregon, Brazil and Chile. They are however more common in storm-dominated seas and larger lakes and bays, where high, but short period (T= 2-5 s) storm

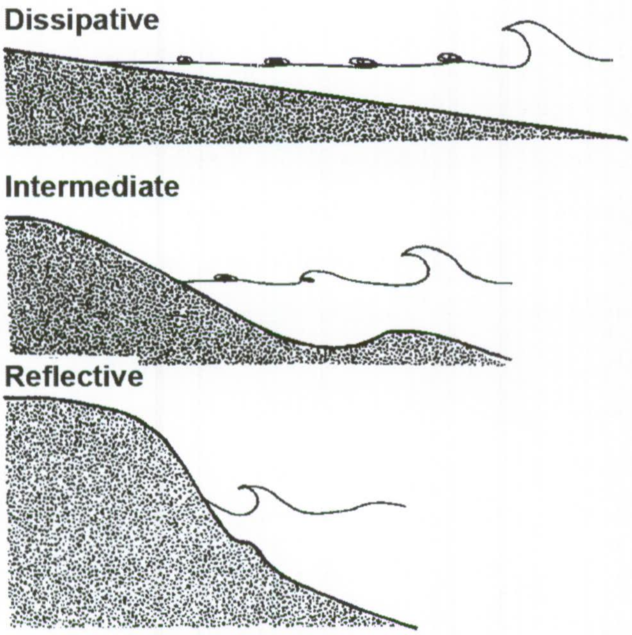


Figure 1.1 Beach types (*source:* Short and Writer, 1983).

waves act on fine sand beaches, such as part of the Artic Ocean, eastern Nicaragua, Great Lakes, Baltic, Mediterranean and North Sea. *Intermediate* beaches refer to beaches that are intermediate between the high energy dissipative and the lower energy reflective beaches. The most obvious characteristic is the presence of a horizontally segregated surf zone with bars and rips, moderate to high waves (0.5 to 2.5 m), fine to medium sand, and longer wave periods. *Reflective* sandy beaches (coarse sand, low waves, and/or long periods) lie at the lower energy end of the beach spectrum, though not necessarily in areas of low waves, always have a relatively narrow beach and swash zone, with beach cusps commonly present. The swash zone is relatively steep, with actual gradient depending on grain size. They have no surf zone and waves move unbroken to the shore where they collapse or surge up the beachface.

Parameter	Beach type	References
Waves height/energy	High energy	DAVIES AND HAYES (1984)
	Low energy	OTVOS (1982a,b)
Wave type	Ocean/swell	DAVIES (1964)
	Sea	NORDSTROM (1992)
	Estuarine	
Tide	Macro (> 4 m)	DAVIES (1964)
	Meso (2-4 m)	HAYES (1979)
	Micro (0-2 m)	DAVIES AND HAYES (1984)
Sediment size	Boulder	DAVIES (1980)
	Cobble/shingle	NORDSTROM (1992)
	Sand	
Climate/latitude	Polar/high	DAVIES (1982a,b,c)
	Temperate/mid	
	Tropical/low	

Table 1.1 Qualitative beach classifications.

The Ecuadorian coast

Ecuador has different ecosystems in its coastal and marine areas with beaches, bays, estuaries, cliffs, coastal lagoons and rocky coasts. AYÓN (1987) described the Coastal region of Ecuador as an area of 530 Km of longitude, situated at the western of the Andes and at the east of the Pacific Ocean and three coastal zones were classified; from north to south: A) Río Mataje-Pedernales, B) Pedernales-Guayaquil and C) Guayaquil-Boca de Capones (Figure 1.2). In the zones A and C the estuarine processes are permanent. The littoral formations in the Ecuadorian coastal zones correspond to:

Littoral drifts: Shoals formed by marine sandy deposits with shell remains. Sometimes the littoral drifts are plugging the mouth of alluvial valleys and so are forming emerged beaches enclosing hypersaline lagoons (Palmar-Ballenita and Santa Elena-Anconcito).
Low cliffs: The rocky projections are forming enclosed beaches protected by low cliffs. Most of the beaches are situated in a deep cove.
High cliffs: Littoral formation on rocks of different lithological composition, including basalts. The beaches are narrow with coarse sands. The erosion produced in the cliffs is due to the stratification by high disintegration of most of the layers and meteorization of the rocks. The weakest layers easy are undermined by the waves and many caves are observed.
Unstable high cliffs: Cliffs formed of soft rocks, which are degraded in blocks. They are unstable sediments, continuously undermined by the surge, producing a diminution of the coastal strip.
Mangroves: Delta zones formed in the mouth of the estuaries.

Studies carried out along the Ecuadorian coast, focus principally on the marine (CORNEJO, 1976; MASSAY, 1983; MORA, 1990; CRUZ *et al.*, 2003; DOMÍNGUEZ *et al.*, 2004; AERTS *et al.*, 2004; and CALLES *et al.*, 2005) and estuarine biota (CRUZ, 1983a; GUALANCAÑAY, 1983; JIMÉNEZ, 1983; VILLAMAR, 1989; and CRUZ, 1998).

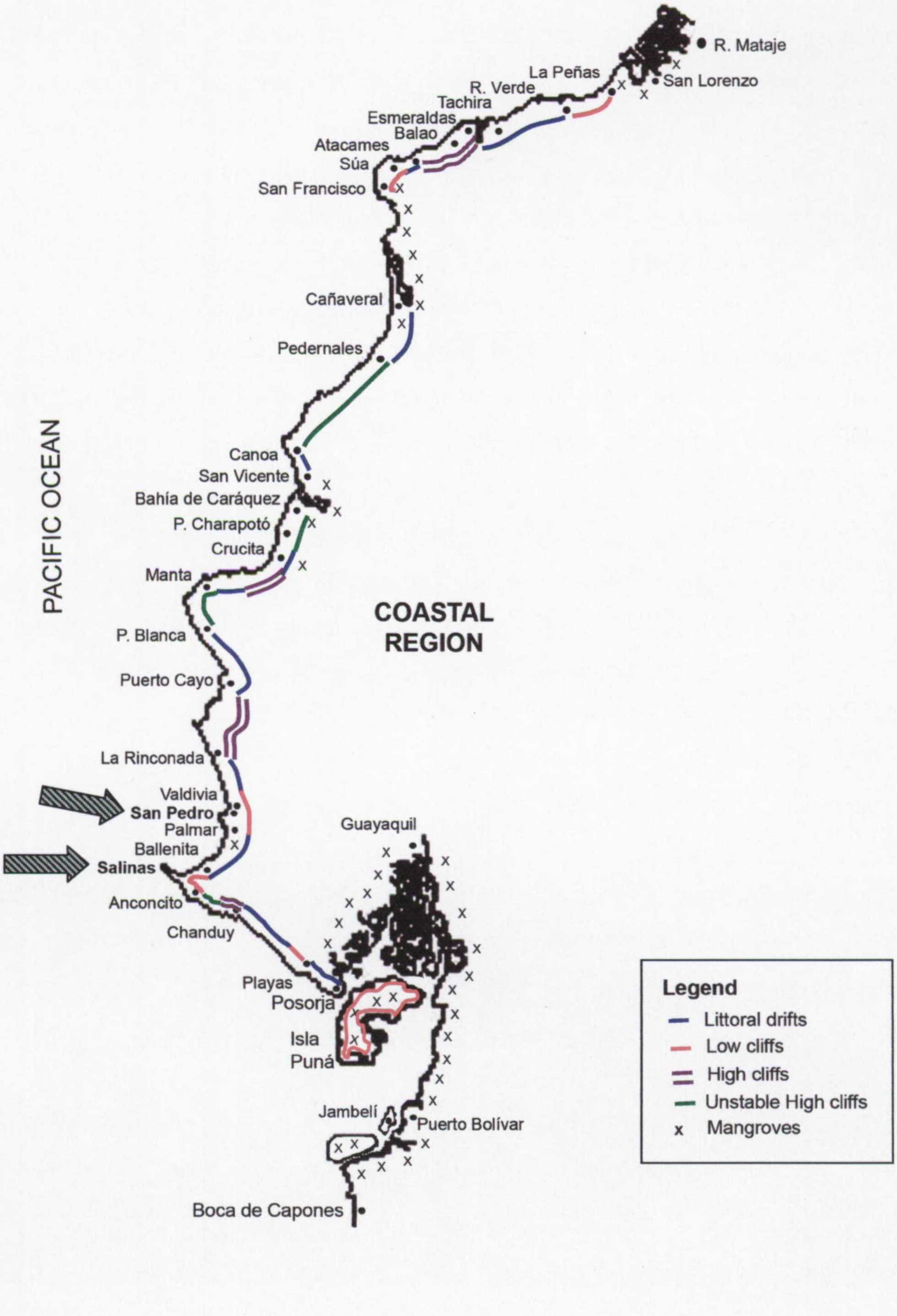


Figure 1.2 Ecuadorian Coastal Classification (AYÓN, 1987).

The benefit of the beach for the local population

The coastal region is of a substantial ecological and economic importance ("values" mainly as input for fisheries). From 1970 onwards the coastal zone was used commonly for the artisanal fishing of shrimp post-larvae, which had a large socio-economic impact on the coastal area and the country in general. From September 2002 onwards this activity was forbidden by the authorities under the law of Fishing and Fishing Development as it was considered as unselective capture and consequently affecting the Ecuadorian marine ecosystem (Acuerdo Ministerial No. 106). The populations of Valdivia and San Pedro de Manglaralto developed these traditional activities, which were important for their income (See Table 1.2) and have maintained their condition of communal centres of artisan, commercial and fishing productions (PMRC, 1993).

For the present meiofauna study, two beaches were chosen base on their differences of beach type and main activities: 'Salinas' situated on a sheltered beach, is a popular destination with high recreational use over the year, while 'San Pedro de Manglaralto', is an exposed beach with fishing activities and supplies products from the sea to the villages around (Figure 1.3).

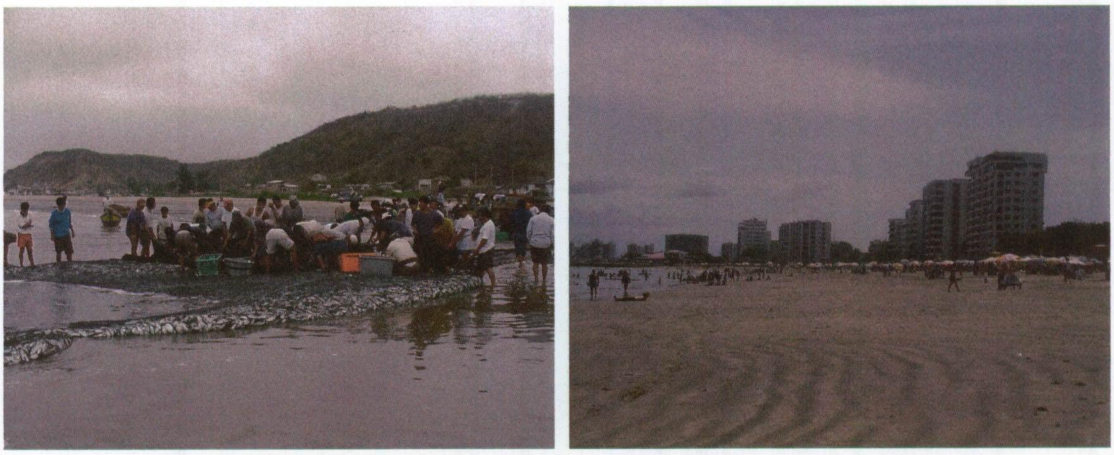


Figure 1.3 ***Left*: Fishermen collecting the capture with a seine net, at San Pedro de Manglaralto. *Right*: tourists at Salinas beach.**

6000 b.C	Horticulture and navigation in canoes.
3000 b.C	Generalized incipient agriculture in the Santa Elena Peninsula.
2000 b.C	Navigation in the open sea with canoes in the Santa Elena Peninsula.
1000 b.C	Intensive agriculture in coastal valleys and Chongón-Colonche Mountain range.
1300	Small fleet of rafts for navigation of long distance. Terraces of culture in coastal valleys and Chongón-Colonche Mountain range.
1850	The straw culture and sale of 'toquilla' (straw) is the main activity. Toquilla is tiled straw to elaborate hats. Salt extraction. The bitumen of the mines of Copey is used on vessels.
1900	Manglaralto is the most important village of Santa Elena in the production and commerce.
1910-1944	Through Manglaralto, 'tagua' (vegetable), straw toquilla, hats and coffee were exported. Sugar plantations, palms, honey and alcohol were produced. Development of livestock between the villages. Manglaralto was port and customs district. The fishing was a secondary activity for personal consumption and for the local market.
1937	The organization law is sent and a regime of communes from 6 of August of 1937 exists. 11 communes were organized along the coast of San Pedro de Manglaralto.
1945-1969	Drought. Crisis of the farming production. Hard pressure on the forest. Manglaralto lost the condition of customs district. Higher migration. The fishing and the commerce are the main activities of San Pedro de Manglaralto. The production was used for the peninsular consumption.
1970-1992 	Most of the artisan fishermen begin to use the catching net, incorporate the motor outside, 'pangas' (boat make with fibre-glass) replace the canoes. Construction of ponds for the shrimp culture and laboratories for shrimp-larvae production (*Litopenaeus vannamei* principally). The harvesting of larvae (1984-92) is the activity that concentrates the greater manual labour (75000 persons). The horticulture and floriculture in charge of farming industrialists are developed basically in Manglaralto and Valdivia.
2000-Actual	Fishing and tourism.

Table 1.2 Chronology of the relation of old and modern societies with the natural resources of San Pedro de Manglaralto and surroundings (PMRC, 1993).

Major impacts on Ecuadorian beaches

The Coastal Ecuadorian population is growing under deteriorated surroundings. This situation is getting worse with the implantation of processors of fish, industrial factories, salt extraction and shrimp operation fisheries without compliance with control regulations. Impacts can be grouped into five main categories (CRUZ *et al.*, 2003):

- Global climate change
- Fisheries operations
- Pollution from the industries
- Alterations of physical habitat
- Tourism

The oceanographic and atmospheric conditions of the region are influenced by the seasonal contribution of water masses with defined characteristics:

The **El Niño Current** is an annual flow of warm tropical surface waters (25-27 °C) with low salinity (<34 UPS), going from North to South, from the Panamá bay to the coasts of Ecuador until the north of Perú, approximately from December to April; also the current is characterized by low nutrient concentrations (Figure 1.4). Historically, the name of this current was given by the fishermen of the south of Ecuador and north of Perú, its origin must to that these warm waters appear every year near of Christmas time (El Niño is Spanish for the Christ Child). The flow of this current gives beginning of the warm and humid climate in the coastal region of Ecuador denominated 'the rainy season' (Cucalón, 1989).

The **Humboldt Current** is an annual flow of cold subtropical surface waters (18-19 °C) with salinity around 35 UPS. This current flows towards the north throughout the coast of Perú; it is characterized to have high nutrient concentrations (due to the upwelling at the Peruvian coast) (Figure 1.4). During the 'dry season' of Ecuador (May-November), the Humboldt Current is more intense and flows towards the north until approximately 5°S and from there it is turned towards the west, to be jointed with the **Equatorial Subcurrent** (or Cromwell Current) in the Galápagos Islands. In the transition between the flow towards the north and the west, a part of the water flows towards the north pressed by the winds of the south that blow parallel to the coast and converges near the equatorial line with the warm tropical water of the north, forming the denominated **Frente Ecuatorial** (Enfield, 1976).

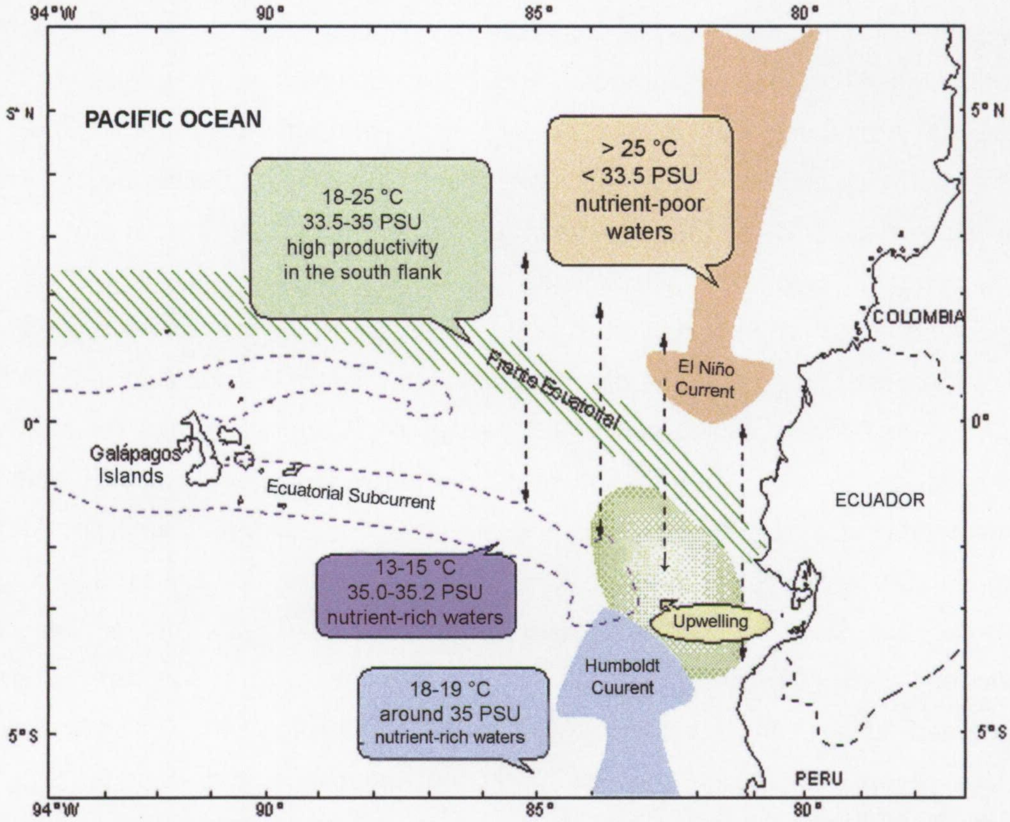


Figure 1.4 **Eastern Pacific area showing the interactions between the currents and masses of surface waters which influence the climatology of Ecuador (*source*: www.cenaim.espol.edu.ec, elaborated by Johnny Chavarría).**

An important long-term meteorological influence on the region is the **El Niño Southern Oscillation (ENSO)**. In the western Pacific, the marine currents and their heat content undergo marked seasonal and interannual variations. The ocean circulation can reverse itself in the equatorial zone for periods that can exceed one year. ENSO events are occurring by the interaction between the ocean and the atmosphere in the region of the tropical Pacific Ocean, with a recurrence period around 2-8 years (Santos, 1999). ENSO events display two components: El Niño and the Oscillation of the South. The first refers to the changes in the temperatures of the sea and the atmosphere, whereas the Oscillation of the South refers to an oscillation in the surface pressure (air masses) between the south-eastern tropical Pacific and the Australian-Indonesian regions. In addition to the mentioned components, ENSO events have two phases: a warm one that denominates *El Niño*, and a cold phase named *La Niña*. In normal conditions, the pressure differential between the centre of high pressure of the south-eastern tropical Pacific and the centre of low pressure of Indonesia and north of Australia govern the equatorial trade winds that blow towards the west, being these more forts when greater is the pressure differential between both centres. During ENSO events the pressure differential between these two centres is reduced to a minimum (the causes for these fluctuations totally are not known); consequently, the equatorial trade winds are debilitated. The collapse of these winds generates in the western Pacific internal waves Kelvin (subsurface waves) who travel towards the east throughout the equator (parallel 0°), reaching the South American coast in 2 to 3 months (particularly in front of Ecuador and Perú). The waves Kelvin have two effects: they intensify the circulation towards the east and deepen the thermocline in the eastern Pacific. Both effects tend to warm up the surface of the sea: the first, transporting warm water from the west; and the second, not to allow the transport of deeper water (colder nutrient-rich water) to shallow levels (upwelling process) (Espinoza, 1996; Patra, 1996, Zambrano, 1996). During ENSO events, the warm water accumulation throughout the Ecuadorian coast is excessive; the stock of pelagic fishes practically disappears. In addition, the Ecuadorian coast mainly undergoes forts precipitations due to an abnormal displacement towards the south of the Convergence Inter-tropical Zone of winds; this produces severe damages to the cultures of the region due to the floods (Cucalón, 1986b). In contrast La Niña impacts are positive in the fisheries based on small pelagic fish such as sardines, while there are negative impacts on shrimp exports. In shrimp aquaculture the impact is negative, because during cold events wild shrimp larvae availability decreases (Cornejo, 1998). According to Santos (2006) the presence of ENSO events in South America is felt in two ways: a) trough its effects on the atmosphere and ocean systems, and b) trough its impact on natural ecosystems (both marine and terrestrial) and on socio-economic sectors (like fisheries, health and agriculture). The main effects of El Niño/La Niña are:

- Increase/decrease of the sea surface temperature and salinity.
- Increase/decrease of sea level and wave activity
- Increase/decrease of air temperature and amount of ultra violet radiation reaching the surface of the earth
- Changes in the rainfall and evaporation patterns.

Use of meiofauna in ecological studies

The 'meiofauna' is defined on a methodological basis as all metazoa retained on a sieve of 42 µm (MARE, 1942). A total of 23 invertebrate phyla are represented, including species that remain throughout their life cycles, the 'permanent' meiofauna: such as Nematoda, Copepoda, Turbellaria, Gastrotricha and Tardigrada, and the species of some specialized or immature members of primarily larger phyla, the 'temporary' meiofauna: Gastropoda, Holothuroidea, Nemertina and Sipuncula (HIGGINS AND THIEL, 1988). Meiofauna is primarily detrital feeders or indiscriminate feeders on diatoms and bacteria (*i.e.* nematodes and copepods elaborate mucus to trap bacteria). However some meiofauna species are themselves predators on other infauna (WATZIN, 1983; AMBROSE, 1984; MARTENS AND SCHOCKAERT, 1986; and MENN AND ARMONIES, 1999). Predatory nematodes (*i.e. Enoploides longispiculosus*) may not only impact prey nematode communities (MOENS *et al.*, 1999; GALLUCCI *et al.*, 2005) but also other metazoan meiobenthos (MOENS AND VINCX, 1997) and perhaps macrobenthos through predation on settling larvae (WATZIN 1983). Meiofauna plays an important role in marine benthic communities, both directly, by processes such as bioturbation (organic decomposition, nutrient cycling, redistribution of organic material, oxygenation of the sediment) and the stimulation of bacterial metabolism, and also as the main food sources for the juvenile stages of many commercially important marine species at the higher trophic level including fish and crustaceans (WARWICK, 1987; COULL, 1988; GEE, 1989; VINCX, 1996; and MENN, 2002).

Most biological assessment of marine environmental health has traditionally included large visible organisms such as macrofauna that can readily be counted and identified. Microscopic components such as meiofauna have much less been included. This omission of a complete section of the biological spectrum is potentially counterproductive because much interaction between pollutants and the biosphere occurs at low levels of phylogenetic organization. Meiofauna is shown to have advantages that include their sessile habitat, high abundance, high species diversity, short generation time, direct benthic development and ubiquitous distribution of marine sediments (littoral, estuarine, coastal and oceanic) as well as in vegetated habitats such as sea grass beds. Disadvantages include their small size, high level of spatial and temporal variability, potential cost of samples processing and limited taxonomic literature accessible to non-specialists (WARWICK *et al.*, 1990; KENNEDY AND JACOBY, 1999; and SCHRATZBERGER *et al.*, 2000).

A number of taxa have been found to flourish in organically enriched sediments, while being rare or absent from clean sediments. Typical representatives include large oncholaimid nematodes, such as *Pontonema* and the harpacticoid genus *Bulbamphiascus* (MOORE AND BETT, 1989). The evidence suggests that a range of meiofaunal species is associated with particular types of perturbation. Higher numbers of these taxa indicate not only that pollution is occurring but also the identification of the pollutant (KENNEDY AND JACOBY, 1999).

Studies of marine meiofaunal taxonomy and ecology have increased considerably in the last 25 years and meiobenthic assemblages have increasingly been used to assess the effects of perturbations in the marine environment (SCHRATZBERGER *et al.*, 2002). Management decisions should be based on scientific information that exhibits quantitative data and its inherent variability and site-specific to aid in defining impacts in space and time (GORDON, 1987). Meiofauna provides a sensitive and clear measure of the benthic ecosystem status, as they are sedentary and respond to the changes of their local environment.

Since in general organisms are subject to differing stress agents in nature, the multiple measurement of their state of health is required in order to be able to identify and separate the effects caused directly or indirectly by human activity from the natural effects of lack or food reduction of habitat quality. Within the benthic infauna, the free-living nematodes are considered **indicators of environmental quality of sediments** (PLATT, 1984; SANDULLI AND NICOLLA, 1991; SCHRATZBERGER AND WARWICK, 1999; and GHESKIERE *et al.*, 2005). Nematodes are ecologically a very successful group which is also demonstrated by their high species diversity (HEIP *et al.*, 1985). The characteristics of nematodes (Table 1.3) allow the analysis of presence and abundance of individual taxa (BONGERS AND FERRIS, 1999).

The nematodes range in reproductive potential from explosive opportunists to conservative survivalists and they vary in sensivity to pollutants and environmental disturbance. So, although their prime importance in many shore environments may be their key positions as primary and intermediate consumers and as food for higher organisms in soil food webs; the evaluation and interpretation of the abundance and function of their faunal assemblages or community structure offers an *in situ* assessment of disruptive factors (PLATT AND WARWICK, 1980 and SHAW *et al.*, 1983).

Some nematode species are resistant to anaerobiosis, they are often the last metazoan to survive in grossly polluted sediments (VINCX AND HEIP, 1991). The use of nematodes in monitoring thus requires at least some knowledge of nematode systematic, as the response of different species may be very different whereas overall parameters such as density may remain unaffected as some species decrease but others increase (HEIP *et al.*, 1985).

(i) Nematodes are among the simplest metazoa. They occur in any environment that provides a source of organic carbon, in every soil type, under all climatic conditions and in habitats that vary from pristine to extremely polluted.

(ii) Their permeable cuticle provides direct contact with their microenvironment.

(iii) Short generation times and high diversity enables a nematode population to respond quickly to alterations in the nature of the food supply.

(iv) They do not rapidly migrate from stressful conditions and many species survive dehydration, freezing or oxygen stress (although others are more sensitive). The community structure is indicative of conditions in the soil horizon that it inhabits.

(v) Nematodes occupy key positions in soil food webs. They feed on most soil organisms and are food for many others.

(vi) Because nematodes are transparent, their diagnostic internal features can be seen without dissection. They can therefore be identified without biochemical procedures.

(vii) There is a clear relationship between structure and function: the feeding behaviour is easily deduced from the structure of the mouth cavity and pharynx.

(viii) Nematodes respond rapidly to disturbance and enrichment: increasing microbial activity leads to changes in the proportion of bacterial feeders in a community.

Table 1.3 The characteristics of nematodes useful for biomonitoring (*source:* BONGERS AND FERRIS, 1999).

AIMS AND THESIS OUTLINE

The development of traditional (agriculture, harvesting of shrimp larvae, fishing) and new productive activities, as well as the implementation of programs for coastal resources management need the knowledge of the conditions in which these activities are developed and also the study of physical and biological parameters that affect the coast.

Most of the biodiversity research on sandy beaches has mainly concentrated on macrofauna (>1 mm) (e.g. review by MCLACHLAN AND JARAMILLO, 1995). In contrast, sandy beach meiofauna has received less attention despite their high structural and functional density and diversity (ANSARI *et al.*, 1990). Nematodes are usually the dominant group and account for between 90-95% of the total meiofauna (GIERE, 1993). Although nematodes are among the most abundant metazoans in marine sediments, only few papers, apart from purely taxonomic ones, have described the nematode species composition at sandy beaches such as: BLOME, 1982, 1983; GOURBAULT *et al.*, 1995; GHESKIERE *et al.,* 2002, 2004, 2005; and URBAN-MALINGA *et al.*, 2004. From the South-eastern Pacific region no data on interstitial fauna is available for sandy beaches. The Ecuadorian coast is strongly influenced by anomalous El Niño and La Niña events every 2-8 years (SANTOS, 2006). This causes fluctuating climatic conditions, which can have an effect on several sensitive marine living organisms. Consequently, inventories describing species diversity and community structure are needed to evaluate the impact of environmental changes in the Ecuadorian coast. The present study was conducted within the VLIR-ESPOL Program. In project 4, "Environmental Management System in Agriculture and Aquaculture" part of the research is focused on meiofauna composition and their distribution at the intertidal zone in the Ecuadorian sandy beach, and more in detail on free-living marine nematodes. The sampling campaigns included short-term period (fortnightly) from June 2000 until July 2001, and long-term period (quarterly) from August 1999 until February 2001, during the strong La Niña following the 1997-1998 El Niño. The results from the current study should serve as baseline information for future investigations to understand the ecology of meiofauna as an important benthic group and is a first step to detect effects of climatic variability on the coastal ecosystem.

The specific objectives in this study are:

- To compare patterns of nematode density and diversity (genus level) over a larger time scale (August 1999-February 2001) on two Ecuadorian sandy beaches (pristine and disturbed).

- To contrast the density and diversity (species level) of intertidal nematofauna at the upper and the lower part of an exposed Ecuadorian sandy beach.

- To assess the temporal variability in view of seasonality (dry versus rainy season) of the nematode dominant species over a one-year period in a pristine site.

- To investigate the effect of the environmental variables such as temperature, salinity, pluviosity, chlorophyll, organic matter and median grain size on the structure of the meiofaunal and nematode community.

- To describe some dominant new nematode species.

The thesis is divided in two main parts. In the first part, the ecology of the meiofauna and nematode community (density, diversity, feeding and zonation pattern) (Chapters: II-V) was described while in the second part, the taxonomy of the dominant species was described (Chapter VI). The general discussion and conclusions are presented in Chapter VII. REFERENCES are listed at the end of the thesis. The recorded nematode species and their taxonomic position are listed in the ANNEX 1, the meiofauna and nematode densities (ind./ 10 cm^2), and the environmental values per sampling site are given in the ANNEXES 2-12.

CHAPTER II: *"Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches"* deals with the meiofauna and nematode community differences between a sheltered beach characterized by fine grain size (extensively used by tourists) and an exposed beach (fishing village) with fine-medium grain size. The main aims are to describe (1) the meiofauna and nematode assemblage structure in both sandy beaches; (2) biodiversity of the nematode community and (3) the relationship with the environmental factors: salinity, temperature, chlorophyll *a*, suspended particular matter (SPM) and particulate organic matter (POM). This chapter has been published as CALLES, A., VINCX, M, CORNEJO, P, & CALDERÓN, J. 2005. Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches. *Meiofauna Marina* 14, 121-129.

CHAPTER III: *"Tropical sandy beach meiofauna: a case study on the temporal patterns of a high and low water station in Ecuador"*. This research described the fortnightly variability from June 2000 until July 2001 of the intertidal meiofauna, (1) to contrast the density and composition at the upper and the lower part of an exposed Ecuadorian sandy beach (2) to assess the temporal variability in view of seasonality (dry versus rainy season) and (3) to investigate the effect of the environmental variables such as temperature, salinity and pluviosity on the structuring of the meiofaunal community. This chapter has been submitted to Revista Chilena de Historia Natural.

CHAPTER IV: *"Temporal variability in the composition and biodiversity of free-living marine nematodes in a tropical beach (Ecuador)"*. This study described the monthly variability from June 2000 until July 2001 at lower tide level, of the free-living nematode densities, diversity (at species level) and assemblage and their relationship with the environmental factors (sea surface temperature, salinity, pluviosity, chlorophyll *a*, suspended and particular organic matter and median grain size). This chapter has been prepared for a Special Issue of Remote Sensing of Environment on Earth Observation for Biodiversity and Ecology (2006) which will focus on in-situ, aerial and satellite observation for characterizing and monitoring the status and trends of biodiversity and ecosystems. Submitted.

CHAPTER V: *"The dominance of predatory nematodes at the high water level in an Ecuadorian sandy beach"*. This chapter aims to report on the biodiversity of the free-living marine nematodes (at species level), their densities, assemblage and trophic structure at the highest watermark in an exposed sandy beach over a monthly sampling from June 2000 until July 2001. A comparison of diversity and taxonomic distinctness between the nematode species from highest (this study) and lower tide level (previous chapter) was established to detect a zonation pattern across the Ecuadorian beach.

CHAPTER VI: Taxonomic description of some dominant nematode species from San Pedro de Manglaralto beach (Ecuador): *Ceramonema adrianae* sp. n., *Rhynchonema ronaldi* sp. n. and *Gonionchus ecuadoriensis* sp. n.*

"Description of Gonionchus ecuadoriensis sp. n., (Xyalidae, Nematoda) a dominant species on Ecuadorian sandy beaches". An identification key of the genus *Gonionchus* is provided separating the thirteen species into two groups, principally on the presence or absence of longitudinal ornamentations in the cuticle. This paper has been submitted to "*Nematology*".

CHAPTER VII: General discussion and conclusions.

---

* The descriptions of the 3 new species are submitted to *Nematology* and *Zootaxa*. Throughout the thesis, *Ceramonema adrianae* sp. n. has been named *Ceramonema* sp. 1, *Rhynchonema ronaldi* has been named *Rhynchonema* cf. *hirsutum* and *Gonionchus ecuadoriensis* sp. n. was used throughout the text.

CHAPTER II

Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches

Paper published as

CALLES A, VINCX M, CORNEJO P, CALDERÓN J (2005)

Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches. *Meiofauna Marina* 14, 121-129.

ABSTRACT

Meiofauna was studied at two sandy beaches along the Ecuadorian coast between August 1999 and February 2001 (with seasonal intervals), a sheltered beach with high recreational use and an exposed beach with fishing activities. Meiofauna densities ranged between 376 and 2388 ind./10 cm^2. Despite the La Niña event, no clear seasonal trends could be detected in the meiofauna abundances. Nematodes represented between 22-81% of the total meiofauna at the sheltered beach and 76-95% at the exposed beach, followed by turbellarians and gastrotrichs. A total of 40 genera belonging to 19 families were identified. *Neochromadora*, *Daptonema, Metadesmolaimus* and *Omicronema* were the dominant genera at the sheltered beach, while *Metachromadora*, *Rhynchonema, Paracyatholaimus, Ceramonema* and *Gonionchus* were more dominant at the exposed site. Despite the different genus composition, the general genus diversity was similar in both sites. However, a clear difference was present in the feeding types. Non-selective deposit feeders were dominant (42%) followed by predators/omnivores (26%) and epistrate feeders (24%). Multivariate analysis demonstrated that the meiofauna and nematode communities remain different between the two beaches with regard to the temporal variation as well: so each beach, although only 28 km apart from each other, but clearly different in sediment texture, do have their own meiofauna and nematode composition.

KEY WORDS: Intertidal, composition, diversity, exposed beach, sheltered beach.

INTRODUCTION

Meiofauna plays an important role in pollution research. HEIP (1980) has discussed the possibility of nematodes as tools in monitoring the biological effects of pollution. Some nematode species are resistant to pollution and anaerobiosis, they are often the last metazoans to survive in grossly polluted sediments (VINCX AND HEIP, 1991). They range in reproductive potential from explosive opportunists to conservative survivalists and vary in sensitive to pollutants and environmental disturbance (BONGERS AND FERRIS, 1999). The present study was aimed to examine the effects of meiofauna (especially nematodes) community in two Ecuadorian sandy beaches, under different "disturbance" pressure, such as sediment types, human activities carried out in the surf zone (*i.e.* the penaeids shrimp post-larvae capture in San Pedro de Manglaralto, this was forbidden on 2002 onwards in our coast), by comparing the different seasonal and spatial patterns. The results provide the first data available from the Ecuadorian coast reporting on composition and density range of the meiofauna.

MATERIAL AND METHODS

The sites are located along the Ecuadorian coast in Santa Elena Peninsula (Figure 2.1). The area is characterized by two seasons[1]: rainy (January-March) and dry (April-December). 'Salinas' (Chipipe bay) is a sheltered beach, characterized by fine grain sand and extensively used by tourists. 'San Pedro de Manglaralto' is an exposed beach, situated in a fishing village; the sediment is composed of fine to medium grain sand.

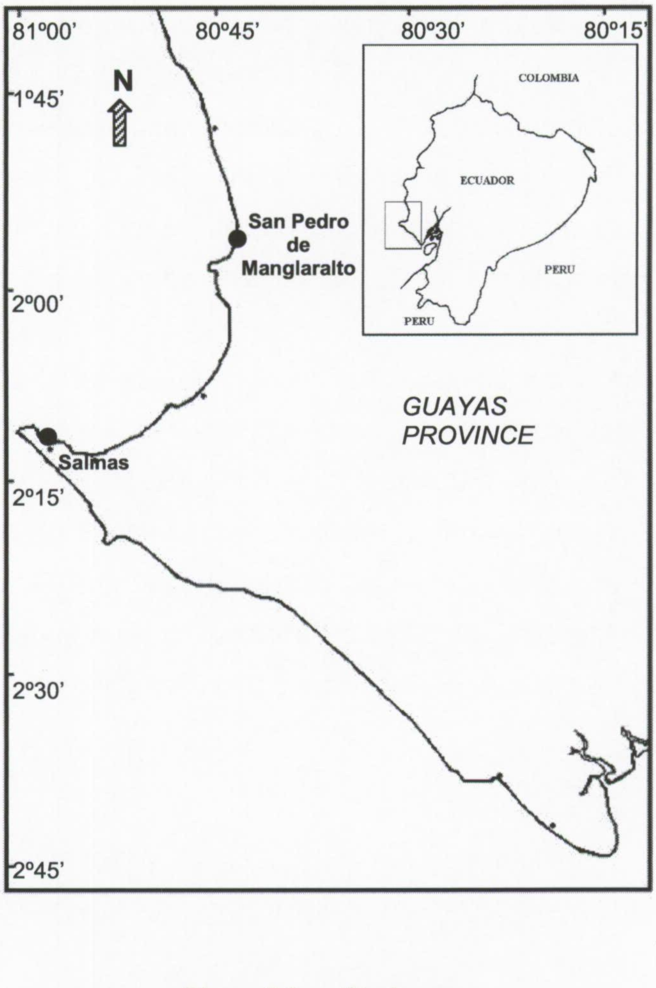


Figure 2.1 Study area.

---

[1] The dry and rainy season mentioned here corresponded to the data set of the environmental sampling campaigns of the present study.

The sampling was carried quarterly from August 1999 to February 2001 (presence of an anomalous period, "La Niña" cold phase after the 1997-1998 El Niño). Meiofauna samples were collected with cores (3.6 cm diameter), preserved with hot (60 ºC) formaldehyde 4%, retained in a 38 µm sieve and extracted by centrifugation with Ludox HS 40 (density 1.18 g/cm^3). Higher taxa were counted and sorted under a stereomicroscope and 200 nematodes were picked out in each replicate, prepared in glycerin solution and mounted on slides for further identification at the genus level (PLATT AND WARWICK, 1988). Nematode feeding types according to WIESER (1953): 1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate feeders and 2B, predators/omnivores were analyzed[1].

In situ salinity and temperature were measured using a refractometer and a mercury thermometer. Water samples were taken and passed through Whatman GF/C filters for the determination of chlorophyll *a* (*Chl a*) by acetone-methanol extraction[2], suspended particulate matter (SPM) was measured by weight difference (filters were dried at 60 °C/48h) and particulate organic matter (POM) by subsequently burning filters at 550 °C. Median grain size was analysed by Coulter LS and classified to the Wentworth scale (BUCHANAN, 1984).

Hill's diversity indices were calculated on nematode genera (HILL, 1973). Diversity profiles were visualized by *k*-dominance curves (LAMBSHEAD *et al.*, 1983). Classification was performed by Two Way Indicator Species Analysis (TWINSPAN) and Principal Component Analysis (PCA) ordination (MCCUNE AND MEFFORT, 1999), using the higher meiofauna taxa (%) and total nematode[3] density (ind./10 cm^2). Mann-Whitney U test was used to assess the significance of differences between samples sites ($p<0.001$-very highly significant, $p<0.01$-highly significant, $p<0.05$-significant).

---

[1] Samples were collected at low tide level and two replicates were used to the data analysis.

[2] The chlorophyll *a* was measured by spectrophotometer (PARSONS *et al.*, 1984).

[3] Genus composition.

RESULTS

Environmental factors

Temperature ranged between 22° and 29 °C. Salinity varied from 34 to 36 PSU. The median grain size ranged between 184-224 µm in Salinas, corresponding to fine sand while in San Pedro de Manglaralto it ranged between 201 and 260 µm (fine to medium sand). The *Chl a* values increased in the rainy season, the concentrations ranged from 0.11 to 3.74 mg/l. SPM concentrations varied from 10.1 to 290.15 mg/l at Salinas and 218.7-1392.4 mg/l at San Pedro de Manglaralto, while POM varied from 3.2 to 53.5 mg/l at Salinas and between 20 and 78.3 mg/l at San Pedro de Manglaralto.

Meiofauna community

Total meiofauna density ranged from 461±101.5 to 1848±7 ind./10 cm^2 at Salinas (sheltered beach) and from 376±21.5 to 2388±161.5 ind./10 cm^2 at San Pedro de Manglaralto (exposed beach). An opposite trend was observed between both stations regarding the temporal variability; at San Pedro de Manglaralto the maximum densities were registered in August 1999 and followed by a subsequent decline until November 2000, while at Salinas, a progressive increase was observed until May 2000, followed by a decline and to increase in February 2001 (Figure 2.2a). However, no significant differences were observed. Nematodes dominated at San Pedro de Manglaralto (76-95%), while in Salinas nematodes represented between 22 and 81% of the total meiofauna density. The temporal variation (Figure 2.2b) was characterized by lower densities (374±61.5 ind./10 cm^2) during dry season at Salinas, while at San Pedro de Manglaralto they were highest (2273±125.5 ind./10 cm^2). Turbellarians represented between 7 and 76% of the total meiofauna density at Salinas and 0.3-13% at San Pedro de Manglaralto. The maximum densities were registered in May 2000 and February 2001, corresponding to warm periods (Figure 2.2c). Gastrotrichs were the third most important taxon, accounting for 6 to 11% of the total meiofauna density (Figure 2d). Other meiofauna groups included rotifers (0.34-1.12%), copepods (0.23-0.32 %), ostracods (0.30%) and polychaetes (0.06-0.24%), while tardigrades, isopods, cnidarians (registered in San Pedro de Manglaralto) and bivalves (registered in San

Pedro de Manglaralto) represented less than 0.05% of the total meiofauna. Spearman rank correlation confirmed the positive relationship between harpacticoids, polychaetes ($p<0.05$) and rotifers ($p<0.001$) with median grain size and negative relationship for turbellarians ($p>0.001$) and isopods ($p<0.01$).

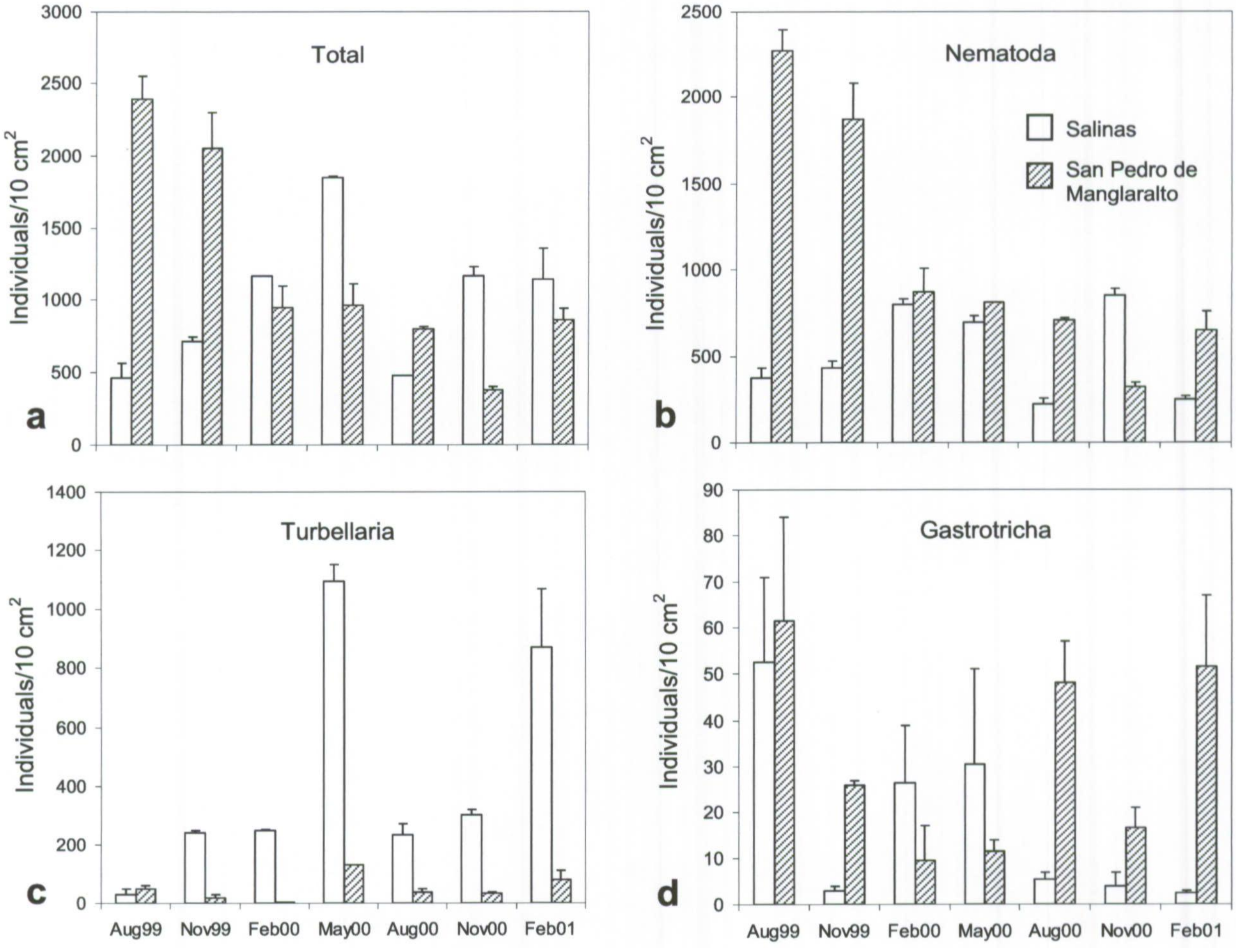


Figure 2.2 **Mean density (a) total, (b) nematodes, (c) turbellarians and (d) gastrotrichs from August 1999 until February 2001; mean values and standard error of the mean (bar±SE).**

Twinspan showed the separation of meiofauna samples for Salinas and San Pedro de Manglaralto beaches. PCA distinguished the temporal variation of meiofauna into seasonal groups (Figure 2.3). At Salinas: Group 1 (August 1999) influenced by "La Niña" event; Group 2 (November 1999-February 2000 and August-November 2000), characterized by the most tourist month (February) and Group 3 (May 2000, February 2001) where the highest turbellarians density was observed. At San Pedro de Manglaralto two groups were detected, corresponding to the chronological sampling done (August 1999-February 2000 and May 2000-February 2001.

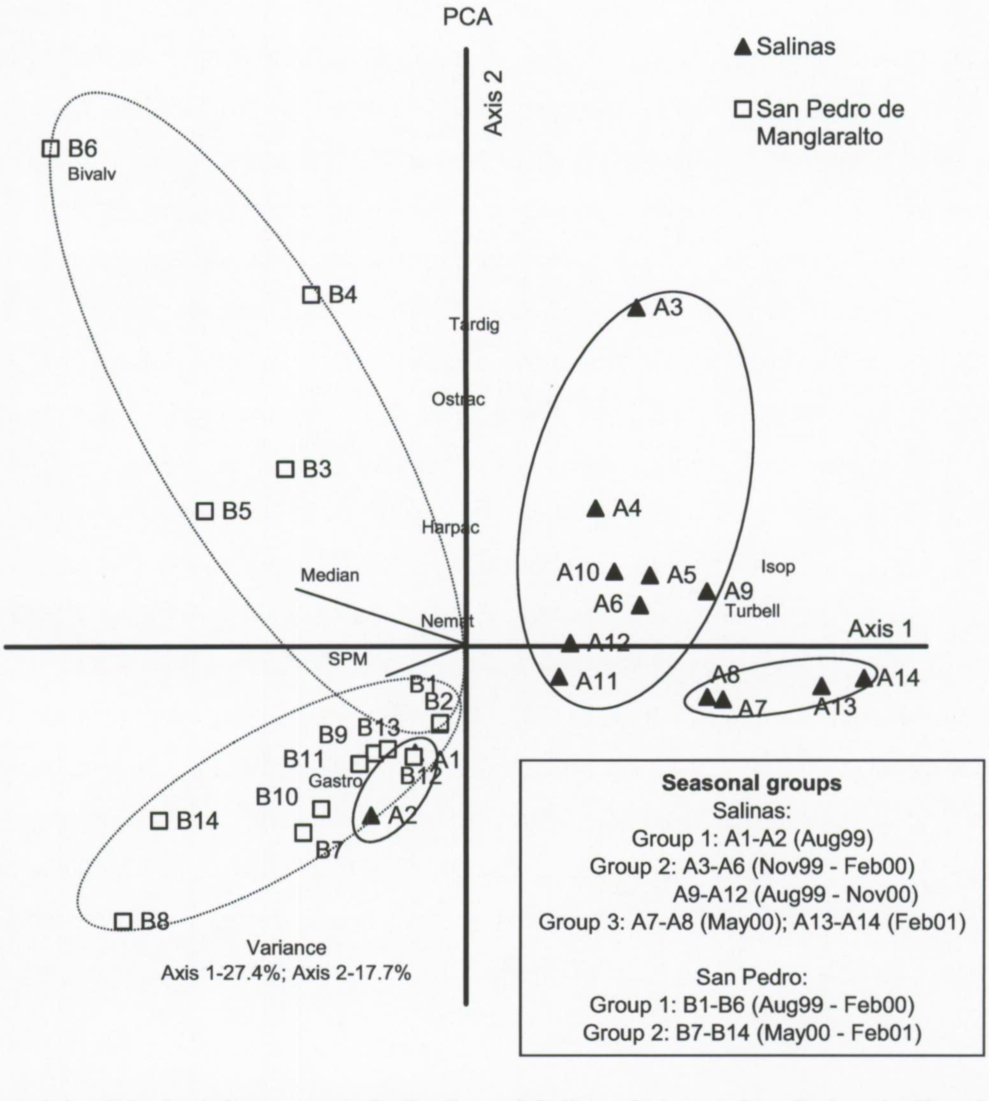


Figure 2.3 **Principal Component Ordination of Salinas (▲) and San Pedro de Manglaralto (□). Nemat= Nematoda, Turbell= Turbellaria, Gastro= Gastrotricha, Harpac= Harpacticoida, Ostrac= Ostracoda, Tardig= Tardigrada, Isop= Isopoda and Bivalv= Bivalvia.**

Nematode community

A total of 40 genera belonging to 19 families were identified (See Table 2.1). At Salinas Xyalidae (with the genera *Rhynchonema, Daptonema, Metadesmolaimus, Omicronema, Paramonohystera* and *Pseudosteineria*) represented 49% of the nematode community, followed by Chromadoridae (genera: *Dichomadora* and *Neochromadora*) represented 21% and Desmodoridae (17%), while at San Pedro de Manglaralto Xyalidae represented 44%, Desmodoridae (22%) and Cyatholaimidae (13%).

Neochromadora represented 20% of the total nematode density at Salinas and ranged between 3±0.6 (August 2000) and 319±68.3 (November 2000) ind./10 cm^2. The densities increased from August 1999 until May 2000, after a steep density decline was registered in August 2000 and February 2001; indicating that higher nematode densities were observed during the transitional months (from dry to rainy season or vice versa). At San Pedro de Manglaralto low densities were registered along the sampling period (Figure 2.4a). *Daptonema* represented 19 % at Salinas (from 33±2.1 to 238 ± 11.5 ind./10 cm^2) and 10% at San Pedro de Manglaralto (from 8±5.7 to 388±4.2 ind./10 cm^2). The temporal patterns showed similar trends during February-August 2000 at both sites (Figure 2.4b). *Metachromadora* represented 17% at Salinas and 22% at San Pedro de Manglaralto. The densities peaked in February 2000 at Salinas (335±70.9 ind./10 cm^2) and in November 1999 (649±10.4 ind./10 cm^2) at San Pedro. The temporal variation to the subsequent period showed similar fluctuations at both sites (Figure 2.4c). *Metadesmolaimus* ranged between 10±6.1 and 220±68.4 ind./10 cm^2 (Figure 2.4d). *Rhynchonema* was the second dominant genus at San Pedro de Manglaralto ranging from 32±1.2 to 509±179.9 ind./10 cm^2, represented 17% of the total density (Figure 2.4e). *Paracyatholaimus* registered the highest density at San Pedro de Manglaralto (410±53.6 ind./10 cm^2) (Figure 2.4f). *Ceramonema* represented 11.6% of the total nematode density at San Pedro, while at Salinas scarce individuals were found. The temporal pattern differed along the sampling period with the maximum density in February 2001 (Figure 2.4g).

		Salinas			San Pedro de Manglaralto		
Family	Genera	Mean	Min - Max	%	Mean	Min - Max	%
Thoracostomopsidae	*Enoplolaimus*	4,1	0 - 13	0,80	1,8	0 - 5	0,16
Anoplostomatidae	*Anoplostoma*	0,1	0 - 1	0,03			
Anticomidae	*Anticoma*				1,0	0 - 5	0,10
	Odontanticoma	1,9	0 - 6	0,36	37,5	11 - 65	3,50
Oxystominidae	*Halalaimus*	1,0	0 - 3	0,19	1,4	0 - 5	0,13
	Nemanema				0,3	0 - 2	0,03
Oncholaimidae	*Metoncholaimus*	0,2	0 - 2	0,05			
	Oncholaimellus	2,7	0 - 12	0,52			
	Oncholaimus	0,1	0 - 1	0,02			
	Viscosia	26,3	4 - 56	5,08	8,4	2 - 24	0,78
Enchelidiidae	*Ditlevsenella*				0,4	0 - 3	0,04
	Eurystomina				0,6	0 - 5	0,06
	Pareurystomina				0,1	0 - 1	0,01
Tripyloididae	*Bathylaimus*				16,5	0 - 57	1,54
Chromadoridae	*Dichromadora*	5,6	0 - 23	1,07	3,2	0 - 18	0,30
	Neochromadora	103,7	3 - 319	20,05	10,1	0 - 63	0,95
Comesomatidae	*Sabatieria*	5,1	0 - 21	1,00			
Cyatholaimidae	*Paracyatholaimus*	5,0	0 - 32	0,97	127,3	13 - 410	11,88
	Pomponema	0,5	0 - 4	0,10	7,3	0 - 16	0,68
Selachinematidae	*Synonchiella*	0,2	0 - 1	0,04			
Desmodoridae	*Metachromadora*	87,1	2 - 335	16,83	233,3	44 - 649	21,77
	Spirinia	0,1	0 - 1	0,02			
Microlaimidae	*Microlaimus*				9,9	0 - 28	0,93
Leptolaimidae	*Camacolaimus*	0,3	0 - 2	0,07	0,3	0 - 2	0,02
	Leptolaimus				0,2	0 - 1	0,02
Ceramonematidae	*Ceramonema*	0,8	0 - 2	0,16	124,4	55 - 209	11,61
Xyalidae	*Cobbia*				0,2	0 - 1	0,02
	Daptonema	99,8	33 - 238	19,29	109,3	8 - 388	10,20
	Gonionchus				81,9	12 - 195	7,64
	Metadesmolaimus	62,7	10 - 204	12,12	69,9	12 - 220	6,53
	Omicronema	35,6	9 - 91	6,89	25,0	1 - 56	2,34
	Paramonohystera	28,9	0 - 126	5,58	1,9	0 - 7	0,18
	Pseudosteineria	2,2	0 - 14	0,42			
	Rhynchonema	26,3	2 - 40	5,08	180,6	32 - 509	16,85
Sphaerolaimidae	*Sphaerolaimus*	0,1	0 - 1	0,03			
Linhomoeidae	*Eumorpholaimus*	1,6	0 - 10	0,31			
	Paralinhomoeus	0,2	0 - 1	0,03			
Axonolaimidae	*Axonolaimus*				0,5	0 - 4	0,05
	Odontophora	0,1	0 - 1	0,03			
	Parodontophora	14,9	5 - 48	2,89	18,1	0 - 55	1,69

Table 2.1 Nematode genera density (ind./10 cm^2) at Salinas and San Pedro.

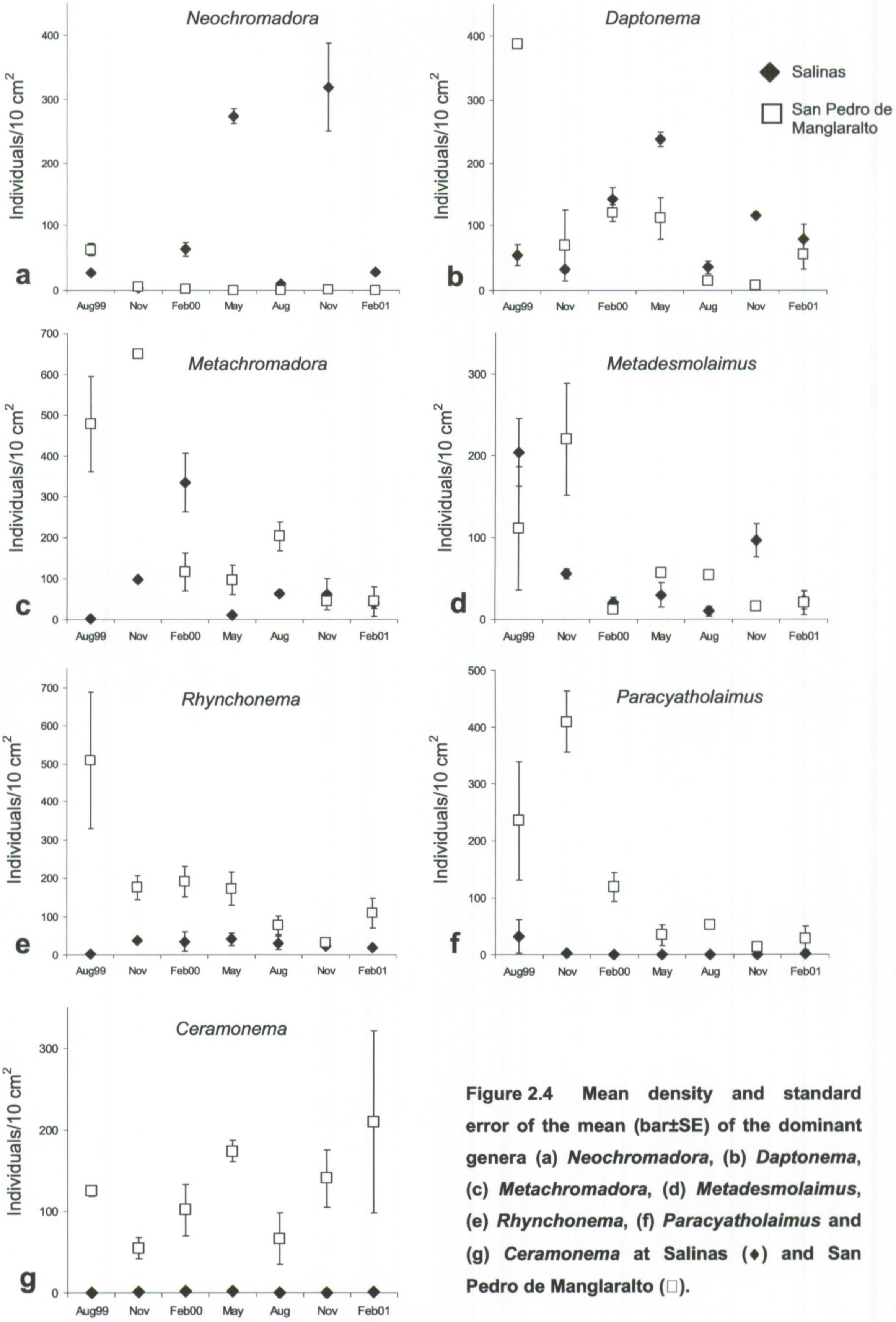


Figure 2.4 Mean density and standard error of the mean (bar±SE) of the dominant genera (a) *Neochromadora*, (b) *Daptonema*, (c) *Metachromadora*, (d) *Metadesmolaimus*, (e) *Rhynchonema*, (f) *Paracyatholaimus* and (g) *Ceramonema* at Salinas (♦) and San Pedro de Manglaralto (□).

The diversity was similar at both beaches: lowest in August 1999 and highest in the rainy season (Table 2.2)[1]. The *k*-dominance curves (Figure 2.5) also showed similar patterns.

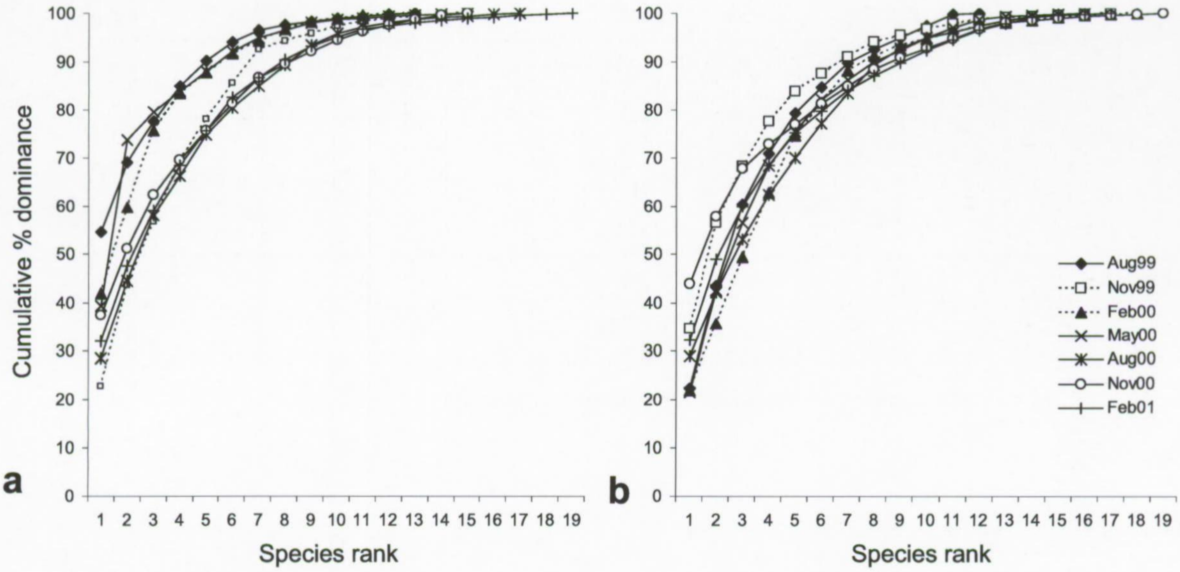


Figure 2.5 ***K*-dominance curves of nematode assemblages for Salinas (a) and San Pedro de Manglaralto (b) beaches.**

Non-selective deposit feeders predominated: at Salinas represented 51% (*Daptonema, Metadesmolaimus* and *Omicronema* contributed with 38%), while at San Pedro de Manglaralto represented 38% (*Rhynchonema* and *Daptonema* contributed with 27%). At Salinas predators/omnivores represented 26% of the trophic structure, followed by epistrate feeders (23%), while the selective deposit feeders were less abundant. At San Pedro de Manglaralto epistrate feeders and predator/omnivores represented 25.2 and 25.1% respectively, followed by selective deposit feeders (12%) where *Ceramonema* contributed with 11.7% (Figure 2.6). PCA results of the Nematoda genera densities showed that the samples formed two groups[2] (like meiofauna community) but not displayed any seasonal trend.

---

[1] See Annex 2.1 in this article (page 39).

[2] See Annex 2.2 in this article (page 40).

Salinas beach	Aug99	Nov99	Feb00	May00	Aug00	Nov00	Feb01
N_0	13	15	13	15	17	15	19
N_1	4.74	8.30	5.86	5.15	9.06	8.10	8.79
N_2	2.97	6.75	4.10	3.54	6.73	5.28	6.13
N_{inf}	1.83	4.40	2.38	2.54	3.52	2.67	3.13
H'	1.56	2.12	1.77	1.64	2.20	2.09	2.17
San Pedro beach	**Aug99**	**Nov99**	**Feb00**	**May00**	**Aug00**	**Nov00**	**Feb01**
N_0	12	17	18	16	16	19	17
N_1	8.17	7.19	9.63	9.15	9.50	7.48	9.00
N_2	6.70	5.04	7.74	7.20	7.05	4.30	6.13
N_{inf}	4.47	2.89	4.54	4.67	3.47	2.28	3.10
H'	2.10	1.97	2.26	2.21	2.25	2.01	2.20

Table 2.2 **Diversity indices (Hill's numbers N_0, N_1, N_2, N_{inf} and Shannon-Wiener index H') of the nematode community at Ecuadorian sandy beaches.**

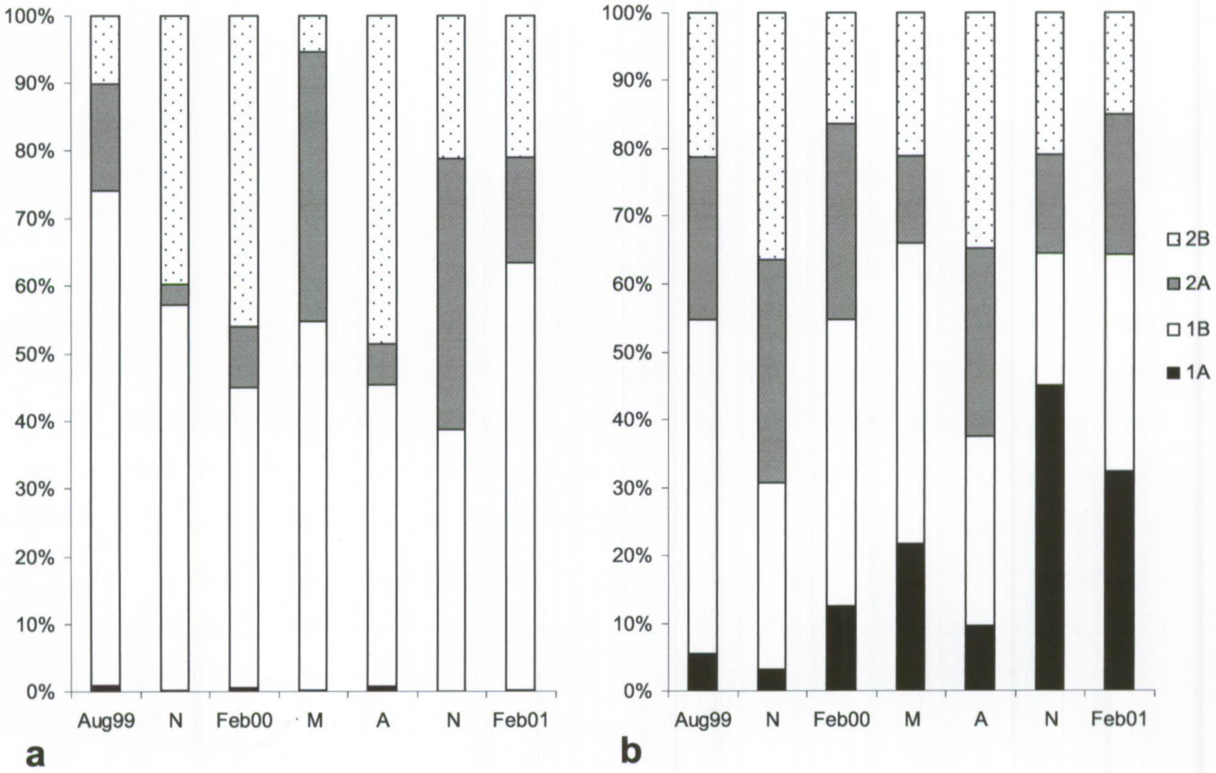


Figure 2.6 **Nematode feeding types at Salinas (a) and San Pedro de Manglaralto (b). 1A= selective deposit feeders, 1B= non-selective deposit feeders, 2A= epistrate feeders and 2B= predators/omnivores.**

DISCUSSION

The first sampling took place during strong La Niña phase of the El Niño South Oscillation (ENSO) cycle. There is some evidence that ENSO has a substantial influence on meiofauna of sandy beaches (NEIRA *et al.*, 2001). During the anomalous conditions several of the most abundant genera collected, such as *Neochromadora, Daptonema* and *Rhynchonema* registered highest densities, especially in San Pedro de Manglaralto; while at Salinas this period attained lowest densities.

The hydrodynamics of each area could influence the infaunal densities by producing differential responses of nematode assemblages to physical disturbance and organic enrichment. In relation to the wave exposure rate, pioneer studies (e.g. MCLACHLAN *et al.*, 1981) suggested that meiofauna in sandy beaches is not negatively affected by the increases in exposure rate and coarser sediments.

The meiofauna composition in the Ecuadorian sandy beaches could be in accordance with the beach characteristics, where the highest meiofauna densities were registered in the exposed beach and the lowest at the sheltered beach. In the Caribbean beaches the nematode generic composition was highly variable at the more wave-exposed locations, but less so at the more sheltered locations (GOURBAULT *et al.*, 1998).

SCHRATZBERGER AND WARWICK (1999) reported that in treatments of physical and biological disturbance, the nematodes show most extreme changes as a result of organic enrichment. In our study the turbellarians were more abundant in Salinas (waste water is deposited directly into the bay) during warm months, turbellarians have been demonstrated being very common in wave-protected areas with little mixing of the sediments (CANNON AND FAUBEL, 1988). On the other hand the organic enrichment caused by intensive fish farming in coastal sediments showed evident changes on meiofaunal densities, which were 50% lower than in a non disturbed site (MAZZOLA *et al.*, 2000).

Non-selective deposit feeders (1B) such as Xyalidae are normally associated with exposed beaches (NICHOLAS AND HODDA, 1999), while the predator/omnivores (2B) such as Oncholaimidae are more associated with water-movement disturbance (NETTO *et al.*, 1999). The dominance of 1B species is associated with lower maturity indexes, which mean the disturbance on nematode fauna (BONGERS *et al.*, 1991). In this study we observed a dominance of Xyalidae, Chromadoridae and Desmodoridae at Salinas (with fine sand), while that Xyalidae, Desmodoridae and Cyatholaimidae dominated at

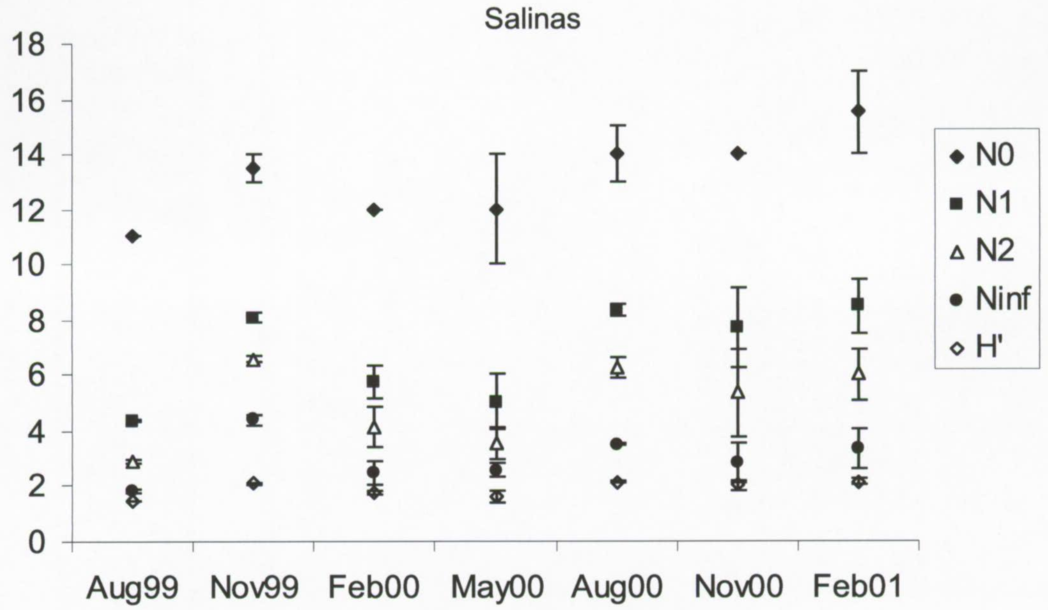
San Pedro de Manglaralto (with fine-medium sand). The proportion of non-selective deposit feeders ranged from 51% (Salinas) to 38% (San Pedro de Manglaralto).

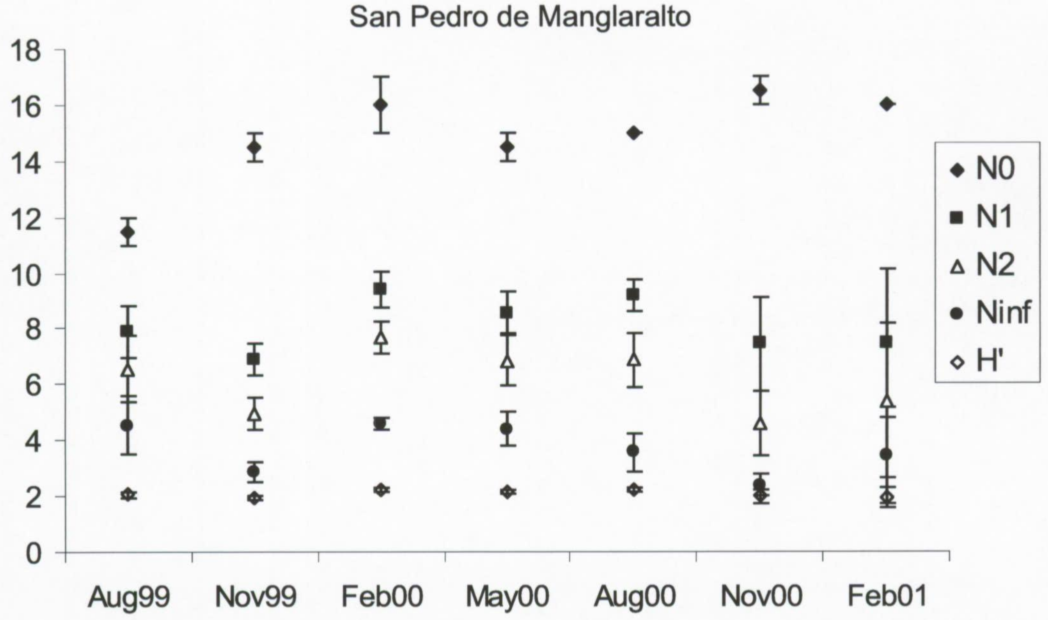
The spatial and seasonal patterns of meiobenthos in the two Ecuadorian sandy beaches showed differences in terms of composition and density but not in diversity. At the higher taxon level, turbellarians were significantly more abundant in the sheltered area compared to the exposed site.

ACKNOWLEDGEMENTS

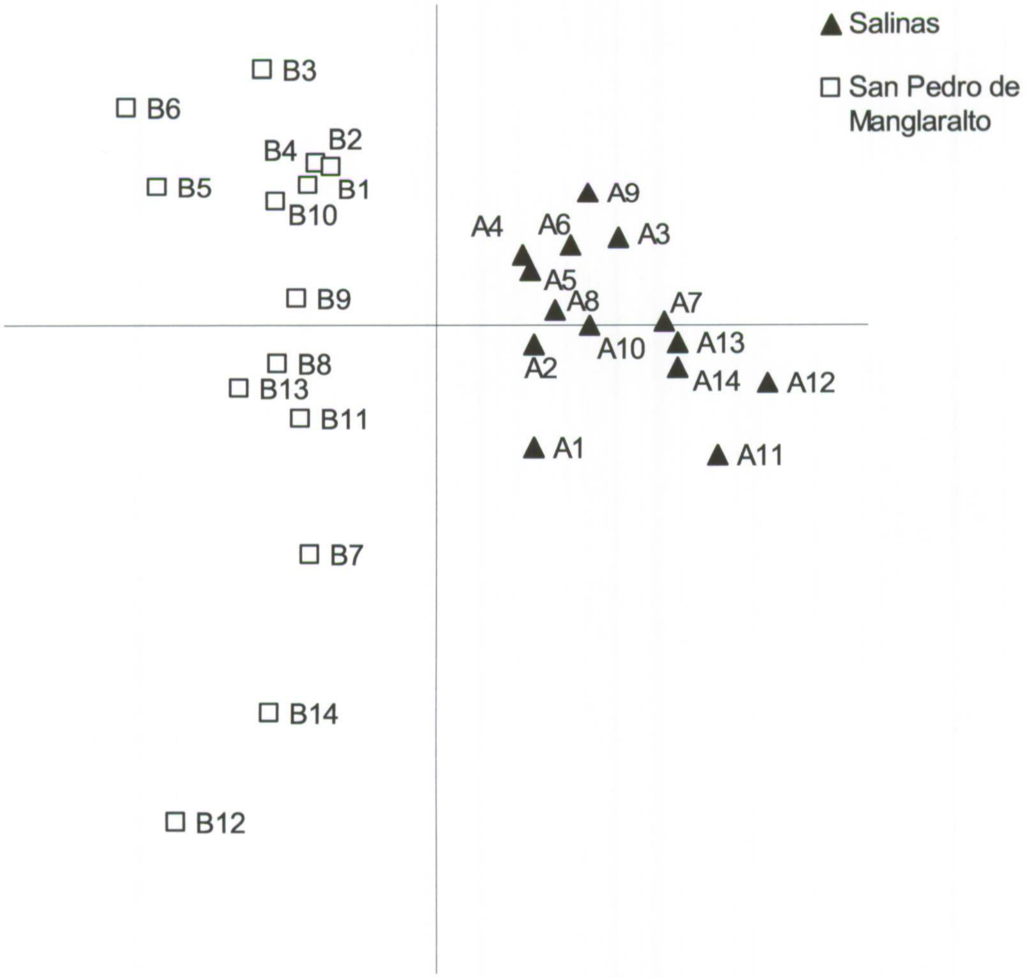
This study was supported within the framework of the VLIR-ESPOL Program. The authors are indebted to Nancy Fockedey, Jan Wittoeck, Sonnia Guartatanga, Verónica Ruíz and Luis Domínguez for their assistance in the field and Dr. F. Arcos for his comments on the manuscript.

ANNEX TO THE ARTICLE





Annex 2.1 **Mean and standard error of Hill's numbers (N_0, N_1, N_2 and N_{inf}) and Shannon-Wiener (H') diversity at Salinas and San Pedro de Manglaralto beaches.**



Annex 2.2 **Principal Component Ordination of Salinas (▲) and San Pedro de Manglaralto (☐) based on Nematoda genera densities.**

CHAPTER III

Tropical sandy beach meiofauna: a case study on the temporal patterns of a high and low water station in Ecuador

Paper prepared as

Calles A, Degraer S, Vanagt T, Gheskiere T, Cornejo M.P, Vincx M.
(submitted)

Tropical sandy beach meiofauna: a case study on cross-shore and seasonal patterns in Ecuador. Revista Chilena de Historia Natural.

ABSTRACT

The meiofauna on a cross-shore gradient at an intermediate-reflective Ecuadorian sandy beach was studied fortnightly from June 2000 until July 2001 (this period had undergone a strong La Niña event), in order to analyse the patterns in abundance between upper and lower station at the intertidal zone and to assess the temporal variability in view of seasonality (dry versus rainy season). The sea surface temperature ranged between 21.4 and 27.5 °C, the pluviosity was restricted between January and March 2001 (151-114 mm), the salinity ranged between 32 and 34 PSU and the median grain size between 215 and 290 µm at the upper station and 191-301 at the lower station, corresponding to fine-medium sand. The meiofauna samples were collected with plastic cores (3.6 cm diameter) to 20 cm depth. Fifteen meiofauna taxa were registered, with Nematoda the dominant taxon on the beach (61% at the upper station and 83% at the lower station). The total meiofauna density ranged from 186±14 ind./10 cm^2 to 3907±408 ind./10 cm^2 at the upper station and from 417±5 ind./10 cm^2 to 1940±166 ind./10 cm^2 at the lower station; however no significant differences on the average meiofauna densities were detected between the stations. Multi-dimensional scaling ordination based on higher meiofauna taxa densities showed cross-shore differences, caused by highest densities of copepods at the upper station (275±86 ind./10 cm^2) and highest densities of nematodes (738±64 ind./10 cm^2), with a near absence of copepods at the lower station. At the lower station the total meiofauna and nematode densities showed a significant negative correlation with the distance (as a proxy for elevation): a decreasing density was found lower on the beach; and a significant positive correlation with the rainfall. A seasonal respond to the total meiofauna and nematodes at the lower station were detected. At the upper station no correlation were found. Compared with other cross-shore patterns illustrated in the literature, the nature of the meiofauna data from the Ecuadorian beach increases even at the high spatial and temporal variability of the interstitial meiofauna present in different sandy beaches around the world. Therefore, there is not something like a 'typical' sandy beach meiofauna.

KEY WORDS: meiofauna, Ecuador, intertidal zone, intermediate-reflective beach, temporal variability, tidal level.

INTRODUCTION

In the intertidal beach, physical variables such as temperature, movement of sediment and salinity are more variable than in the subtidal, and may greatly influence the faunistic composition and distribution within and between intertidal areas (HICKS AND COULL, 1983). MCLACHLAN AND TURNER (1994) described the intertidal environment of sandy beaches as a continuum with at one extreme the coarse-grained, reflective beach state characterized by high water percolation and, consequently, high oxygenation, and at the other extreme dissipative beaches with finer sands and a lower permeability which tend to harbour higher organic inputs and anaerobic conditions.

Exposed sandy shores are often considered to be merely an edge of the sea or the land, but they also constitute an important ecotone with food chains based on decomposers, grazers and suspension feeders (MCLACHLAN, 1981). The physical harshness of the eroding, intermediate shore may be counterbalanced by oxygen-rich conditions. On the accreting, dissipative shore a pronounced chemocline (sharp gradient in chemical concentration) favours a dominance of nematodes (MENN, 2002). Differences in availability of major food resources between the shores may also affect the meiofauna. The longer the period between swashes, the better the conditions for the fauna on exposed sandy beaches. MCLACHLAN *et al.* (1993) have suggested that the swash climate directly controls the composition and structure of the sandy beach communities. The interstitial fauna of marine beaches has been studied at different latitudes and localities (e.g. HEIP *et al.*, 1985 for an overview; COULL, 1988) but not so much along cross-shore and temporal gradients in tropical areas (GOURBAULT *et al.*, 1998). From the South-eastern Pacific region no data on interstitial fauna are available for sandy beaches. This study provides the first information about the meiofauna composition and their distribution at the intertidal zone in the Ecuadorian sandy beach over a one year period. The aims of this study were: 1. to contrast the density and composition of intertidal meiofauna at the upper and the lower part of an exposed Ecuadorian sandy beach; 2. to assess the temporal variability from June 2000 until July 2001, in view of seasonality (dry versus rainy season) and 3. to investigate the effect of the environmental variables such as pluviosity, temperature, salinity, distance (as a proxy for elevation) and median grain size on the structuring of the meiofaunal community. The study period undergone a strong La Niña phase, after the 1997-98 El Niño (McPhaden, 1999).

MATERIAL AND METHODS

Study site

The beach of San Pedro de Manglaralto is part of the denominated cove San Pedro-Montañita and is an exposed sandy beach that displays a concavity with direction SO-NE. The sampling station was located at the southern limit of the Centro Nacional de Acuicultura e Investigaciones Marinas (CENAIM), (1°56'30"S, 80°43'30"W) (Figure 3.1). The beach has a semi-diurnal, mesotidal regime (DAVIES, 1964) with a tidal range between 2-2.4 m. The Ecuadorian coastal climate is characterized by two seasons: a dry-cool season (May-December) and a wet-warm season (January-April) and is influenced by currents in the Pacific Ocean. From July until October the area is subjected to the relatively cold (<22 °C) Humboldt-current, heading North, while during the months January until April the warm (>25 °C) El Niño-current, heading South, dominates. In addition, wide inter-annual fluctuations of the weather can occur due to the ENSO phenomenon (FIEDLER, 2002).

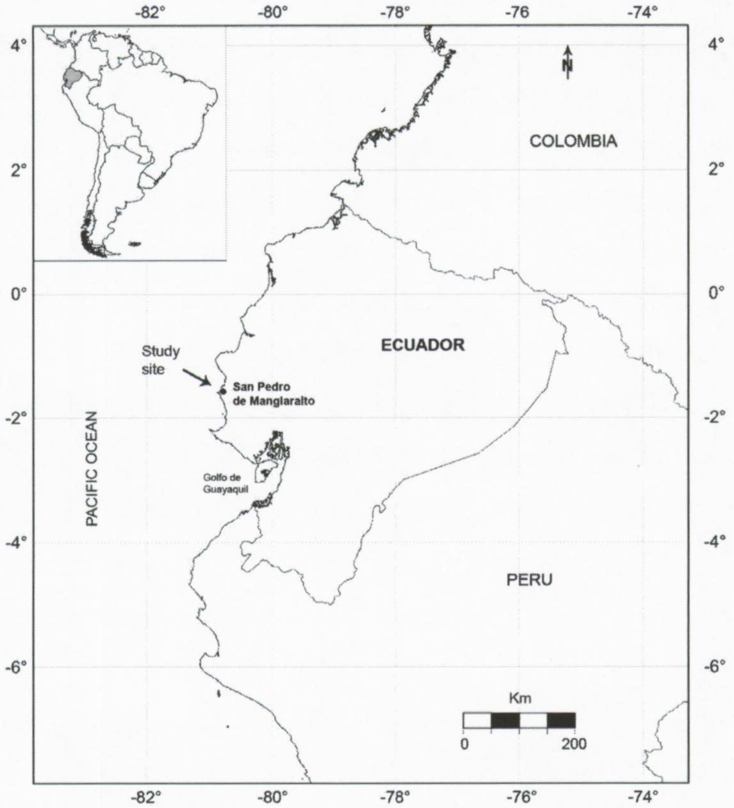


Figure 3.1 Location of the study site.

Sampling strategy and laboratory work

Sampling was performed fortnightly from June 2000 until July 2001 at spring tides (full moon and new moon). At the beach two stations were sampled: one at low and one at high tide level. The position of both stations was assessed based on predicted time and elevation of high and low water (La Libertad data, Instituto Oceanográfico de la Armada). At each station, three replicate samples were collected for meiofauna samples. They were obtained by forcing a hand core (3.6 cm diameter) (HIGGINS AND THIEL, 1988) to 20 cm depth in the sediment and fixed with a heated (60 °C) 4% buffered aqueous formaldehyde solution (VINCX, 1996).

Additional sediment samples were collected for granulometric analyses. Sea Surface Temperature (SST) and salinity data were taken from 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.

Sediment particle-size distribution was determined using Coulter LS 100© particle size analyzer. The sediment fractions were defined according to the Wentworth scale (BUCHANAN, 1984).

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.

In the laboratory, meiofauna samples were rinsed with a gentle jet of freshwater 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. Meiofauna was counted by using a counting dish and identified at the higher taxon level under a stereomicroscope. The presence of archiannelids (Polychaeta) was observed in the samples but it was not possible to include them in the counting because the specimens were fragmented.

Data analysis

Beaches can be classified by three variables: The modal breaker height (H_b), in meters; the modal wave period (T), in seconds; and sediment fall velocity (W_s), in meters per second. The W_s was calculated from the median grain size following GIBBS *et al.* (1971). The values to this study were: H_b= 0.4 m, T= 3 s and W_s= 0.03 m/s. These parameters were combined into the dimensionless fall velocity $\Omega = H_b / W_s T$ or Dean's parameter (SHORT, 1999). When $\Omega < 1$ beaches tend to be *reflective*, when $\Omega > 6$ they tend to be *dissipative* and in between ($1 < \Omega < 6$) are the so-called *intermediate* beaches (MASSELINK AND SHORT, 1993). The 'dry' (April-December) and 'rainy' (January-March) seasons were defined according to the data set of the sampling year (See figure 3.3). In order to detect temporal and cross-shore patterns in the meiofauna data, the multivariate analyses were done after square-root data transformation. Lower triangular similarity matrices were constructed using the Bray-Curtis similarity measure to find a faunal structure with visual inspection of a clustering dendrogram. Patterns in the meiofauna data were analyzed by non-metric Multi-Dimensional Scaling (nMDS). One-way crossed analysis of similarities or ANOSIM (CLARKE, 1993) was used to test the significant differences in meiofauna assemblage composition between beach stations. The similarity percentage analyzer or SIMPER (CLARKE, 1993) was applied to determine the contribution of higher meiofauna taxa to the discrimination between the beach stations. The multivariate analyses were performed using PRIMER v5 software package (CLARKE AND GORLEY, 2001). The univariate analyses were applied to the average meiofauna densities of three replicates. The faunal densities were expressed in individuals per 10 cm^2 (ind./10 cm^2). Analysis of variance (ANOVA) was applied to check the existence of significant differences between dry and rainy season per station. Pearson's correlation was applied to assess the relationship between meiofauna taxa (at the upper and at the lower station) and environmental factors such as pluviosity, temperature, salinity, distance (as a proxy for elevation) and median grain size. The normal distribution of the data was checked by the Kolmogorov-Smirnov test. Levene's test was used to verify the homogeneity of variances prior to the analysis. When conditions for the use of a parametric test were not fulfilled, the nonparametric 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 employed at two independent samples. Statistical analysis was performed using the STATISTICA v6.0 software package (STATSOFT, 2001).

RESULTS

Physical environment

The width of the intertidal zone at the different sampling locations ranged from 90 to 120 m. The beach slope varied between 1:21 and 1:41. At the upper station, samples were taken between 34-54 meters from the reference point (0), and at the lower station the sampling distance ranged from 84 to 118 meters (Figure 3.2). In function of the Dean's parameter Ω, the study site is an intermediate beach (Ω =1.2) but near the reflective characteristics.

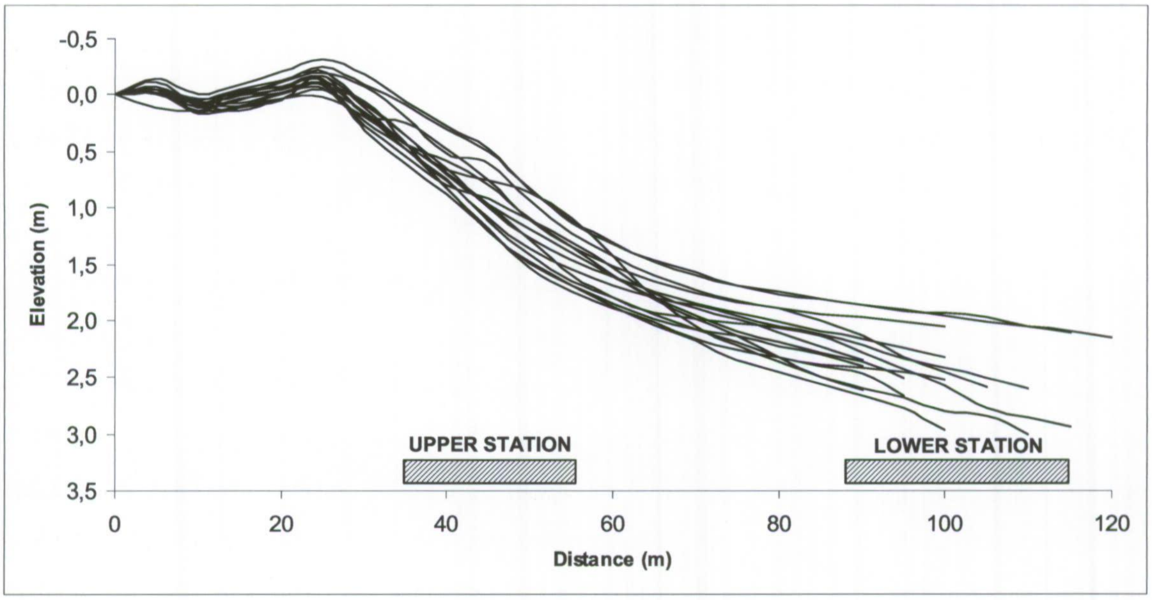


Figure 3.2 **Beach profile at San Pedro de Manglaralto (June 2000-June 2001). The indication bars 'upper station' and 'lower station' refer to the sampling distance over which the actual samples were taken during the one year period (cf. text), following the water line at high and low tide level. The vertical scale is exaggerated in relationship to the horizontal. The origin (0) is named reference point in the text.**

The fine to medium sand fractions dominated the sediment. Median grain size ranged from 215 to 290 µm at the upper station and from 191 to 301 µm at the lower station (Table 3.1). The SST ranged between 21.4 and 27.5 °C and was highest in the rainy season; salinity ranged between 32 to 34 PSU and was lowest in the rainy season; the rainfall was mainly restricted from January 2001 (151 mm) to March 2001 (114 mm) (Figure 3.3).

Sediment		**Upper station**				**Lower station**			
		Mean	SE	Min	Max	Mean	SE	Min	Max
Median grain size	(µm)	258	± 3	215	- 290	230	± 6	191	- 301
% silt and clay	(<63 µm)	0.0	± 0.0	0.0	- 0.0	0.7	± 0.1	0.0	- 1.5
% very fine sand	(63-125 µm)	1.7	± 0.2	0.0	- 4.8	8.7	± 0.8	1.0	- 18.9
% fine sand	(125-250 µm)	45.6	± 1.1	34.3	- 61.9	46.3	± 1.1	33.7	- 57.1
% medium sand	(250-500 µm)	46.9	± 1.0	31.4	- 54.1	28.7	± 1.3	14.7	- 42.6
% coarse sand	(500-1000 µm)	5.2	± 0.6	1.3	- 16.1	14.0	± 1.6	5.5	- 48.6
% gravel	(>1000 µm)	0.5	± 0.1	0.0	- 3.6	2.5	± 0.3	0.0	- 6.4

Table 3.1 Sediment characteristics at high tide level (upper station) and at low tide level (lower station): mean of granulometric values and standard error of the mean (SE).

Meiofauna assemblage structure: upper versus lower beach

Multidimensional scaling (Figure 3.4) and cluster analysis (not shown) clearly reveal the differences in meiofauna assemblage structure between the high water and the low water positions: the sampling points of both stations are clearly separated during the full sampling period.

One-way ANOSIM results confirmed that the composition of the meiofauna assemblages differed significantly between stations at the beach (R = 0.78, p<0.001). Following the SIMPER analysis, higher copepod densities at the upper station and higher nematode densities and near absence of the copepods at the lower station mainly caused the differences.

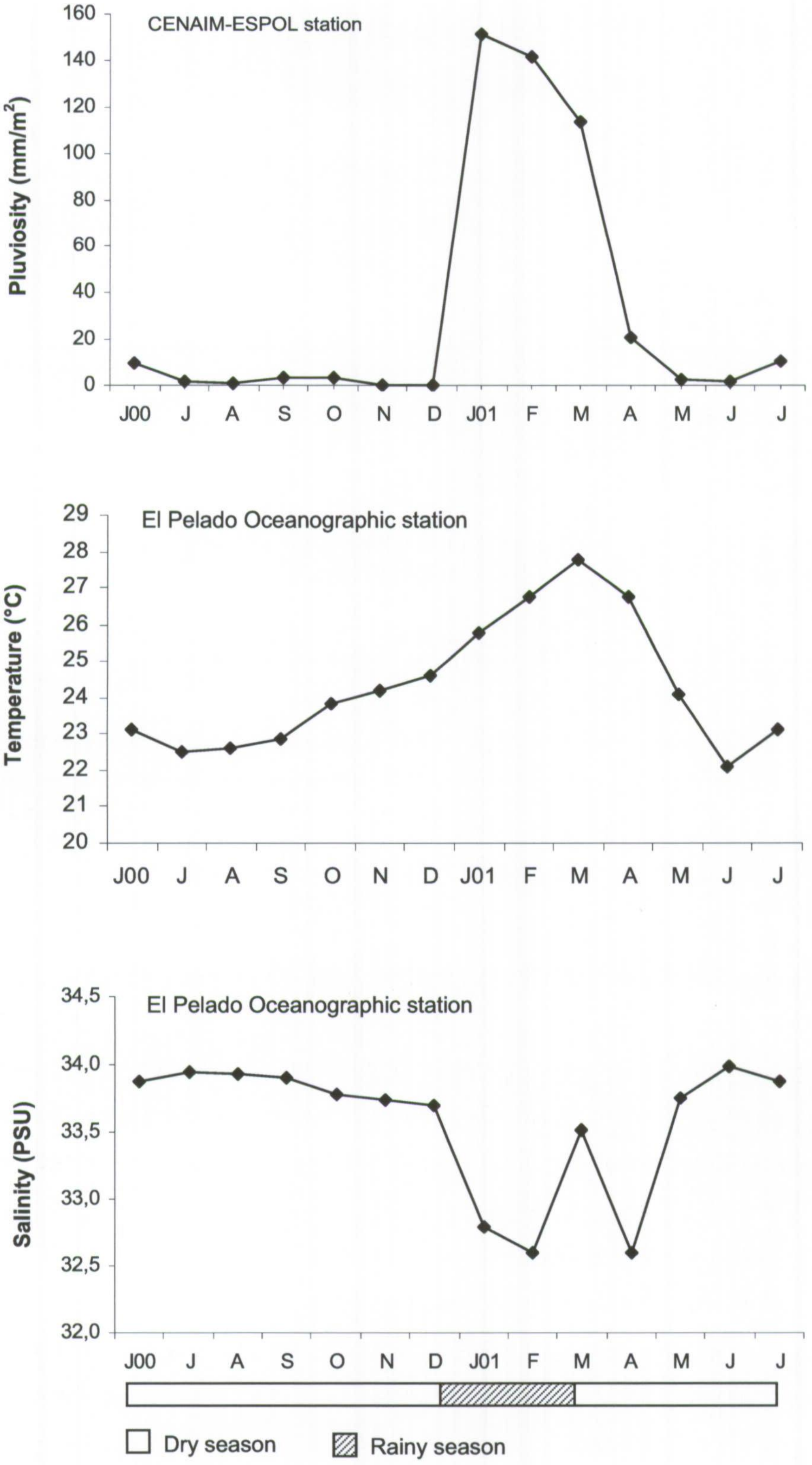


Figure 3.3 **Temporal fluctuation of the environmental variables: pluviosity, temperature and salinity.**

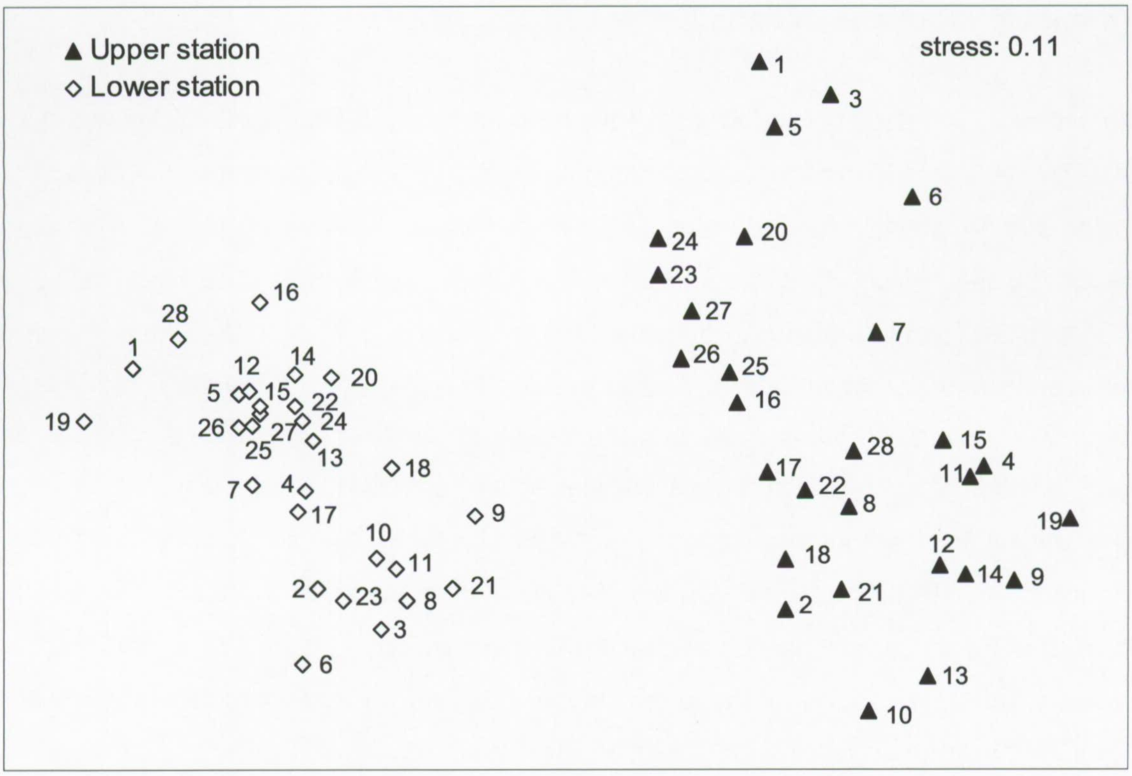


Figure 3.4 **Output of non-metric multi-dimensional scaling (nMDS) on square-root transformed abundance data of the higher taxa of the meiofauna (numbers indicate the fortnightly sampling in a chronological order from June 2000 to July 2001).**

At the upper station, Nematoda was the dominant taxon (61%) with a mean density value of 587±84 ind./10 cm^2, followed by Copepoda Harpacticoida (29%) with a mean density value of 275±86 ind./10 cm^2, Tardigrada (4%) with 42±20 ind./10 cm^2, naupliar larvae (3%) with 29±6 ind./10 cm^2 and Turbellaria (1%) with a mean density value of 13±2 ind./10 cm^2. Other meiofauna groups represented less than 1% of the total meiofauna density: Polychaeta, Isopoda, Cladocera, Rotifera, Ostracoda, Bivalvia, Halacaroidea, Insecta and Oligochaeta.

At the lower station, the meiofauna was even more dominated by Nematoda (83%) with a mean density of 783±64 ind./10 cm^2, followed by Gastrotricha (9%) with 82±11 ind./10 cm^2 and Turbellaria (6%) with a mean density of 49±8 ind./10 cm^2. Other meiofauna groups represented less than 1% of the total meiofauna density: Copepoda Harpacticoida, naupliar larvae, Polychaeta, Isopoda, Rotifera, Ostracoda, Tardigrada, Bivalvia, Halacaroidea, Insecta and Oligochaeta.

Temporal variations of densities

Total meiofauna density ranged from 186±14 ind./10 cm^2 in October 2000 (new moon) to 3907±408 ind./10 cm^2 in June 2000 (full moon) at the upper station; while at the lower station density ranged from 417±5 ind./10 cm^2 in April 2001 (full moon) to 1940±166 ind./10 cm^2 in January 2001 (new moon) (Figure 3.5). The Mann-Whitney test, applied to total meiofauna densities did not show significant differences between the upper and the lower station; nevertheless the average of the total meiofauna density was slightly highest at the upper station than the lower. Meiofauna composition and densities at the upper and the lower station are reported in the table 3.2.

The densities of nematodes ranged from 148±6 ind./10 cm^2 in October 2000 (new moon) to 1673±162 ind./10 cm^2 during May 2001 (new moon) at the upper station and from 298±32 ind./10cm^2 in September 2000 (new moon) to 1652±73 ind./10 cm^2 in January 2001 (new moon) at the lower station; however no significant differences were detected between upper and lower station (ANOVA, $p > 0.05$).

Significant differences between the upper and the lower station concerning densities of the several taxa recorded were detected by the Mann-Whitney test: Copepoda ($Z=6.4$; $p<0.001$***); Turbellaria ($Z= -4.4$; $p<0.001$***); Isopoda ($Z=2.6$; $p<0.01$**); Tardigrada ($Z=4.7$; $p<0.001$***); Bivalvia ($Z=-2.7$; $p<0.01$**) and naupliar larvae ($Z=4.2$; $p<0.001$***).

At the upper station, the temporal variation of copepods was characterized by highest densities (2322±250 ind./10 cm^2) in June 2000 (full moon) and lowest densities (20±15 ind./10 cm^2) in October 2000 (new moon), while at the lower station the densities reached a maximum of 20±2 ind./10 cm^2 in February 2001 (new moon) (Figure 3.5). The turbellarians registered the highest densities (33±4 ind./10 cm^2) in February 2001 (full moon) at the upper station and 160±25 ind./10 cm^2 in July 2001 (new moon) at the lower station. Gastrotrichs, only present at the lower station, registered maximum densities (245±29 ind./10 cm^2) in August 2000 (new moon) and minimum densities (12±3 ind./10 cm^2) in April 2001 (full moon).

The ANOVA results did not show significant differences between the dry season (April-December) and the rainy season (January-March), both for the upper and the lower station.

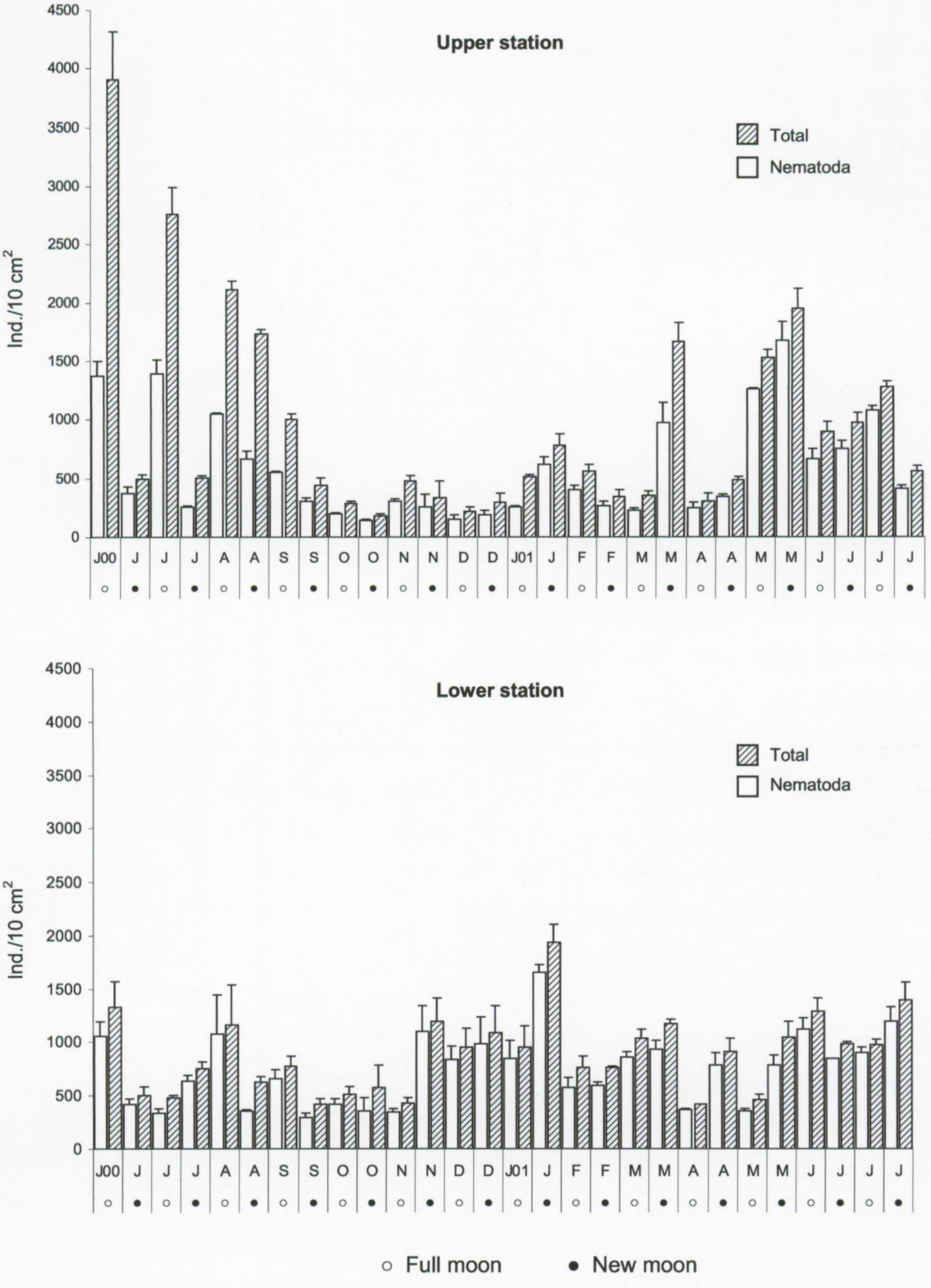


Figure 3.5 **Total meiofauna and nematode densities (ind./10 cm^2) (bars±SE) during the one year sampling period (fortnightly intervals). All calculated by three replicates per date.**

	Upper station				**Lower station**			
Meiofauna	Mean	SE	Min	Max	Mean	SE	Min	Max
Nematoda	586.6	± 83.5	148 (Oct00)	- 1673 (May01)	738.3	± 63.6	298 (Sep00)	- 1652 (Jan01)
Copepoda	274.8	± 86.4	20 (Oct00)	- 2322 (Jun00)	4.5	± 1.1	0	- 20 (Feb01)
Gastrotricha					82.4	± 11.0	12 (Apr01)	- 245 (Aug00)
Tardigrada	42.0	± 20.2	0	- 434 (Aug00)	0.4	± 0.2	0	- 6 (Oct00)
Naupliar larvae	29.1	± 6.3	0 (Jul00)	- 143 (Aug00)	6.1	± 1.1	0 (May00)	- 26 (Oct00)
Turbellaria	13.4	± 1.7	0 (Mar01)	- 33 (Feb01)	48.6	± 7.6	0 (Mar01)	- 160 (Jul01)
Rotifera	7.7	± 2.1	0	- 44 (Jul00)	4.6	± 1.8	0	- 43 (Feb01)
Polychaeta	6.5	± 2.2	0	- 48 (Aug00)	2.4	± 0.5	0 (Sep00)	- 11 (Jan01)
Isopoda	1.0	± 0.3	0	- 5 (Jul00)	0.1	± 0.1	0	- 1 (Feb01)
Halacaroidea	0.9	± 0.2	0	- 5 (Feb01)	0.8	± 0.2	0	- 3 (Mar01)
Ostracoda	0.3	± 0.1	0	- 3 (Sep00)	1.0	± 0.5	0	- 13 (Jun00)
Bivalvia	0.1	± 0.04	0	- 1 (Dec00)	0.6	± 0.2	0	- 3 (Jun00, Jan01)
Oligochaeta	0.1	± 0.1	0	- 2 (Jan01)	0.02	± 0.02	0	- 1
Insecta	0.1	± 0.03	0	- 1 (Mar01)	0.07	± 0.03	0	- 1
Cladocera	0.04	± 0.03	0	- 1 (Mar01)				
Total	962.7	± 166.8	186 (Oct00)	- 3907 (Jun00)	889.9	± 69.0	417 (Apr01)	- 1940 (Jan01)

Table 3.2 Mean of meiofauna taxa densities (individuals/10 cm^2) and standard error of the mean (SE) at the upper and the lower station in San Pedro de Manglaralto beach, from June 2000 until July 2001.

Relationship with environmental data

The relationships between the higher meiofauna taxa densities and the environmental variables such as: pluviosity, SST, salinity, distance (as a proxy for elevation) and median grain size revealed that, the upper station did not show any correlation (only the regression between total meiofauna and nematode densities with distance are given in the figure 3.6). At the lower station, the total meiofauna and nematode densities showed a significant negative correlation with the distance (as a proxy for elevation): a decreasing density was found lower on the beach (Figure 3.6), nevertheless the results of ANOVA did not show significant differences between the dry and the rainy season.

At the lower station the relationship between the residual values of the total meiofauna and the nematodes versus pluviosity indicated that densities deviation from the predicted average value were positively correlated: the more rainfall, the higher total meiofauna and nematode densities (Figure 3.7). The ANOVA results showed significant differences ($p< 0.01$) between the dry and rainy season, indicating a seasonal respond to the total meiofauna and nematode densities.

DISTANCE

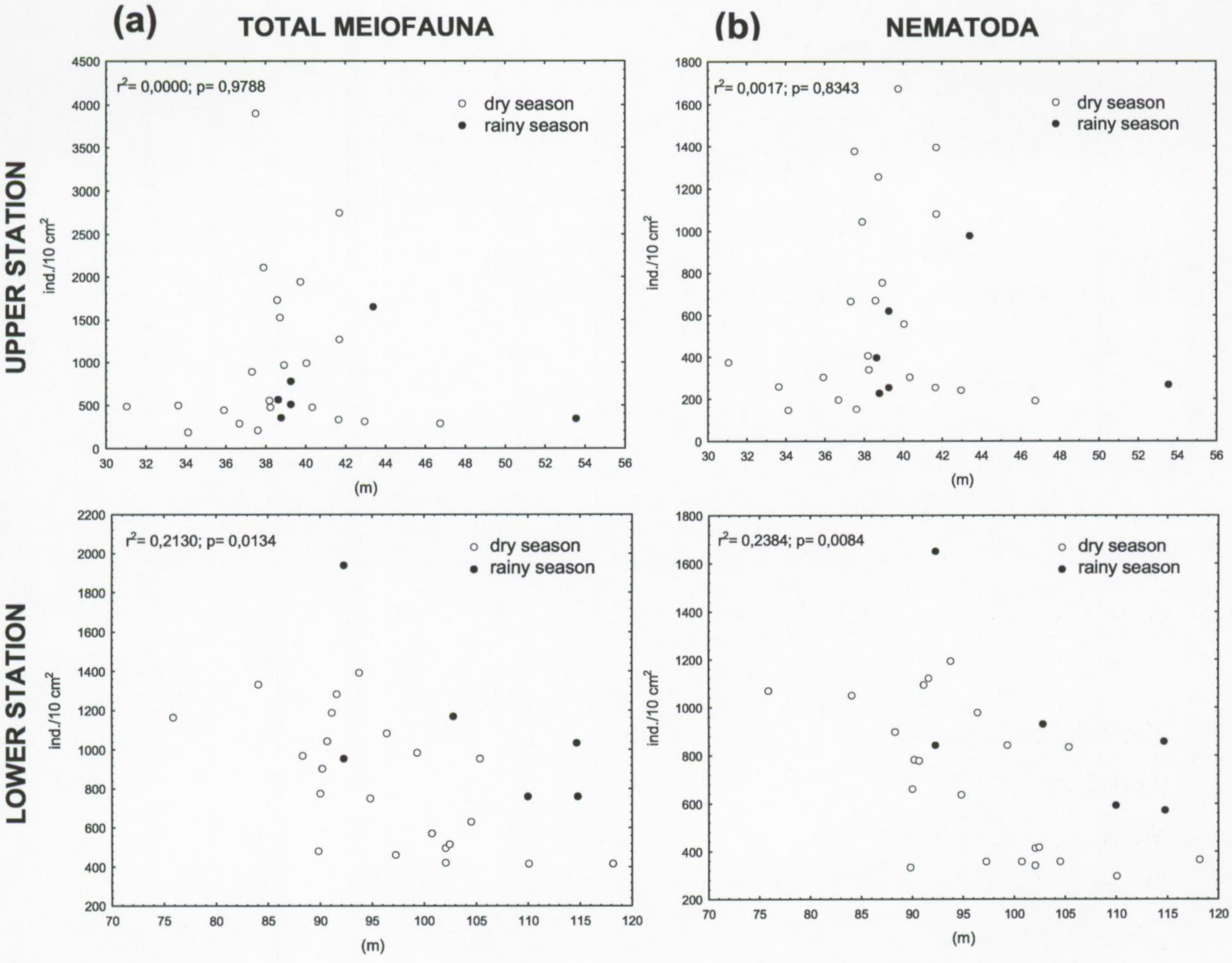


Figure 3.6 **Relationship between the sampling distance (as a proxy for elevation) and (a) the total meiofauna density and (b) the nematode density at upper and lower station; the sampling of the dry and the rainy season are indicated separately.**

PLUVIOSITY

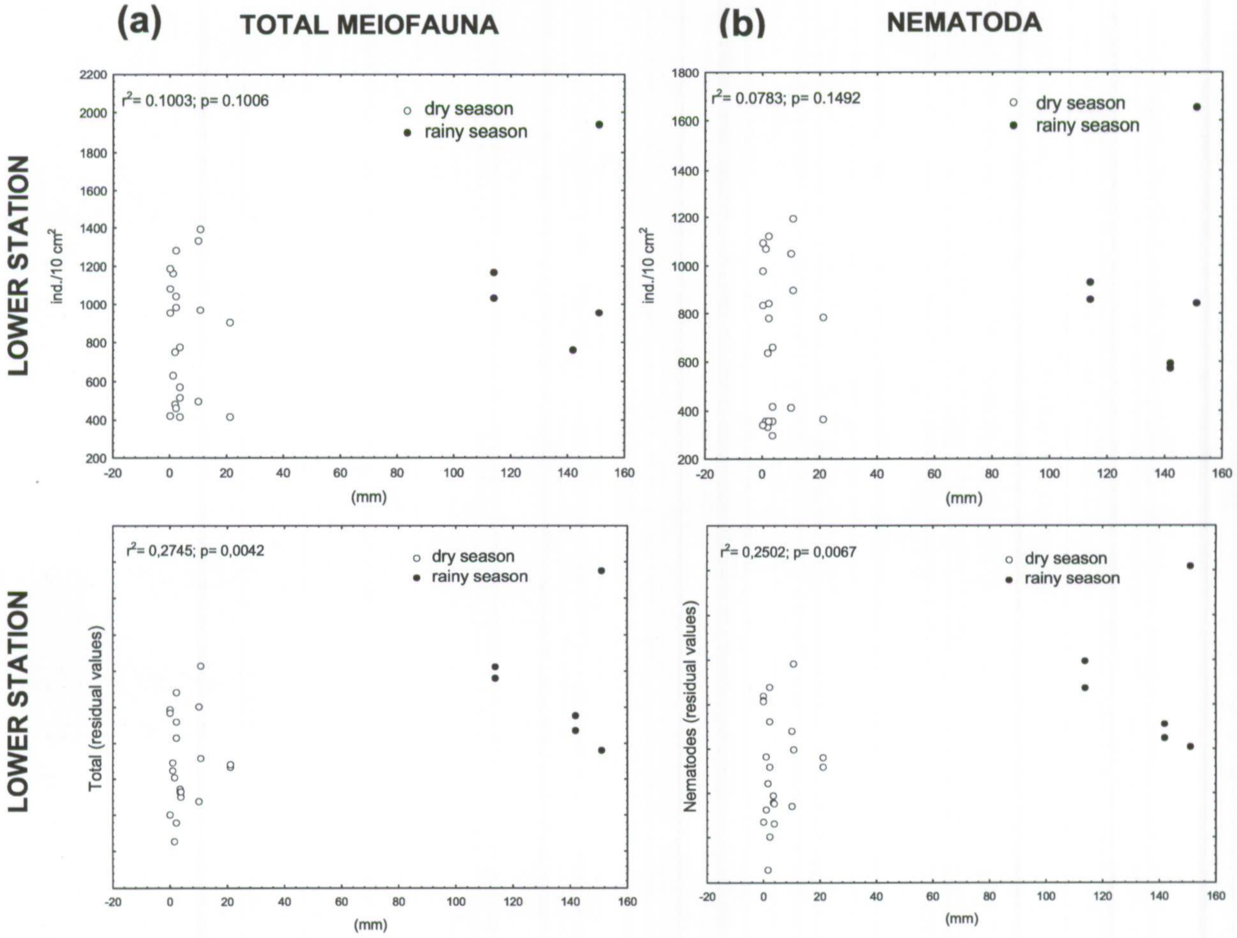


Figure 3.7 **Relationship between the pluviosity and (a) the total meiofauna density and (b) the nematode density at the lower station; the sampling of the dry and the rainy season are indicated separately.**

DISCUSSION

The meiofauna composition of an intermediate-reflective exposed sandy beach in Ecuador shows clear differences between the high tide level (high abundance of nematodes and copepods) and the low tide level (mainly high abundance of nematodes) and with the season (increasing densities during rainy season at the lower station). The beach is under a relatively low anthropogenic pressure, where is almost no tourism (AERTS *et al.*, 2004).

Most studies on the composition of meiofauna of sandy beaches refer to cross-shore variability (ANSARI *et al.*, 1984; OLAFSSON, 1991; RODRÍGUEZ *et al.*, 2001; GHESKIERE *et al.*, 2002; KOTWICKI *et al.,* 2005 and GHESKIERE *et al.*, 2005) and not so much to temporal variability (GOURBAULT *et al.*, 1998; COVAZZI *et al.*, 2000; HOOGE, 1999 and DEUDERO AND VINCX, 2000). The effect of dry-rainy seasonality, as is the case in Ecuador, was not documented yet for the meiofauna assemblage structure of beaches. In general, the very few studies on the composition of intertidal sandy beach meiofauna in the tropics (GOURBAULT *et al.*, 1998; and ANSARI *et al.*, 1984) also reveal very different results regarding temporal and cross-shore patterns.

The 'long term' temporal variability of 23 beaches in Guadeloupe (GOURBAULT *et al.*, 1998) was investigated from April 1979 until November 1984 (divided over 6 sampling dates). No clear patterns could be detected and the spatial variability was much higher than the temporal variability. The higher meiofauna taxa recorded was correlated with sediment grain size and calcium carbonate content. The locations with the coarsest sediment were dominated by harpacticoid copepods and the stations with finer sediments (low calcium carbonate) were generally dominated by nematodes, followed by tardigrades.

At a sheltered sandy beach in Mombasa, Kenya (ANSARI *et al.*, 1984) the highest densities of meiofauna occurred around the high tide level (2502 ind./10 cm^2) and the densities dropped gradually (1268 ind./10 cm^2) towards the low tide level, while at an exposed sandy beach the meiofauna was aggregated downshore and the highest densities were recorded between mid and low tide level (2560 and 2131 ind./10 cm^2 respectively) and decreased towards high tide level (1717 ind./10 cm^2). On both beaches, the meiofauna was dominated by nematodes (48% at the sheltered beach and 62% at the exposed beach) followed by copepods (25 and 13% respectively).

Significant differences in the total meiofauna densities were detected between the sheltered and the exposed beach.

The interstitial fauna of beaches is extremely difficult to compare for the different geographical areas (cf. MCLACHLAN AND TURNER, 1994) since very high variability is present in the morphodynamics of the beaches (gradients from reflective over dissipative), the tidal regime level (macro-micro tidal), the nature of the substrate (volcanic, quartz), the seasonality (polar, temperate, tropical) and the anthropogenic influence on the substrate (e.g. tourism).

In San Pedro de Manglaralto, an exposed and intermediate-reflective Ecuadorian sandy beach, fifteen meiofauna taxa were found and Nematoda were dominant representing 61% and 83% of the total meiofauna density at the high and low tide level respectively, followed by Copepoda (29%) at the upper station, and Gastrotricha (9%) at the lower station. The results showed a trend of decreasing of average meiofauna density from the upper station (963±167 ind./10 cm^2) towards the lower station (890±167 ind./10 cm^2) on the beach; nevertheless not significant differences between both stations were found.

The meiofauna assemblage on the southwest coast of Iceland varied considerably both between and within the beaches (OLAFSSON, 1991). The beaches were different in substrate, ranging from exposed coarse volcanic sands to sheltered sandy beaches. At a very exposed beach consisting of very coarse volcanic sand, the density of turbellarians was highest at the low tide level (up to 490 ind./10 cm^2 or 92 % of the total meiofauna), and the nematodes increased towards the high tide level, from 25 ind./10 cm^2 to 257 ind./10 cm^2, representing 5 and 59% of the total meiofauna respectively. At another beach, classified as rather exposed and consisting of medium fine shell sand, the Gastrotricha dominated the lower station (89%), while nematodes dominated the mid and upper stations (58 and 69% respectively). Copepoda reached 70% of the meiofauna at the upper station of the beach consisting of extremely coarse volcanic sands (highly exposed beach); and at the sheltered beach no group dominated, nevertheless the lowest densities of total meiofauna and nematodes were registered at the high tide level.

Taking into account literature data (including this study) did not show clear meiofauna cross-shore patterns regarding beach type (sheltered versus exposed). However the general increase in nematode densities towards the low tide level is noted in some sandy beaches (MCINTYRE, 1968; GRAY AND RIEGER, 1971; HARRIS, 1972; GHESKIERE *et al.*, 2002; GHESKIERE *et al.*, 2005 and KOTWICKI *et al.*, 2005) although some exceptions with highest densities in the upper beach zone exist (RODRÍGUEZ *et al.*, 2001).

Along the Belgian coast, at De Panne, a macrotidal dissipative sandy beach (GHESKIERE *et al.*, 2002), eleven meiofauna taxa were recorded and Nematoda were dominant (76-97%) followed by Turbellaria. The total meiobenthic densities increased from high tide (56±13 ind./10 cm^2) towards the low tide level (1470±303 ind./10 cm^2) as a consequence of tidal exposure gradients. The study of KOTWICKI *et al.* (2005) confirmed the intertidal zonation trend at De Panne: the average abundance of nematodes decreased from the high tide level (81 ind./10 cm^2) towards the low tide level (2663 ind./10 cm^2).

The Mediterranean and Baltic meiofauna study across the beach slope on microtidal beaches (GHESKIERE *et al.*, 2005) (tidal range between 0.1 and 0.5 m) showed that the meiofauna assemblage structure denoted a clear cross-shore pattern and meiofauna composition was related with anthropogenic impact (tourism). The upper zone was more dissimilar in assemblage composition than the middle and the lower zones, which was attributed to the absence of Insecta, Copepoda and Oligochaeta in the Mediterranean tourist beach.

The patterns in meiofauna abundance and biomass (RODRÍGUEZ *et al.*, 2001) at microtidal (around 2 m) sandy beaches, located in southern Chile were studied along a gradient of morphodynamic beach types. The results showed that, depending on the sediment grain size, the highest average meiofauna density and biomass were found at the reflective beach (6172 ind./10 cm^2) as compare with the intermediate beach (3390 ind./10 cm^2) and the dissipative beach (3667 ind./10 cm^2). Also the highest meiofaunal densities occurred at the upper station of each beach. In the reflective beach with coarse sand, the meiofauna density was 4939 ind./10 cm^2 at the high tide level and 2515 ind./10 cm^2 at the low tide level; in the intermediate beach with medium grain sand, meiofauna densities ranged between 5500 ind./10 cm^2 (HW) and 868 ind./10 cm^2 (LW); and in the dissipative beach with fine grain sand, meiofauna densities ranged between 3619 ind./10 cm^2 (HW) and 2315 ind./10 cm^2 (LW).

According to HOOGE (1999), the distribution of meiofauna abundance on northern California beaches was influenced by the median grain size, air exposure percentage and sediment saturation at mid and low water stations. At a Mediterranean beach, COVAZZI *et al.* (2000) found that the very low absolute meiofauna densities, were consistent with the low sedimentary organic matter content; also clear seasonal changes were related to temperature between summer and winter: nematodes were generally the dominant taxon in winter (on average 77% of the total meiofaunal density) whilst copepods generally dominated in summer (on average 63% of the total meiofaunal density).

In our study, total meiofauna densities ranged from 186±14 ind./10 cm^2 in October 2000 (new moon) to 3907±408 ind./10 cm^2 in June 2000 (full moon) at the upper station; while at the lower station density ranged from 417±5 ind./10 cm^2 in April 2001 (full moon) to 1940±166 ind./10 cm^2 in January 2001 (new moon). At the upper station no correlations between higher meiofauna taxa and the environmental variables were detected; whilst at the lower station the distribution of total meiofauna and nematode density were influence by the distance (as a proxy for elevation). Also the highest total meiofauna and nematode densities were positively correlated with the highest rainfall. The results revealed significant differences in seasonal variability linked to wet and dry seasonality

ACKNOWLEDGEMENTS

This study was done with the financial support of the VLIR-ESPOL program (1999-2008). The first author acknowledges the staff of Marine Biology Section from Gent University for the assistance in the statistical analysis. We are grateful to Nancy Fockedey, Jan Wittoeck, Sonnia Guartatanga, Verónica Ruiz and Luis Domínguez for the sampling campaigns.

CHAPTER IV

Temporal variability in the composition and biodiversity of free-living marine nematodes in a tropical beach (Ecuador)

Paper prepared as

CALLES A, CORNEJO M.P, DEGRAER S, VINCX M.
(abstract submitted)

Temporal variability in the composition and biodiversity of free-living marine nematodes in a tropical beach (Ecuador). *Special Issue on Earth Observation for Biodiversity and Ecology*

ABSTRACT

Free-living marine nematodes are the dominant metazoans in sandy beaches and are considered as indicators for environmental changes. In order to detect the influence of environmental variables such as pluviosity, temperature, salinity, chlorophyll *a*, organic matter and median grain size on the nematode assemblages, inhabiting the lower tide level at an exposed Ecuadorian sandy beach were monthly sampled from June 2000 to July 2001, covering the dry (April-December) and rainy season (January-March). This period had undergone a strong La Niña cold event. Thirty seven nematode species belonging to 30 genera were found, with dominance of *Daptonema* and *Metachromadora*. those species has been reported from estuarine sites and they are able to tolerate salinity changes. The total nematode densities ranged from 359±11 ind./10 cm^2 (April 2001) to 1170±119 ind./10 cm^2 (June 2000), no significant differences between dry and rainy season were detected. The maximum nematode densities registered in Ecuador are 50% lower than in the beaches in the Mediterranean and North Sea, but 90% higher comparing with the Baltic Sea. The non-selective deposit feeders were the most abundant feeding group at the nematode community (43%), although with fluctuating dominance (4-90%). Based on the species composition analysis, sample groups were detected by ordination, reflecting the following temporal pattern: (I) June-December, (II) January and (III) February-May. Dissimilarities (71%) were found between the species of the group II and III, explained principally by highest densities of *Daptonema* sp. 1 (490±197 ind./10 cm^2) and *Rhynchonema* cf. *hirsutum* (163±18 ind./10 cm^2) at the group II; *Ceramonema* sp. 1 (208±50 ind./10 cm^2) and *Ceramonema* sp. 2 (75±15 ind./10 cm^2) at group III. The *k*-dominance curves confirmed this trend, lowest diversity and highest dominance in January 2001 versus lowest dominance and highest diversity between June-December 2000. Evenness and Simpson diversity index revealed significant differences between seasons, with lowest values 0.63 and 0.70 respectively, in January 2001. The temporal variability of *Daptonema* sp. 1 and *Viscosia* sp. 1 is coincides with the pluviosity fluctuations, but only seasonal respond were detected to *Daptonema* sp. 1, which at the maximum rainfall, the density increased.

KEY WORDS: free-living marine nematodes; diversity index; exposed sandy beach.

INTRODUCTION

Although nematodes are among the most abundant metazoans in marine sediments, only few papers, apart from purely taxonomic ones, have described the nematode species composition at intertidal sandy beaches (GOURBAULT *et al.*, 1995; GHESKIERE *et al.,* 2002, 2004, 2005; and URBAN-MALINGA *et al.*, 2004) and their seasonal variability (SHARMA AND WEBSTER, 1983; GOURBAULT, 1998; NICHOLAS AND HODDA, 1999 and NICHOLAS, 2001). This is probably due to the time-consuming species identification process and the overall high species diversities of the nematode assemblages. Free-living marine nematodes do have several favourable features for using them as bio-indicators of environmental conditions (BONGERS AND FERRIS, 1999 and SCHRATZBERGER AND WARWICK, 1999) and it is known from experiments that they are ecologically very heterogeneous and occupy different positions in benthic food webs (AARNIO, 2001). However, quantitative data at the nematode species level from tropical sandy beaches is scarce (CALLES *et al.*, 2005). Geographically located in the equatorial tropical climate region, the Ecuadorian coast is strongly influenced by anomalous El Niño and La Niña events every 2-8 years (SANTOS, 2006). This causes fluctuating climatic conditions, which can have an effect on several sensitive marine living organisms. Baseline data describing the species diversity and community structure are needed to investigate the importance of nematodes for the sandy beach ecosystem and is a first step to detect eventual effects of climatic variability on the coastal ecosystem. In the intertidal habitats, the littoral zones can experience exposures to the atmosphere ranging between a few minutes at spring low tide levels to almost permanent exposure except when covered by sea water once a month during spring high tides. The effect of the differing of cyclical immersion and emersion on the osmotic pressure of the interstitial fluids can vary. Salinity of the upper layers of sediment may reduce due to precipitation and terrestrial surface water run-off (FORSTER, 1998). In their review of marine nematode ecology, HEIP *et al* (1985) compiled an extensive list of marine and estuarine species with their salinity tolerances.

The present study describes the monthly variability from June 2000 to July 2001 of the free-living nematode densities, diversity (at species level) and assemblages and their relationship with environmental factors (pluviosity, sea surface temperature, salinity, distance as a proxy for elevation, chlorophyll *a*, organic matter and median grain size). This period had undergone a strong La Niña phase, after the 1997-98 El Niño

(MCPHADEN, 1999). Three climate seasons were monitored: two dry periods (June-December 2000 and April-July 2001) and one rainy period (January-March 2001). These months are the 'common' rainy and dry seasons along the Ecuadorian coasts (CORNEJO, 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 III, Figure 3.1). The samples were taken in front of the Centro Nacional de Acuicultura e Investigaciones Marinas (CENAIM). The beach is classified as an intermediate beach (Ω =1.2) but near to the reflective characteristics. The width of the intertidal zone is about 120 m with a Relative Tide Range of 4.2 m.

Sampling strategy and environmental factors

Sampling was done monthly from June 2000 until July 2001 during the spring tides (full moon) at low tide level; two replicates were investigated. Samples were obtained by forcing a hand core (sampling surface area 10 cm^2), to 20 cm depth in the sediment. The samples (except those for sedimentological analyses) were fixed at 60 ºC with a 4% buffered formaldehyde water solution. 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 (01º 55' 53" S, 80º 46' 55" W), and pluviosity data from the CENAIM-ESPOL (Escuela Superior Politécnica del Litoral) foundation. *In situ* water samples were taken and passed through Whatman GF/C filters (47 mm ϕ, porosity 1.2 μ) for the determination of chlorophyll *a* (Chl *a*) by spectrophotometry (PARSONS *et al.,* 1984), suspended particulate matter (SPM) was measured by weight difference (filters were dried at 60 °C/48h) and particulate organic matter (POM) by subsequently burning filters at 550°C for 2 hours. The concentration unit of water samples was measured in milligrams per litre (mg/l).

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).

Laboratory treatment and Nematoda identification

In the laboratory, samples were rinsed with a gentle jet of tap water over a 1 mm sieve to exclude macrofauna, decanted ten times over a 38 µm sieve, centrifuged three times with Ludox® HS 40 (at 1.18 density) and stained with Rose Bengal.

Nematodes were counted under a stereomicroscope and 200 individuals from each replicate were picked out randomly using a stereomicroscope, transferred through ethanol-glycerol solutions and mounted on glass slides (VINCX, 1996). The identification to genus level was done using the pictorial keys of Platt and WARWICK (1983, 1988) and WARWICK *et al.* (1998). The identification up to species was done using the librarian collection of the Marine Biology Section of Ghent University and nematode classification up to family level was based 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, were used to investigate the nematode trophic structure.

Data analysis

The analysis were applied to the nematode densities (ind./10 cm^2) of two replicates per sampling location. The number of species per sample (S), the expected number of species present in a population of 100 individuals (ES (100)), (HULBERT, 1971; SANDERS, 1968), Pielou´s evenness (J'), Simpson Index (1-λ') and Hill´s diversity numbers N_1 and N_{inf} (HILL, 1973) were calculated. Diversity patterns were visualized by k-dominance curves (LAMBSHEAD *et al.*, 1983).

Multivariate analysis was performed using standardised non-transformed data. The nematode species composition was ordinated by non-metric Multi-Dimensional Scaling (nMDS). One-way ANOSIM was used to test the significant differences between the species groups. Similarity percentage analysis (SIMPER) was applied to identify the species primarily providing the discrimination between the groups. The multivariate analysis was realized using PRIMER v5 software package (CLARKE AND GORLEY, 2001).

One-way ANOVA was applied to test differences in density and richness measures between dry and rainy season. The relationship between nematode species and environmental factors was analysed using Pearson product-moment correlation. The normal distribution of the data was checked by the Kolmogorov-Smirnov test. Levene's test was used to verify the homogeneity of variances prior to the analysis. Statistical analysis was performed using the STATISTICA v6 software package (STATSOFT, 2001).

RESULTS

Environmental factors

The SST varied from 21.9 °C (July 2000) to 27.5 °C (March 2001). The salinity of the water ranged between 32.5 PSU (February 2001) and 34 PSU (July 2000). The pluviosity registered the maximum values in January 2001 (150.9 mm) and March 2001 (113.8 mm). The chlorophyll *a* ranged from 1.2 mg/l (November 2000) to 11 mg/l (April 2001). POM varied from 10.5 mg/l (July 2000) to 365.4 mg/l (June 2001), while SPM concentrations varied from 111.8 mg/l (July 2000) to 4686.4 mg/l (June 2001). The ratios Chl *a*/SPM and Chl a/ POM were determined as a value of organic matter quality. The median grain size of the sediment ranged between 191-260 µm, corresponding to fine-medium sand (Table 4.1).

months	Chl *a* (mg/l)	SPM (mg/l)	POM (mg/l)	median grain size (um)	distance (proxy for elevation) (m)	SST (°C)	salinity (PSU)	pluviosity (mm)	Chl *a* /SPM	Chl *a* /POM
J00	-	-	-	245	84.0	23.6	33.8	9.9	-	-
J	3.4	111.8	10.5	212	89.8	22.0	34.0	1.5	0.030	10.7
A	1.8	-	-	219	75.8	22.7	33.9	1.0	-	-
S	2.0	478.4	249.0	244	90.0	22.6	33.9	3.3	0.004	1.9
O	2.9	483.2	23.9	260	102.4	24.0	33.8	3.5	0.006	20.2
N	1.2	1392.4	78.3	223	102.0	22.5	33.9	0.0	0.001	17.8
D	3.5	4368.0	147.7	211	105.3	25.1	33.6	0.0	0.001	29.6
J01	1.6	547.6	31.4	223	92.3	25.3	32.9	150.9	0.003	17.5
F	3.4	1331.2	70.1	238	114.8	27.5	32.5	141.6	0.003	19.0
M	2.9	-	-	241	114.6	27.5	33.8	113.8	-	-
A	11.0	295.7	-	194	118.1	27.4	32.5	21.1	0.037	-
M	-	3467.0	284.9	214	97.2	25.4	33.6	2.2	-	12.2
J	7.1	4686.4	365.4	241	91.6	23.1	33.9	1.9	0.002	12.8
J	4.0	128.8	20.7	191	88.3	22.4	33.9	10.5	0.031	6.2

Table 4.1 Environmental factors.

Nematode species composition, density and diversity

5567 specimens of nematodes were identified, belonging to 37 species, 30 genera and 17 families. Among the 17 families, Xyalidae were most dominant in densities (43%), number of genera (8) and number of species (12) (Table 4.2).

The total density of nematodes was highest in June 2000 (1170±119 ind./10 cm^2) and lowest in April 2001 (359±11 ind./10 cm^2), no significant differences between dry and rainy season were detected. However density fluctuations were observed along the year but with an increasing trend in January 2001 (948±233 ind./10 cm^2) (Figure 4.1).

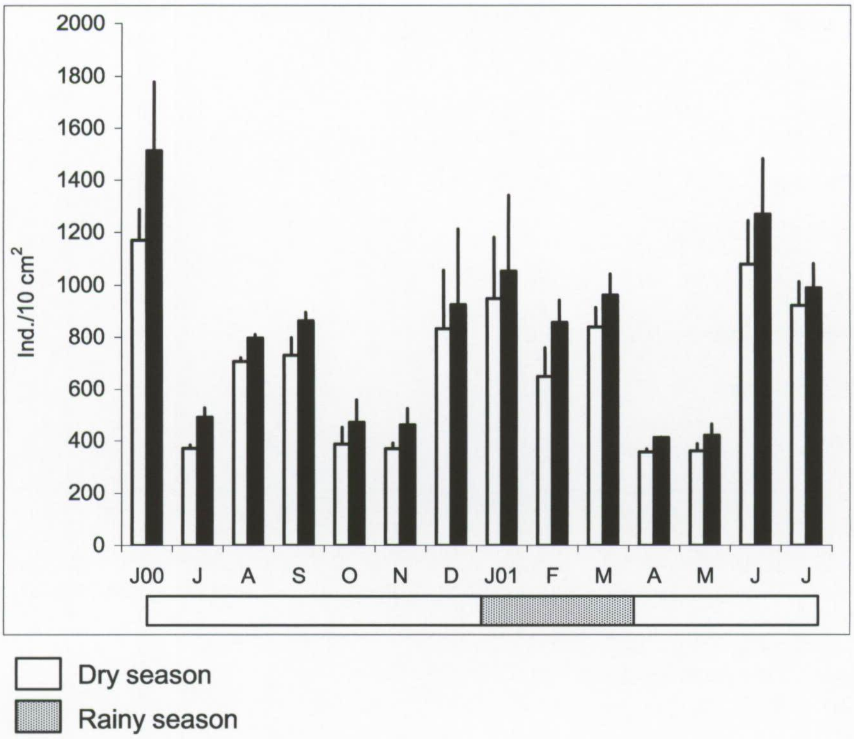


Figure 4.1 **Mean densities and standard errors of the mean (n=2) per month (June 2000-July 2001) for nematode densities (white bars) and total meiobenthic densities (black bars) at San Pedro de Manglaralto beach.**

Family	Percentage of total	Number of genera	Number of species
Xyalidae	42.55	8	12
Ceramonematidae	27.33	2	3
Desmodoridae	11.43	1	1
Cyatholaimidae	4.87	2	3
Axonolaimidae	4.47	1	1
Microlaimidae	3.37	1	1
Oncholaimidae	1.79	1	2
Anticomidae	1.64	1	1
Chromadoridae	0.68	2	2
Tripyloididae	0.62	1	1
Oxystominidae	0.49	1	1
Enchelidiidae	0.28	3	3
Anoplostomatidae	0.18	1	1
Thoracostomopsidae	0.15	1	1
Leptolaimidae	0.10	2	2
Selachinematidae	0.03	1	1
Linhomoeidae	0.03	1	1
TOTAL	100	30	37

Table 4.2 **Overall relative abundance of nematode families collected at San Pedro de Manglaralto beach, listed in descending order of dominance, with indication of the number genera and species found.**

The temporal distribution of the species richness was more or less constant throughout the year; the highest value (21±1 sp.) was registered in April 2001, concomitant with highest Chl *a*, and the lowest (15±3 sp.) in July 2001 (Table 4.3). The evenness and Simpson index expressed as (J') and (1-λ'), respectively, were significantly different ($p<0.05$) between dry and rainy season, being lowest in January 2001, suggesting, together with N_{inf}, a higher dominance of some species (*i.e. Daptonema* sp. 1, *Viscosia* sp. 1).

Months	N	S	J'	ES (100)	1-λ'	N_1	N_{inf}
J	1170 ± 119	17 ± 2	0.86 ± 0.011	14.28 ± 1.25	0.89 ± 0.001	11.03 ± 0.52	5.18 ± 0.41
J	373 ± 12	19 ± 2	0.85 ± 0.002	16.91 ± 1.21	0.89 ± 0.011	12.12 ± 1.00	5.11 ± 0.77
A	706 ± 15	16 ± 0	0.79 ± 0.043	13.32 ± 0.40	0.84 ± 0.035	8.99 ± 1.06	3.38 ± 0.81
S	729 ± 68	18 ± 1	0.76 ± 0.002	13.40 ± 0.63	0.83 ± 0.002	8.71 ± 0.13	2.98 ± 0.05
O	388 ± 64	19 ± 1	0.76 ± 0.016	15.23 ± 0.10	0.84 ± 0.015	9.17 ± 0.25	3.46 ± 0.31
N	371 ± 21	19 ± 2	0.81 ± 0.033	15.90 ± 1.55	0.87 ± 0.023	10.73 ± 1.71	4.17 ± 0.47
D	832 ± 225	18 ± 0	0.86 ± 0.015	15.66 ± 0.12	0.90 ± 0.008	11.96 ± 0.52	6.07 ± 0.72
J	948 ± 233	17 ± 1	0.63 ± 0.071	12.86 ± 1.48	0.70 ± 0.075	6.11 ± 1.43	2.08 ± 0.36
F	650 ± 109	18 ± 1	0.75 ± 0.077	13.88 ± 0.54	0.82 ± 0.067	8.74 ± 2.08	3.68 ± 1.48
M	838 ± 76	19 ± 1	0.75 ± 0.021	14.74 ± 0.33	0.83 ± 0.026	9.02 ± 0.72	3.60 ± 0.85
A	359 ± 11	21 ± 1	0.72 ± 0.055	17.15 ± 1.33	0.81 ± 0.059	9.28 ± 1.84	2.96 ± 0.85
M	362 ± 27	17 ± 1	0.76 ± 0.009	13.25 ± 0.55	0.86 ± 0.002	8.66 ± 0.16	4.48 ± 0.04
J	1078 ± 166	18 ± 1	0.79 ± 0.024	14.27 ± 1.20	0.86 ± 0.007	9.75 ± 0.89	3.87 ± 0.26
J	921 ± 92	15 ± 3	0.65 ± 0.032	11.70 ± 2.60	0.72 ± 0.037	5.92 ± 1.26	2.11 ± 0.13

Table 4.3 **Species number (N), species richness (S), Evenness (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 and standard errors of the mean (n= 2 replicates).**

Temporal variability of the nematode species

The variation of the relative composition of the Nematode species over the sampling year is given in the figure 4.2. Also the list of the nematode species recorded at the lower station and their corresponded densities are given in the table 4.4.

Some species have a limited distribution in time, such as *Camacolaimus* sp., *Ditlevsenella* sp. and *Metadesmolaimus* sp. 2; they are restricted to January-February 2001, February-April 2001 and March-July 2001 respectively (Table 4.4).

The results of ANOVA analysis for differences between seasons for nematode densities are given in the table 4.5. There were no significant differences between rainy and dry seasons, concerning nematode species density recorded, except to *Daptonema* sp. 1, (ANOVA, $p<0.01$).

The temporal variability of the 12 dominant species is showed in the figure 4.3. Several of the most of the dominant species, registered the highest densities between June (2000, 2001) and August 2000. *Ceramonema* sp. 1 had higher relative density (19%) on the overall nematode composition, the highest densities occurred in June (2000 and 2001) and July (2000 and 2001), followed by a decline of the density; the densities remained constant along the sampling year, but a decrease in early rainy season was observed. Similar pattern of density fluctuations were found in *Ceramonema* sp. 2, which represented 8% of the total nematode density, with the highest densities in June (2000 and 2001) and the lowest in January 2001.

Daptonema sp. 1 represented 13% of the total nematode species. The temporal variation of this species is different from *Ceramonema* species. Indeed opposite trends were observed: the highest values were obtained in January 2001 and March 2001 (rainy season), followed by a subsequent density decline; the lowest densities being attained in dry season (May-December 2001).

The third most abundant species was *Rhynchonema* cf. *hirsutum* (12%). There is not a clear trend in the densities occurred along the year; the densities increased from June 2000 until September 2000, where the maximum densities occurred; followed by a decline until November 2000, increasing again between December 2000 and February 2001, followed by a great reduction.

The temporal patterns of *Metachromadora* cf. *gerlachi*, comprised 11% of the total nematode densities; *Metadesmolaimus* sp. 1 and *Gonionchus ecuadoriensis* sp. n., each one comprising 5% of the total nematode densities, were similar. The highest densities occurred between June (2000, 2001) and August 2000 followed by a sharp decline.

The densities of *Parodontophora* sp. 1 (5%), showed a subsequently density increase from June 2000 until March 2001, the maximum densities being reached in May 2001.

The temporal patterns observed in *Paracyatholaimus* sp. 1 (4%) and *Omicronema* sp. 1 (2%) were similar; the highest densities were registered in June 2000 and August 2000 respectively, followed by density fluctuations to increase again in June and July 2001, nevertheless the densities of *Omicronema* sp. 1 disappeared in July 2001.

Microlaimus sp. represented 4% of the total nematode species and registered very low densities between June 2000 and February 2001. However, in March 2001 the densities increased and remained constant until July 2001.

Viscosia sp. 1 represented 2% of the total nematode species. The temporal variation of this species is similar to the trends observed in *Daptonema* sp. 1 species: the highest values were obtained in January 2001, followed by a subsequent density decline until May 2001, and increase again in June and July 2001.

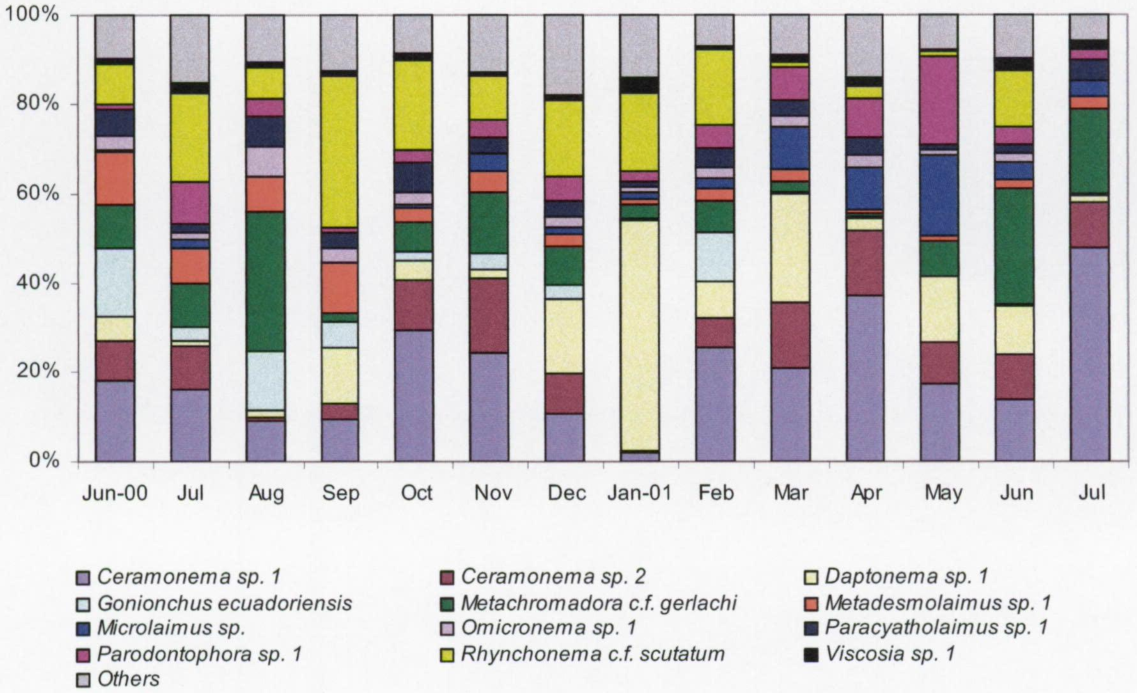


Figure 4.2 **Monthly variation of the relative composition of Nematode species at the lower station in San Pedro de Manglaralto beach (June 2000-July 2001).**

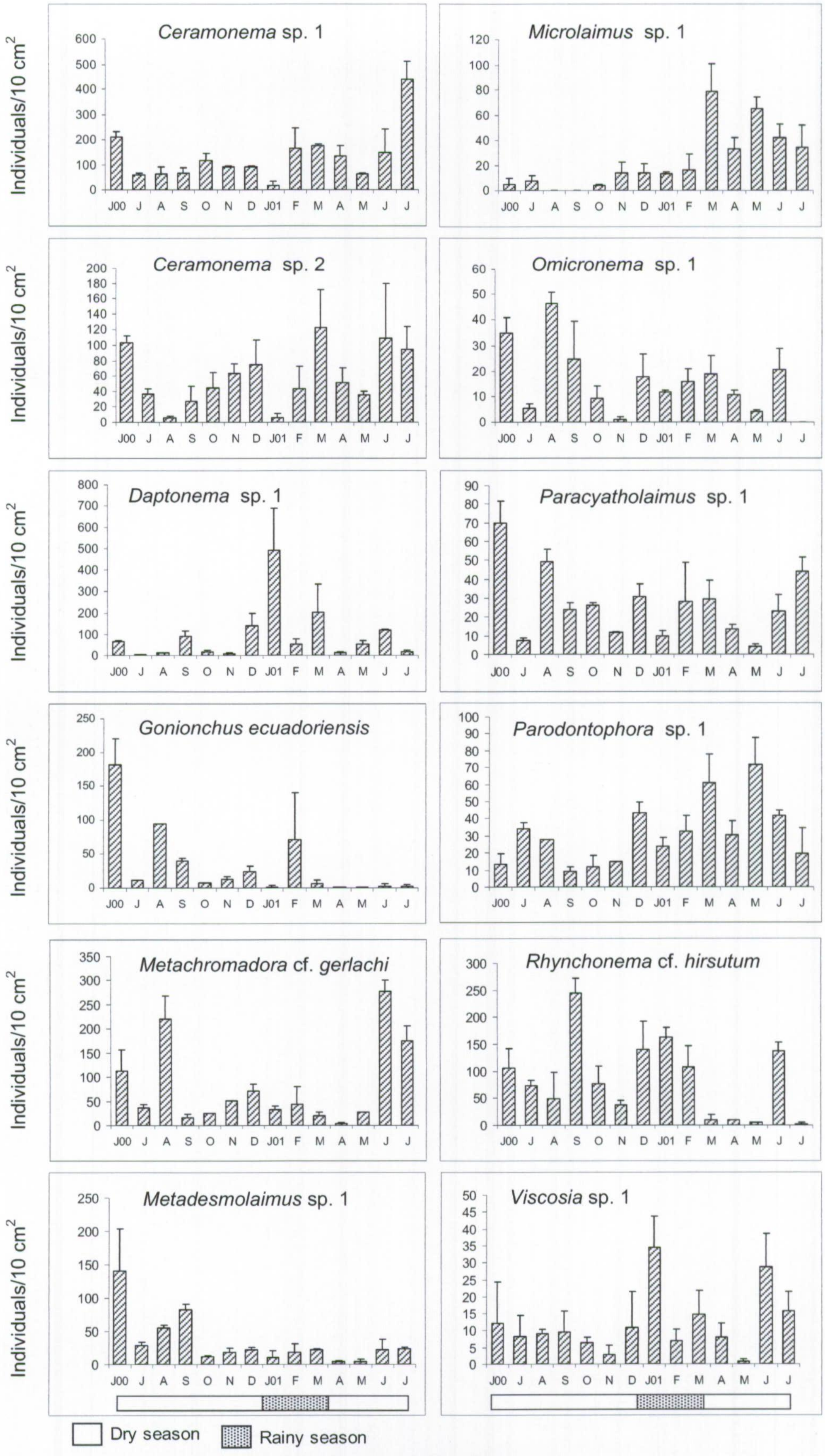


Figure 4.3 **Mean densities and standard errors (n=2) per month (June 2000-July 2001) of the 12 dominant Nematoda genera at San Pedro de Manglaralto.**

Nematode species:			Jun-00	Jul	Aug	Sep	Oct	Nov	Dec	Jan-01	Feb	Mar	Apr	May	Jun	Jul
	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	Av SE
Anoplostoma sp.	1B	0.18	0 ± 0	3 ± 3	0 ± 0	2 ± 2	0 ± 0	0 ± 0	0 ± 0	5 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8 ± 2	0 ± 0
Bathylaimus sp.	1B	0.62	0 ± 0	0 ± 0	9 ± 5	2 ± 2	0 ± 0	0 ± 0	0 ± 0	34 ± 34	0 ± 0	4 ± 4	5 ± 5	1 ± 1	0 ± 0	4 ± 4
Camacolaimus sp.	2A	0.05	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	2 ± 2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
**Ceramonema* sp. 1	1A	18.91	211 ± 20	60 ± 7	64 ± 26	67 ± 20	115 ± 29	90 ± 5	90 ± 6	18 ± 18	165 ± 81	175 ± 8	134 ± 42	62 ± 4	148 ± 96	440 ± 71
Ceramonema sp. 2	1A	8.40	104 ± 9	36 ± 7	6 ± 2	27 ± 20	44 ± 21	64 ± 12	75 ± 32	5 ± 5	43 ± 29	123 ± 48	52 ± 19	35 ± 5	109 ± 71	94 ± 30
Cobbia sp.	2A	0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Daptonema sp.	1B	0.14	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	2 ± 2	0 ± 0	8 ± 4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0
Daptonema sp. 1	1B	13.21	65 ± 4	5 ± 1	11 ± 1	92 ± 22	16 ± 10	7 ± 5	140 ± 57	490 ± 197	55 ± 22	203 ± 129	11 ± 4	53 ± 18	121 ± 1	15 ± 10
Daptonema sp. 2	1B	0.64	2 ± 2	7 ± 1	3 ± 3	4 ± 0	1 ± 1	3 ± 3	9 ± 3	18 ± 11	0 ± 0	0 ± 0	4 ± 2	3 ± 3	2 ± 2	6 ± 6
Daptonema sp. 3	1B	0.37	20 ± 20	3 ± 3	0 ± 0	14 ± 14	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Dasynemoides sp.	1A	0.02	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	1 ± 1	0 ± 0	0 ± 0
Dichromadora sp.	2A	0.03	0 ± 0	0 ± 0	2 ± 2	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ditlevsenella sp.	2B	0.11	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 0	6 ± 2	1 ± 1	0 ± 0	0 ± 0	0 ± 0
Enoplolaimus sp.	2B	0.15	0 ± 0	1 ± 1	0 ± 0	2 ± 2	1 ± 1	0 ± 0	0 ± 0	2 ± 2	0 ± 0	2 ± 2	2 ± 2	0 ± 0	5 ± 5	0 ± 0
Eumorpholaimus sp.	1B	0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 1	0 ± 0	0 ± 0	0 ± 0
Eurystomina sp.	2B	0.07	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	2 ± 2	3 ± 3	0 ± 0	2 ± 2	0 ± 0
**Gonionchus ecuadoriensis*	2A	4.72	181 ± 39	11 ± 1	94 ± 0	40 ± 3	8 ± 1	13 ± 4	25 ± 7	2 ± 2	71 ± 69	6 ± 6	1 ± 1	1 ± 1	3 ± 3	3 ± 3
Halalaimus sp.	1A	0.49	3 ± 3	0 ± 0	2 ± 2	2 ± 2	2 ± 0	5 ± 3	10 ± 1	2 ± 2	1 ± 1	2 ± 2	6 ± 1	4 ± 2	6 ± 6	2 ± 2
Leptolaimus sp.	1A	0.05	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	2 ± 2	0 ± 0	0 ± 0	0 ± 0
Metachromadora cf. *gerlachi*	2B	11.43	112 ± 44	36 ± 7	220 ± 48	16 ± 8	26 ± 0	50 ± 1	72 ± 13	32 ± 7	44 ± 36	20 ± 7	3 ± 3	28 ± 0	277 ± 24	174 ± 32
Metadesmolaimus sp. 1	1B	4.79	141 ± 63	29 ± 4	55 ± 4	82 ± 8	12 ± 1	18 ± 7	23 ± 4	11 ± 11	18 ± 13	23 ± 1	4 ± 2	4 ± 3	22 ± 16	23 ± 3
Metadesmolaimus sp. 2	1B	0.68	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	14 ± 1	15 ± 1	15 ± 4	13 ± 6	9 ± 4
Microlaimus sp.	2A	3.37	5 ± 5	8 ± 4	0 ± 0	0 ± 0	4 ± 1	14 ± 9	14 ± 8	13 ± 1	16 ± 12	79 ± 22	33 ± 9	65 ± 9	42 ± 10	34 ± 17
Neochromadora sp.	2A	0.65	2 ± 2	7 ± 2	0 ± 0	4 ± 0	1 ± 1	1 ± 1	17 ± 5	0 ± 0	0 ± 0	24 ± 24	1 ± 1	1 ± 1	5 ± 5	0 ± 0
Odontanticoma sp. 1	2A	1.64	43 ± 18	8 ± 1	40 ± 5	2 ± 2	10 ± 4	12 ± 1	12 ± 9	3 ± 3	15 ± 13	8 ± 8	4 ± 0	0 ± 0	0 ± 0	2 ± 2
Omicronema sp. 1	1B	2.28	35 ± 6	6 ± 2	46 ± 4	25 ± 15	9 ± 5	1 ± 1	18 ± 9	12 ± 1	16 ± 5	19 ± 7	11 ± 2	4 ± 0	21 ± 8	0 ± 0
Paracyatholaimus sp. 1	2A	3.83	70 ± 11	7 ± 2	49 ± 6	24 ± 4	26 ± 2	12 ± 1	31 ± 6	10 ± 3	28 ± 21	29 ± 10	13 ± 2	4 ± 1	23 ± 9	44 ± 8
Paracyatholaimus sp. 2	2A	0.63	18 ± 9	2 ± 2	3 ± 3	2 ± 2	3 ± 2	3 ± 1	5 ± 5	0 ± 0	10 ± 4	4 ± 4	2 ± 2	2 ± 2	0 ± 0	6 ± 6
Paramonohystera sp.	1B	3.70	23 ± 4	21 ± 1	8 ± 8	59 ± 12	13 ± 3	13 ± 2	92 ± 31	56 ± 19	10 ± 0	2 ± 2	2 ± 2	2 ± 0	60 ± 21	0 ± 0
Pareurystomina sp.	2B	0.10	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	2 ± 2	2 ± 2	0 ± 0	0 ± 0	2 ± 2	1 ± 1	0 ± 0	0 ± 0	2 ± 2
Parodontophora sp. 1	1B	4.47	13 ± 6	34 ± 3	28 ± 0	9 ± 3	12 ± 7	15 ± 0	43 ± 6	24 ± 5	33 ± 9	61 ± 17	31 ± 8	72 ± 16	42 ± 3	20 ± 15
Pomponema sp.	2B	0.41	0 ± 0	3 ± 3	6 ± 2	0 ± 0	1 ± 1	3 ± 3	0 ± 0	0 ± 0	0 ± 0	4 ± 0	0 ± 0	1 ± 1	0 ± 0	22 ± 9
Pseudosteineria sp.	1B	0.03	3 ± 3	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
**Rhynchonema* cf. *hirsutum*	1B	11.95	105 ± 37	74 ± 9	49 ± 49	245 ± 27	77 ± 32	37 ± 9	141 ± 51	163 ± 18	108 ± 38	10 ± 10	10 ± 1	4 ± 0	137 ± 17	2 ± 2
Synonchiella sp.	2B	0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Viscosia sp. 1	2B	1.74	12 ± 12	8 ± 6	9 ± 1	10 ± 6	6 ± 2	3 ± 3	11 ± 11	34 ± 9	7 ± 3	15 ± 7	8 ± 4	1 ± 1	29 ± 10	16 ± 6
Viscosia sp. 2	2B	0.05	0 ± 0	2 ± 2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

* Descriptions in Chapter VI

Table 4.4 Nematode densities (ind./10 cm^2) at the lower station in San Pedro de Manglaralto, from June 2000 to July 2001.

No significant differences between the relative abundance of the 4 feeding types were found between dry and rainy season (Table 4.5). On a yearly basis, non-selective deposit feeders are the most dominant (average of 43%), but with highly fluctuating patterns. The relative composition (Figure 4.4) of the nematode trophic structure ranged from 0% to 63% (January 2001 and July 2001 respectively) for selective deposit feeders (1A), 4-90% (July 2001 and January 2001 respectively) for non-selective deposit feeders (1B), 3-31% (January 2001 and June 2000 respectively) for epistrate feeders (2A) and 3-41% (September 2000 and August 2000) in predators/omnivores (2B).

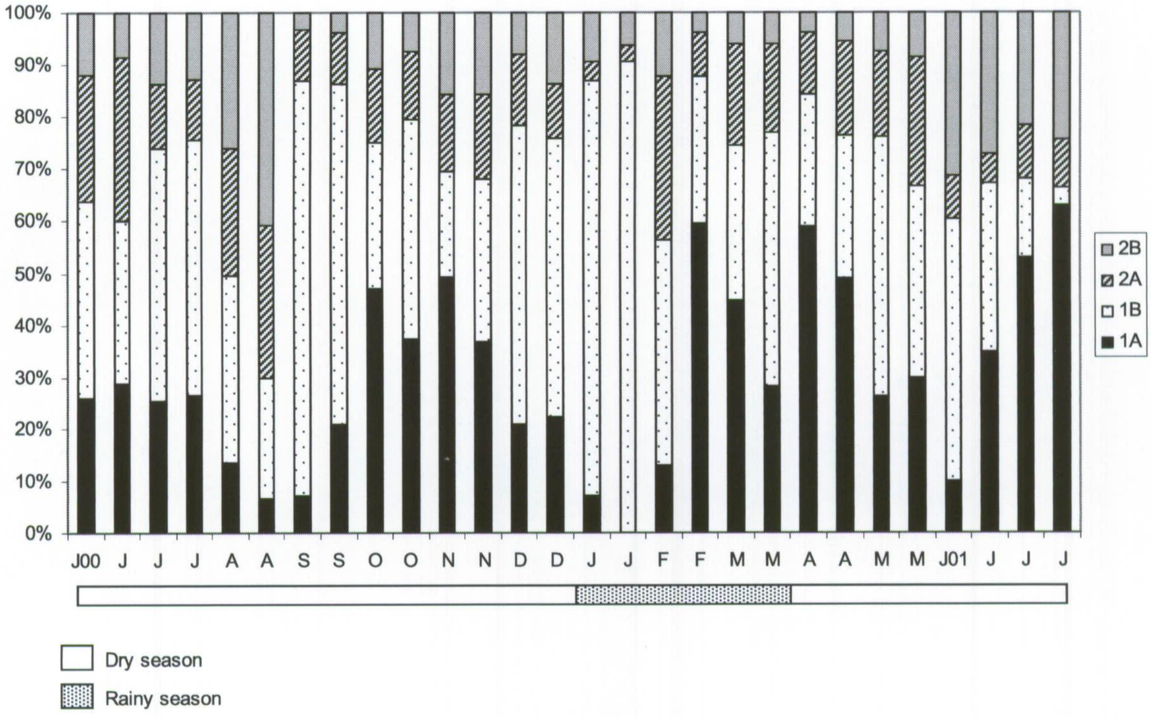


Figure 4.4 **Nematode feeding types according to Wieser (1953) at San Pedro de Manglaralto beach.**

	f-value	**p-value**
Ceramonema sp. 1	0,0179	0,8946
Ceramonema sp. 2	1,4004	0,2474
Daptonema sp. 1	9,7797	0,0043 *
Gonionchus ecuadoriensis sp. n.	0,0015	0,9690
Metachromadora cf. *gerlachi*	1,1865	0,2860
Metadesmolaimus sp. 1	2,2134	0,1488
Microlaimus sp.	2,6584	0,1151
Omicronema sp. 1	0,8164	0,3745
Paracyatholaimus sp. 1	0,0788	0,7811
Paramonohystera sp.	0,0485	0,8273
Parodontophora sp. 1	0,0042	0,9487
Rhynchonema c.f *hirsutum*	0,0146	0,9049
Viscosia sp. 1	1,5997	0,2172
Number of species (S)	0,0003	0,9866
Evenness (J')	4,8710	0,0363 *
ES(100)	0,8301	0,3706
Simpson index (1-λ')	4,2735	0,0488 *
N_1	3,2847	0,0815
Ninf	2,1074	0,1585
Selective deposit feeders (1A)	0,5478	0,4659
Non-selective deposit feeders (1B)	2,8423	0,1038
Epistratum feeders (2A)	0,2063	0,6534
Predators/omnivores (2B)	3,1128	0,0894

Table 4.5 **Results of one-way ANOVA fro mean univariate indices. F-values and p-values are reported (p<0.05* - significant).**

Assemblage structure

The results of the nMDS-analysis (Figure 4.5) and Cluster (not shown) divided the total nematode community into three different sample groups based on species composition, reflecting the seasonal periods (wet and dry): group (I) species registered at the period corresponding to June-December 2000; February (replicate 1) and June 2001 group (II) the nematode species registered in January 2000 (maximum rainfall) and group (III) species at the period February-May 2001 and July 2001. The MDS-ordination showed a considerable degree of similarity and low stress value (0.13), indicating a good and useful 2-D representation of the groups.

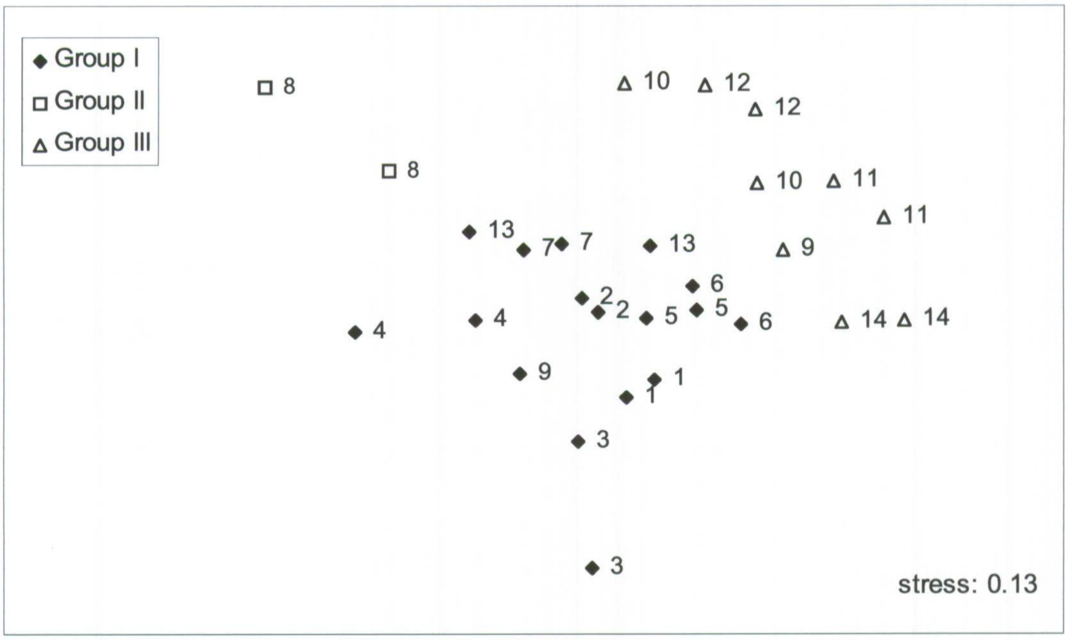


Figure 4.5 **Nematode assemblages: Output of non-metric Multi-Dimensional Scaling (nMDS) on standardised untransformed species abundance data (all replicates) with indication of the three sample groups. Numbers indicated the monthly sampling in a chronological order from June 2000 to July 2001.**

One-way ANOSIM results (Table 4.6) indicated that the composition of the nematode assemblages differed significantly between the three sample groups. The average dissimilarity between sample groups was 61%. The SIMPER analysis indicated a strong dissimilarity between the species groups II and III (71%). These significant differences were largely the result of high abundances of *Daptonema* sp. 1 (490±197 ind./10 cm^2), *Rhynchonema* cf. *hirsutum* (163±18 ind./10 cm^2), and *Paramonohystera* sp. (56±19 ind./10 cm^2) in group II; while *Ceramonema* sp. 1 (208±50 ind./10 cm^2), *Ceramonema* sp. 2 (75±15 ind./10 cm^2), *Metachromadora* cf. *gerlachi* (51±24 ind./10 cm^2), *Microlaimus* sp. (50±9 ind./10 cm^2), *Parodontophora* sp. 1 (43±9 ind./10 cm^2) and *Paracyatholaimus* sp. 1 (21±6 ind./10 cm^2) were abundant in group III.

	Nematode community structure		
	Dissimilarity	R-value	p-value
Global test	61%	0.668	0.001
Groups compared			
I>II	59%	0.761	0.012
I>III	53%	0.617	0.001
II>III	71%	0.934	0.018

Table 4.6 **Results of the ANOSIM and pair-wise tests for difference on nematode community structure between species groups of San Pedro de Manglaralto beach. Dissimilarities as calculated by SIMPER-analyses. (Analyses performed on standardise no transformed data).**

This is also clear from the SIMPER-lists, showing the percentages and feeding type of the dominant species for each sample groups (Table 4.7).

Figure 4.6 clearly indicated that the curve of species group I (June-December 2000) situated at the lower position, as the most diverse and the curve of species group II (January 2001) situated at the upper position as the lowest diverse. As these *k*-dominance curves are based on an unequal number of dates per sample groups, this can lead to a misleading interpretation. However, calculation of individual *k*-dominance curves per date (Figure 4.7) indicated the same patterns (*i.e.* January 2001: lowest diversity, highest dominance; June 2000: lowest dominance, highest diversity).

Analysis of the feeding types showed the dominance of non-selective deposit feeders (1B) in the group I and II and the selective deposit feeders (1A) dominated the group III (Figure 4.8).

Species Group I		
Ceramonema sp. 1	19 %	1A
Rhynchonema cf. *hirsutum*	18 %	1B
Metachromadora cf. *gerlachi*	13 %	2B
Ceramonema sp. 2	8 %	1A
Metadesmolaimus sp. 1	7 %	1B
Daptonema sp. 1	6 %	1B
Paracyatholaimus sp. 1	5 %	2A
Gonionchus ecuadoriensis sp. n.	5 %	2A
Paramonohystera sp.	5 %	1B
Parodontophora sp. 1	4 %	1B

Species Group II		
Daptonema sp. 1	56 %	1B
Rhynchonema cf. *hirsutum*	21 %	1B
Paramonohystera sp.	7 %	1B
Viscosia sp. 1	5 %	2B
Metachromadora cf. *gerlachi*	3 %	2B

Species Group III		
Ceramonema sp. 1	40 %	1A
Ceramonema sp. 2	16 %	1A
Microlaimus sp.	10 %	2A
Parodontophora sp. 1	8 %	1B
Daptonema sp. 1	7 %	1B
Metachromadora cf. *gerlachi*	4 %	2B
Paracyatholaimus sp. 1	3 %	2A
Metadesmolaimus sp. 2	2 %	1B

Table 4.7 SIMPER-lists, showing the contribution percentages for each sample groups and their feeding strategy according Wieser (1953).

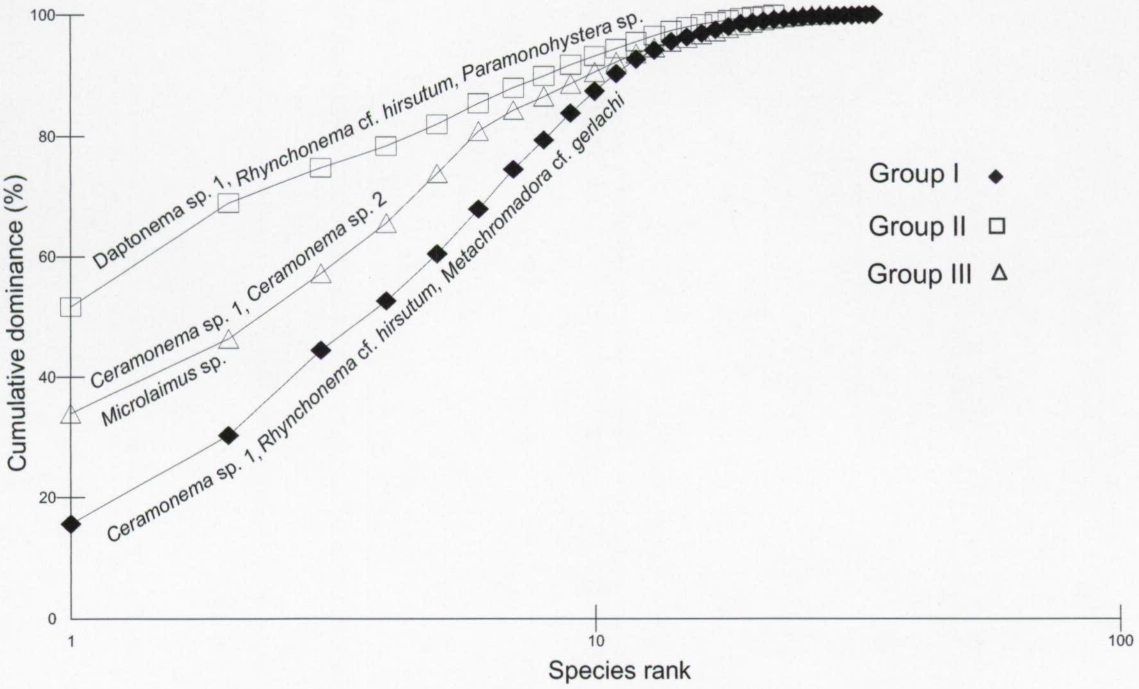


Figure 4.6 ***K*-dominance curves for nematode sample groups, with indication of the three most dominant species.**

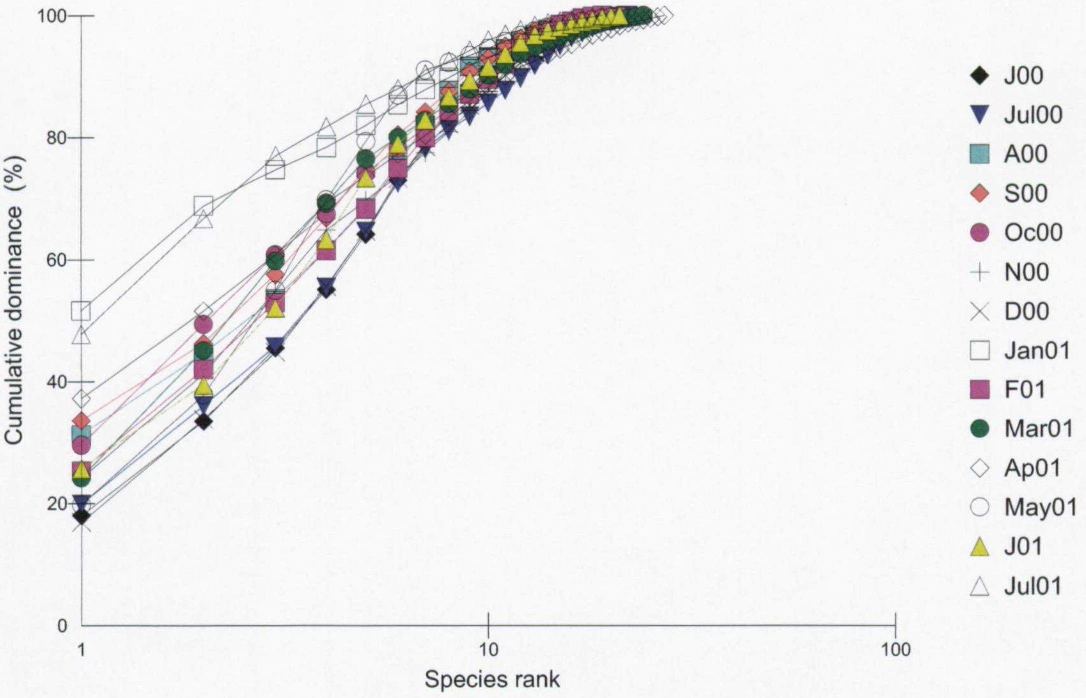


Figure 4.7 ***K*-dominance curves for nematode species per month.**

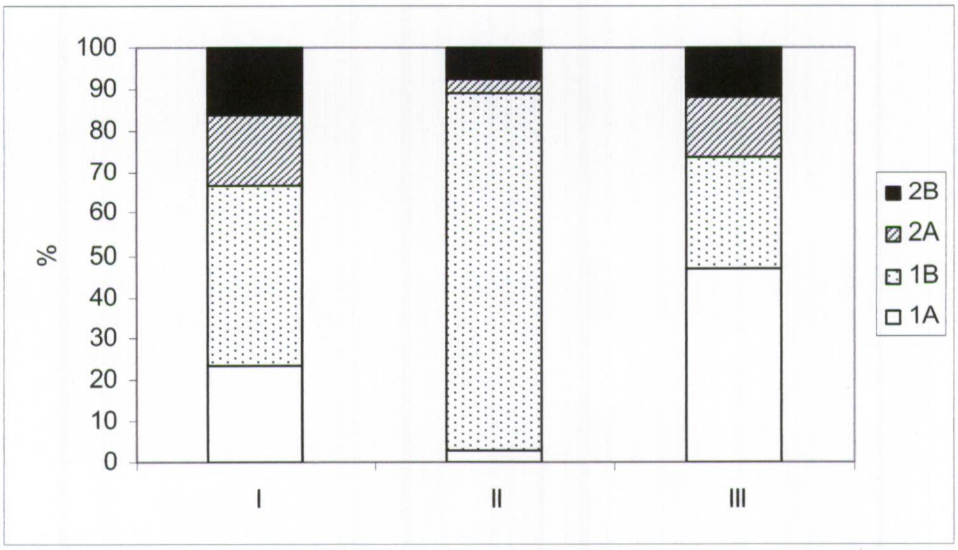


Figure 4.8 **Nematodes feeding types according Wieser (1953) at San Pedro de Manglaralto for sample groups (I= June-December 2000, June 2001; II= January 2001; III= February-May 2001 and July 2001).**

Relationship between nematode (density, diversity indices, trophic group) and environmental factors

Table 4.8 shows the results of the correlation analysis between dominant nematode species and environmental factors. Significant correlations were found between *Parodontophora* sp. 1 and SPM, *Microlaimus* sp. 1 with POM and SST. *Rhynchonema* cf. *hirsutum* with median grain size, between *Metachromadora* cf. *gerlachi* and distance and *Daptonema* sp. 1 with pluviosity. The relationship between *Daptonema* sp. 1 and pluviosity is showed in the figure 4.9.

The residual values were obtained from the nematode species densities and the distance (as a proxy for elevation). The nematode species residual values were correlated with the pluviosity. No relationships were found.

The ANOVA results showed significant differences between dry and rainy season, concerning densities of *Daptonema* sp. 1 (p<0.01). The number of species was positive correlated with distance indicating higher number of species lowest on the beach. The eveness, Simpson index and Hill's number (N_1) decreased when the pluviosity increased.

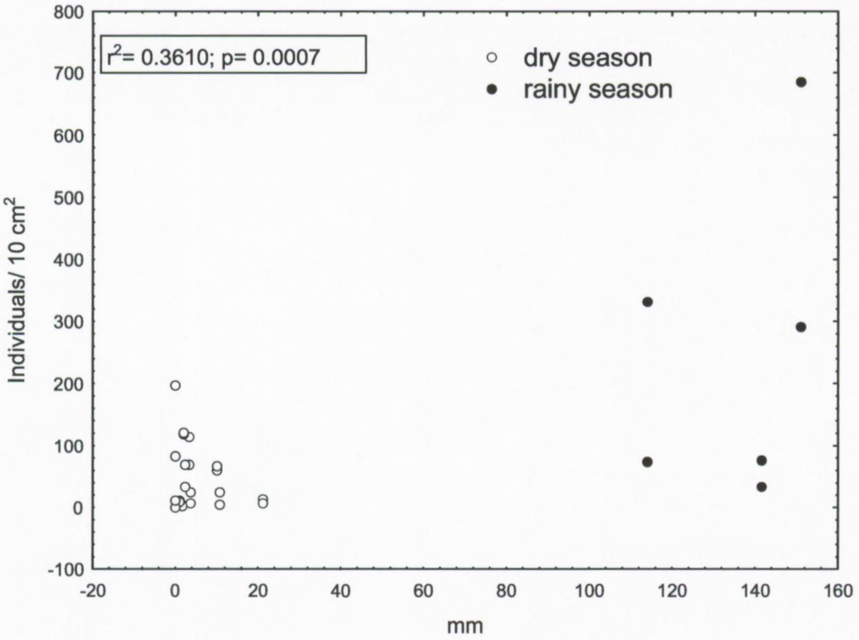


Figure 4.9 **Relationship between *Daptonema* sp. 1 and pluviosity; the sampling of the dry and the rainy season are indicated separately.**

		Chl *a*	SPM	POM	median grain size	distance (proxy for elevation)	SST	Salinity	Pluviosity	Chl *a* / SPM	Chl *a* POM
Nematode species	*Ceramonema* sp. 1	0.21	-0.16	-0.18	-0.22	-0.01	-0.06	0.11	-0.05	0.42	0.27
	Ceramonema sp. 2	0.23	0.34	0.21	0.09	0.18	0.07	0.21	-0.07	0.08	0.00
	Daptonema sp. 1	-0.21	0.07	-0.02	0.11	0.02	0.27	-0.25	**0.60**	-0.33	-0.26
	Gonionchus ecuadoriensis sp. n.	-0.28	-0.02	-0.03	0.29	-0.37	-0.12	0.06	-0.05	-0.22	-0.15
	Metachromadora cf. *gerlachi*	0.09	**0.48**	0.40	-0.05	**-0.56**	**-0.45**	0.37	-0.30	-0.04	-0.01
	Metadesmolaimus sp. 1	-0.37	-0.15	0.23	0.32	**-0.48**	-0.33	0.32	-0.21	-0.10	-0.03
	Microlaimus sp.	0.32	**0.44**	**0.49**	-0.15	**0.39**	**0.46**	-0.05	0.20	0.04	-0.22
	Omicronema sp. 1	-0.11	0.26	0.41	0.32	**-0.38**	-0.06	0.11	-0.04	-0.30	-0.35
	Paracyatholaimus sp. 1	-0.14	0.01	-0.11	0.18	-0.37	-0.16	0.24	-0.12	0.06	0.04
	Paramonohystera sp.	-0.10	**0.46**	0.32	0.14	-0.13	-0.15	0.08	-0.05	**-0.43**	-0.32
	Parodontophora sp. 1	0.23	**0.61**	**0.45**	-0.18	0.29	**0.44**	-0.08	0.14	-0.14	-0.16
	Rhynchonema cf. *hirsutum*	-0.25	0.11	0.26	**0.42**	-0.22	-0.19	0.00	0.10	**-0.46**	-0.31
	Viscosia sp. 1	0.05	0.10	0.07	0.05	-0.18	-0.01	-0.08	0.34	-0.07	-0.04
Diversity index	S	0.40	-0.09	-0.04	-0.01	**0.51**	0.30	-0.28	0.00	0.21	0.05
	J'	-0.05	0.41	0.23	0.22	-0.10	-0.23	0.37	**-0.46**	-0.17	0.03
	ES (100)	0.32	-0.02	-0.12	-0.03	**0.38**	0.11	-0.09	-0.19	0.23	0.21
	1-λ'	0.00	0.41	0.31	0.25	0.01	-0.15	0.33	**-0.45**	-0.21	-0.04
	N_1	0.06	0.30	0.11	0.13	0.06	-0.14	0.23	**-0.38**	-0.05	0.10
	N_{inf}	-0.05	**0.51**	0.18	0.09	0.03	-0.07	0.24	-0.33	-0.22	0.01
Trophic	1A	0.25	-0.02	-0.08	-0.15	0.06	-0.01	0.15	-0.06	0.36	0.21
	1B	-0.22	0.27	0.27	0.26	**-0.39**	-0.13	0.04	0.26	-0.40	-0.31
	2A	-0.17	0.24	0.10	0.25	-0.25	0.03	0.13	0.00	-0.16	-0.17
	2B	0.21	**0.50**	0.34	-0.22	0.18	0.37	-0.08	0.34	0.00	-0.04

Table 4.8 Pearson's correlation values between nematode species density, diversity indices and trophic group with environmental factors (significant correlation in bold numbers).

DISCUSSION

The few quantitative studies on the nematode species composition of sandy beaches use different sampling and extraction techniques and moreover, sandy beaches can be very different from a hydrodynamical point of view (e.g. tidal regime and exposure) reflected in different beach morphodynamics (GOURBAULT AND WARWICK, 1994). Nematode densities reported from two microtidal intermediate beach in Italy (Mediterranean coast) (130-2001 ind./10 cm^2) and Poland (Baltic coast) (102-120 ind./10 cm^2), (GHESKIERE *et al.*, 2005) and from a macrotidal ultradissipative beach in Belgium (North Sea coast) (320-2784 ind./10 cm^2) (GHESKIERE *et al.*, 2004) are very different. The temporal variability in nematode densities of this mesotidal intermediate Ecuadorian beach (359-1170 ind./10 cm^2) is within the range of the nematode densities of the North Sea and Mediterranean coast. The maximum value in Ecuador is however 50% lower in densities than the ones in the study of GHESKIERE *et al.* (2004, 2005) (Italy and North Sea), but *ca*. 90% higher compared to the Baltic coast.

The temporal variability of free-living marine nematode species has only been studied in detail along two Canadian Pacific beaches (SHARMA AND WEBSTER, 1983), the Caribbean island of Guadeloupe (GOURBAULT *et al.,* 1998) and one beach on the south coast of New South Wales, Australia (NICHOLAS AND HODDA, 1999).

SHARMA AND WEBSTER (1983) found significantly more species occurred in the summer than in the winter season. The temporal variability of the species registered at Belcarra Park and at Iona Island, showed different patterns. The highest densities of *Sabatieria pulchra*, a dominant species at Iona Island occurred during the autumn months (October and December), whereas at the other site, the highest densities of the nematodes were registered during May, concomitant with the highest carbon content. GOURBAULT *et al.* (1998) found that the nematode generic composition was highly variable at the more wave-exposed locations, but less at the sheltered sites. The nematode composition was affected by the grain size. No temporal patterns were detected among the 23 beaches studied. NICHOLAS AND HODDA (1999) found significant differences between the nematode densities at the different tide level sampled, with density decreased at the low tide level; however no significant differences in diversity between the tide levels or times of sampling (summer and winter) were detected.

A total of 37 species belonging to 30 genera were registered at the Ecuadorian beach; while in Australia (NICHOLAS AND HODDA, 1999) 58 species belong 48 genera were found and 122 species belonging to 112 genera at Guadeloupe island (GOURBAULT *et al.*, 1998). The dominance of Xyalidae (43%) in our study (with 12 species) is comparable with the dominance of Xyalidae (21%) in Australia (NICHOLAS AND HODDA, 1999) with 11 species registered and GHESKIERE *et al.* (2004) also found that Xyalidae was the dominant in densities (30%) with 20 species at the Panne beach in Belgium.

The *k*-dominance curves for the temporal variation did not show a trend at the different stations in the tropical beaches of Guadeloupe (GOURBAULT *et al.*, 1998). In contrast, the Ecuadorian beach showed lowest diversity and highest dominance during the month with the highest pluviosity (January).

SHARMA AND WEBSTER (1983) found that the dominant species at one Canadian beach were non-selective deposit feeders and epigrowth feeders, while at the other beach a more even distribution of feeding groups was found. At the Ecuadorian beach the non-selective deposit feeders were dominant although with fluctuating values (16-91%).

Although no significant differences in the total nematode densities and species richness between dry and rainy season were detected, some species had a limited distribution in time such as *Camacolaimus* sp., *Ditlevsenella* sp. and *Metadesmolaimus* sp. 2, which were only registered in January and February (rainy season). In contrast, *Linhomoeus undulatus*, *Desmolaimus zeelandicus* and *Eleutherolaimus stenosoma* were recorded mostly during spring months at the Canadian beaches and significantly more species occurred in summer (August) than the winter (December and February). At a Belgian sandy beach (GHESKIERE *et al.*, 2004) non-selective deposit feeders were dominant along the beach profile (upper to lower).

Three nematode sample groups were found in our study, reflecting seasonal periods. Group I (June-December) is characterized by a high dominance of *Ceramonema* sp. 1 (19%), *Rhynchonema* cf. *hirsutum* (18%) and *Metachromadora* cf. *gerlachi* (13%). In group II (January), the non-selective deposit feeder *Daptonema* sp. 1 was dominant (56%). Group III (February-May) was characterized by the dominance of *Ceramonema* sp. 1 and *Ceramonema* sp. 2, which represented 40% and 16%, respectively, of the total nematode fauna of the group. While, GOURBAULT *et al.* (1988) found two genera groups related with the median grain size (finer and coarser sand).

In our study, *Daptonema* sp. 1 and *Viscosia* sp. 1, registered highest densities in January 2001; nevertheless only in *Daptonema* sp. 1 significant differences between dry and rainy season were detected. Both species follows the pluviosity fluctuations, and the period also characterized by lowest salinity and an increase of SST (Table

4.1). The abilities of free-living species of nematodes to survive short term salinity fluctuations were investigated by FORSTER (1998) in two sites on the east coast of England; throughout the year the salinity ranges between 33 and 35 PSU. *Axonolaimus paraspinosus* and *Cervonema tenuicauda* from the upper intertidal zone; *Daptonema oxycerca* from lower intertidal zone and *Sabatieria punctata* from subtidal zone, were studied to assess their ability to osmoregulate under various conditions (3.3, 16.6, 33.3 and 66.6 PSU) of osmotic stress. The results demonstrated that all species were able, to differing extents, to regulate water content. In general, in hypotonic solutions, an initial influx or loss of water was followed by a gradual recovery to water content values approaching those of nematodes in 33.3 PSU. However specific differences in the rate and efficiency of osmoregulation were distinct ranged from no change in body diameter content (*A. paraspinosus*; hypotonic solutions) to extreme expansion and rupture of the cuticle (*D. oxycerca*; hypotonic solutions). The species from the upper shore demonstrated the greatest capacity to osmoregulate and/or tolerate periods of raised body water content. Those results suggested that ability to overcome salinity fluctuations is a factor in determining horizontal distribution of nematode assemblages in littoral habitats. It would be expected that species found at the upper intertidal sites will be able to tolerate osmotic changes and resist the effects of the associated stress more effectively than species from lower intertidal or subtidal sites. In the natural environment, loss of motility during periods of osmotic stress will result in the cessation of normal activities such as feeding. This may be an important negative selection factor for it will undoubtedly have an effect on the long term survival of nematode species in intertidal habitats.

The presence of El Niño and La Niña events in the Ecuadorian coast causes fluctuating climatic conditions, which can have an effect on the meiofauna composition, but more studies will be necessary to compare the temporal patterns under normal and anomalous conditions. The nematode *Daptonema* sp. 1 could be studied as an indicator of the pluviosity fluctuations at the Ecuadorian coast. Nevertheless, the species that occur in estuary habitats are well adapted, not only to low or high salinities, but especially to fluctuations (HEIP *et al.*, 1985). The nematode species community along the Ecuadorian beach is more like an 'estuarine' community (with dominance of *Daptonema*, *Metachromadora*), than a real marine community. In the paper of HEIP *et al* (1985) it has been recorded nematodes such as *Daptonema oxycerca* and *Metachromadora remanei*, can survive in low salinity conditions up to 35

PSU. Another striking factor on Ecuadorian beach is the lack of Epsilonematidae and Draconematidae typical for Guadeloupe (12% and 10% respectively), Italy (42 and 4% respectively), Australia (only Epsilonematidae with less to 5%), Kenya (RAES, *et al.*, submitted) (6 and 10% respectively) and Zanzibar (RAES, *et al.*, submitted) (2 and 8% respectively).

CONCLUSIONS

The changes in nematode assemblages were associated with the seasons. Highest dominance of nematode species was found during January 2001 (maximum rainfall month); at the same time lowest diversity was registered. Seasonal respond was found in *Daptonema* sp. 1, the highest densities were correlated with the pluviosity fluctuations.

ACKNOWLEDGEMENTS

This study was done with the financial support of the International University Collaboration program (1999-2008) between VLIR and ESPOL. The first author acknowledges the staff of Marine Biology Section from Gent University especially to Thom Gheskiere and Annick Verween for the assistance in the statistical analysis. We are grateful to Nancy Fockedey, Jan Wittoeck, Sonnia Guartatanga, Patricia Urdiales, Verónica Ruiz and Luis Domínguez for support during the sampling campaigns and to CENAIM for the logistic support.

CHAPTER V

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

CALLES A, VINCX M, DEGRAER S, ARCOS F, GHESKIERE T

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 cm^2 (December 2000) to 1488±100 ind./10 cm^2 (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 cm^2 and 1-302 ind./10 cm^2 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 cm^2), 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 $N_{1,}$ 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 Λ^+ 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 μm (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).

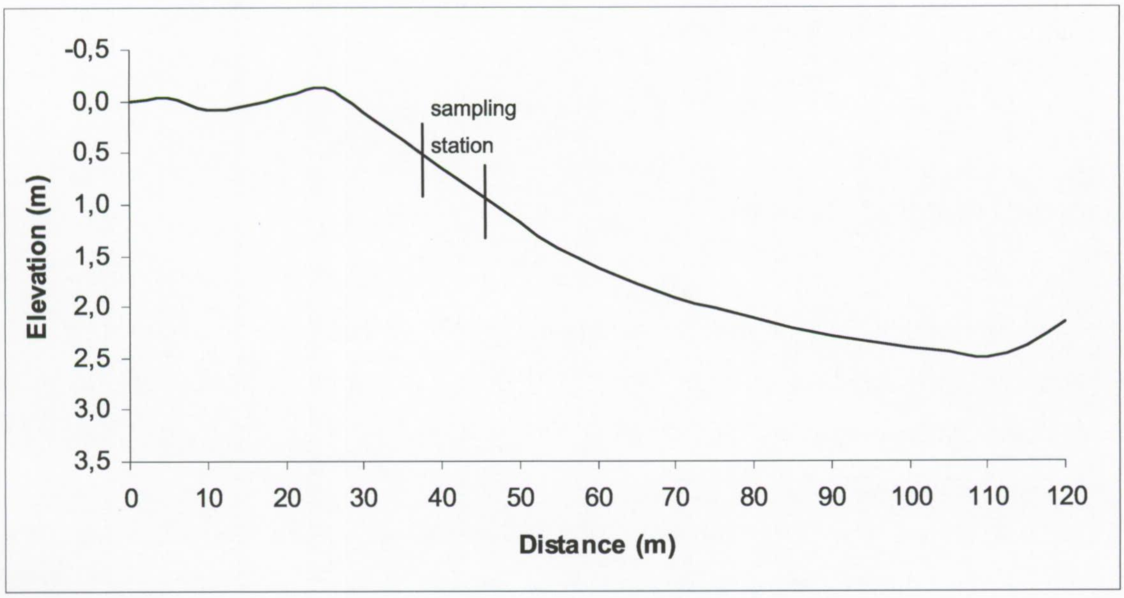


Figure 5.1 **Average beach profile at San Pedro de Manglaralto. The indication lines refer to the sampling distance over which the actual samples were taken during the one-year period (June 2000-June 2001). The vertical scale is exaggerated in relationship to the horizontal. The origin (0) is named reference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

Nematode community

Densities and composition

Total nematode densities (mean±standard error of the mean) varied from 183±28 ind./10 cm^2 (December 2000) to 1488±100 ind./10 cm^2 (June 2000). The overall average density was 662±91 ind./10 cm^2. 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%.

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 cm^2) and July 2000 (322 ind./10 cm^2), followed by a decline until November 2000 (55 ind./10 cm^2), after which an slightly increase was observed between December 2000 and February 2001 (91-105 ind./10 cm^2). Over the sampling period lowest densities occurred in March 2001 (4-12 ind./10 cm^2). 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 cm^2) and an other one in July 2001 (255 ind./10 cm^2) were observed. Over the sampling year the densities remain lower, between 0-113 ind./10 cm^2 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		Jul		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	0 ±	0	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	0 ±	0	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	0 ±	0	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
Daptonema sp. 2	1B	0,06	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	5 ±	4	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0	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	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	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	0 ±	0	0 ±	0	0 ±	0	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	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	0 ±	0	0 ±	0	0 ±	0	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 ±	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 cm^2) 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 cm^2) 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 cm^2) and May (147 ind./10 cm^2) 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 cm^2). The juveniles were dominant.

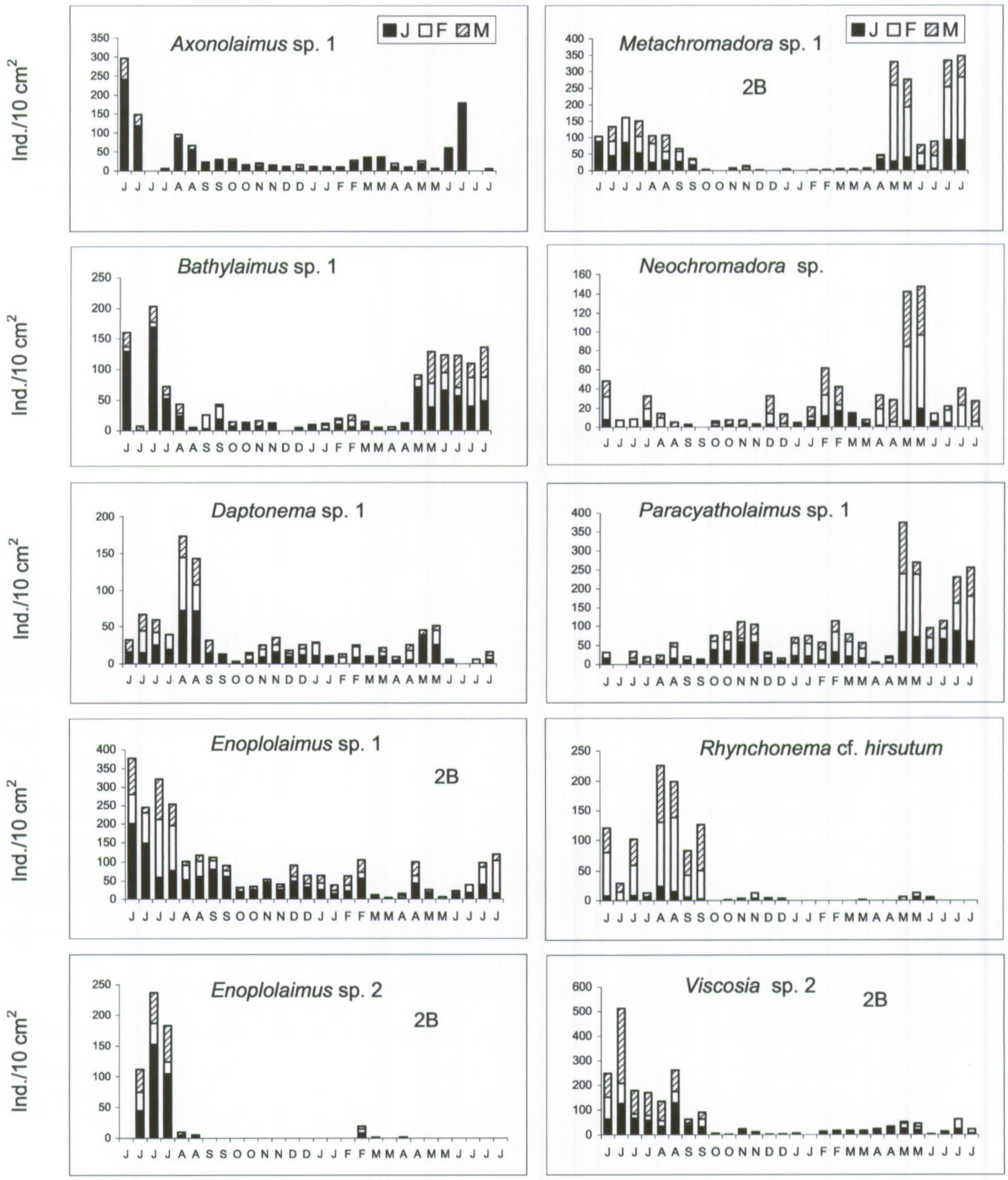


Figure 5.2 **Distribution of the ten dominant species at the upper station, San Pedro de Manglaralto beach, from June 2000 until July 2001. Legend on the figure: J= juveniles, F= females, M= males. 2B= nematode predator/omnivore.**

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
A	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
O	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
A	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).

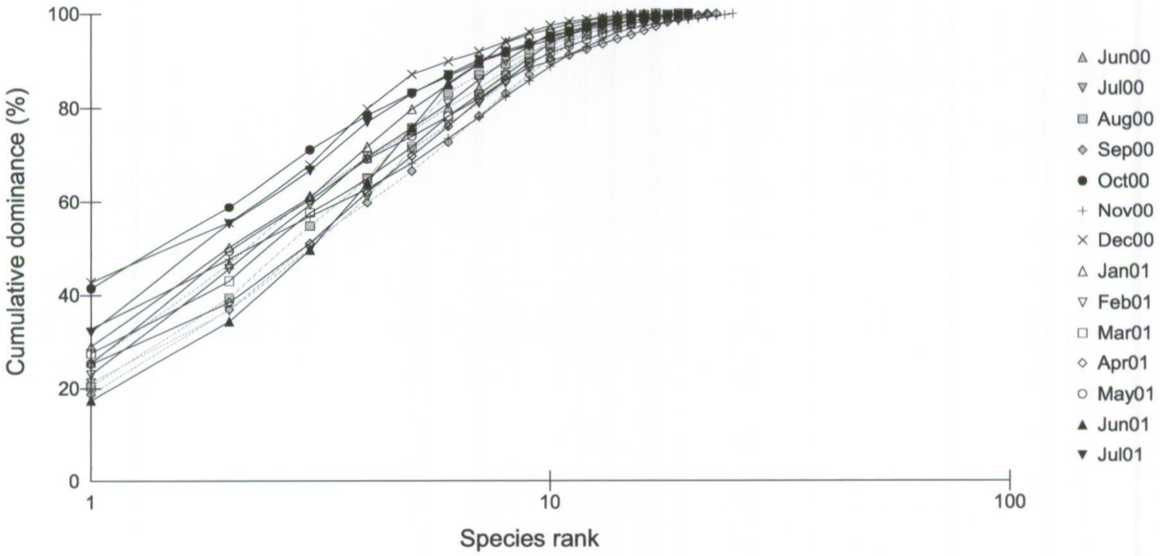


Figure 5.3 ***K*-dominance curves per month at upper station, San Pedro de Manglaralto beach.**

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%.

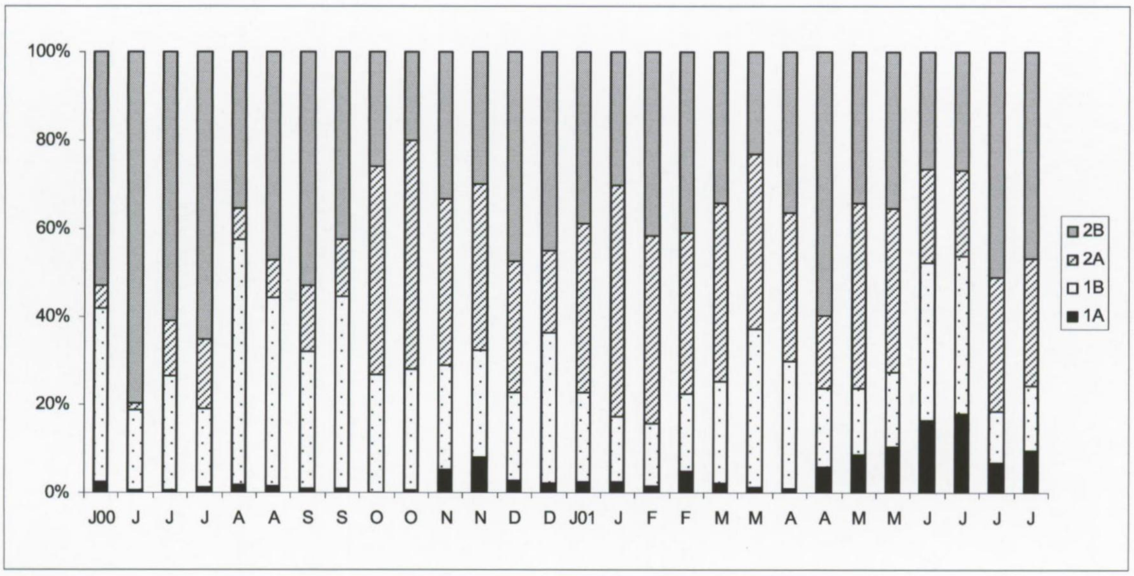


Figure 5.4 **Trophic composition of the nematode community at upper station, San Pedro de Manglaralto beach.**

Nematode age structure

The reproduction was continuous, the juveniles were present throughout the sampling period, and the highest densities (654±156 ind./ 10 cm^2) were coupled with peak densities of the nematode populations (1488±100 ind./10 cm^2). 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).

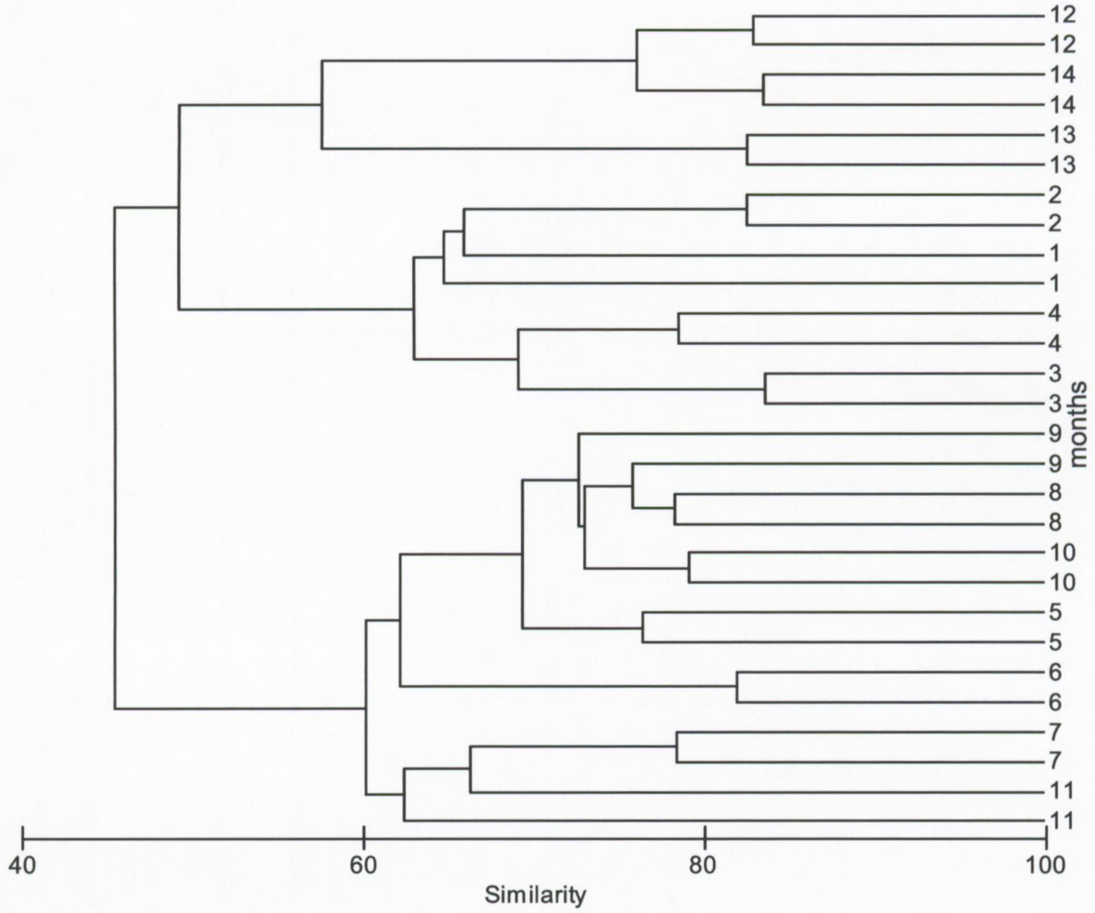


Figure 5.6 Dendogram resulting from Cluster analyses on square-root nematode species densities. Numbers indicated the monthly sampling in a chronological order from June 2000 to July 2001.

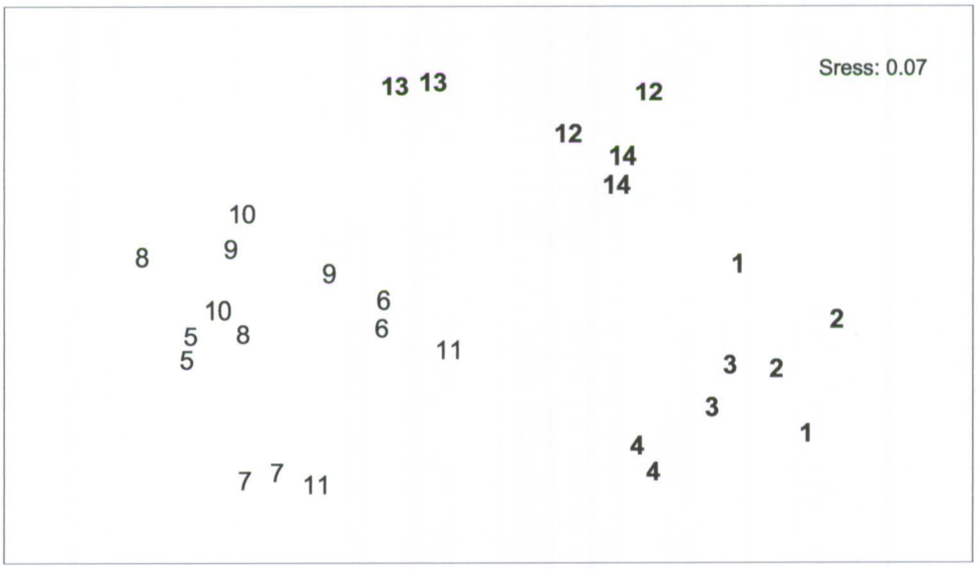


Figure 5.7 **Multi-Dimensional Scaling (MDS) on square-root species abundance data at upper station. Numbers indicated the monthly sampling in a chronological order from June 2000 to July 2001. Bold numbers (Group 1: June-September) and Clear numbers (Group 2: October-April)**

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
Daptonema 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
*significant; **highly significant; *** very highly significant

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

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).**

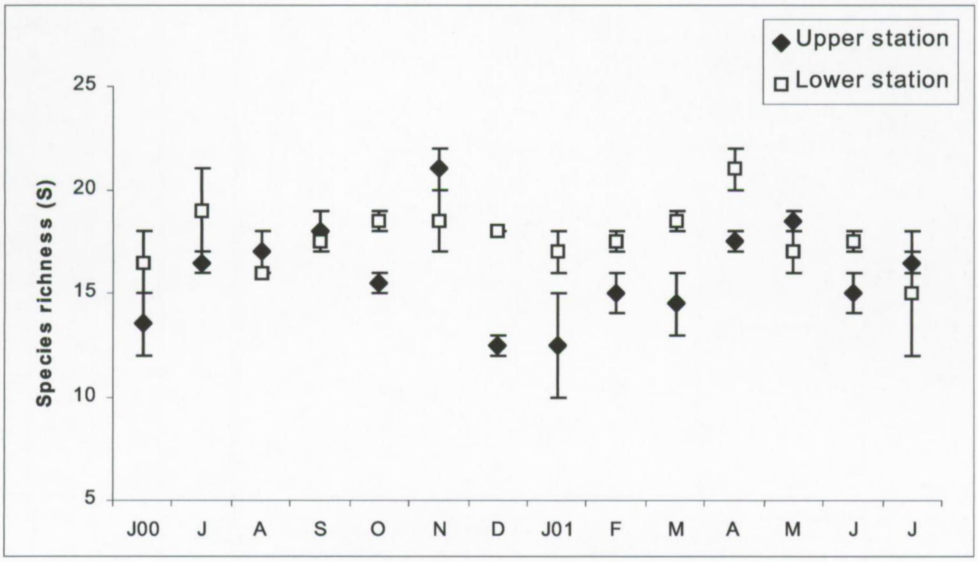


Figure 5.8 **Mean nematode species richness (± standard errors of the mean) at upper and lower station, San Pedro de Manglaralto beach.**

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.

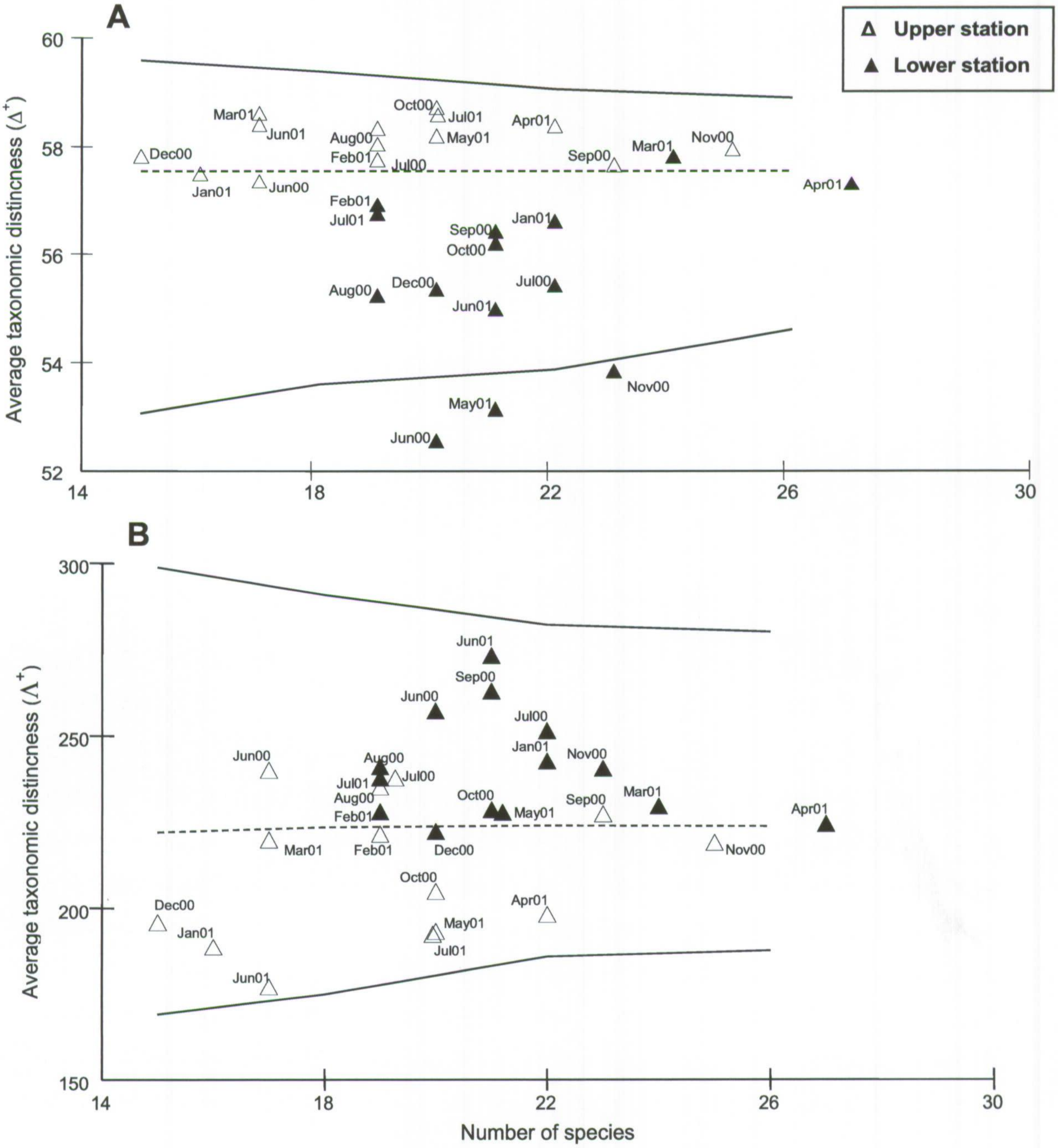


Figure 5.9 The 95% probability funnels for average taxonomic distinctness (Δ^+) and Variation in Taxonomic distinctness (Λ^+) plotted against the number of species on upper and lower station at San Pedro de Manglaralto beach. Dashes lines indicated the simulated mean Δ^+ and Λ^+ from 1000 random selections 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 cm^2) and *Metachromadora* sp. 1 (340±7 ind./ 10 cm^2) 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).

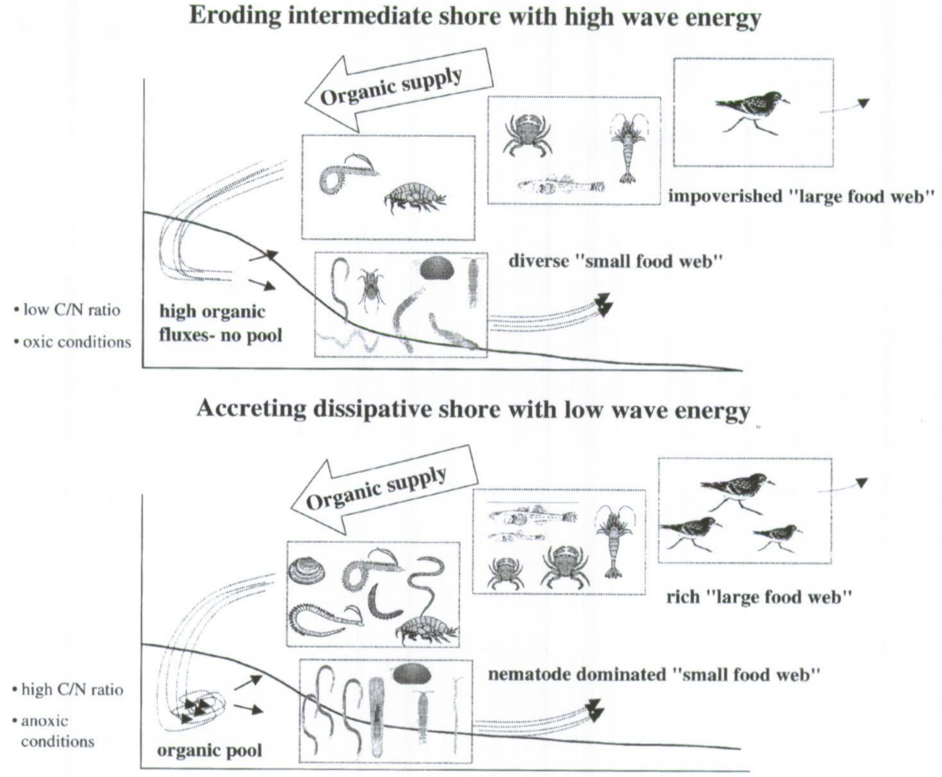


Figure 5.10 **Food web structure on cold-temperate shores. Arrows indicated flow of organic and mineralized substrates (*source:* MENN, 2002).**

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 cm^2) 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 cm^2) and highest densities of nematodes at the lower station (738±64 ind./10 cm^2), 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 LIST	BEACH STATION	
	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	x
Daptonema sp. 2	x	x
Daptonema sp. 3		x
Dasynemoides sp.		x
Dichromadora sp.	x	x
Ditlevsenella sp.		x
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**	x	
Metadesmolaimus sp. 1	x	x
Metadesmolaimus sp. 2		x
Metalinhomoeus sp.	x	
Microlaimus sp.	x	x
Molgolaimus sp.	x	
Neochromadora sp.	x	x
Odontanticoma sp. 1	x	x
Omicronema sp. 1	x	x
Paracyatholaimus sp. 1	x	x
Paracyatholaimus sp. 2	x	x
Paracyatholaimus sp. 3	x	
Paramonohystera sp.	x	x
***Pareurystomina* sp.**		x
Parodontophora sp. 1	x	x
***Pomponema* sp.**		x
Pseudosteineria sp.	x	x
Rhynchonema cf. *hirsutum*	x	x
***Synonchiella* sp.**		x
***Syringolaimus* sp.**	x	
***Trissonchulus* sp.**	x	
***Viscosia* sp. 1**	x	x
***Viscosia* sp. 2**	x	x
***Viscosia* sp. 3**	x	
Wieseria sp.	x	

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.

CHAPTER VI

Taxonomic description of some dominant nematode species from San Pedro de Manglaralto beach (Ecuador)

INTRODUCTION

In total 72 free-living marine nematode species were recorded in the Ecuadorian sandy beaches, among them some are new to science.

This chapter will describe one new species of the family Ceramonematidae: *Ceramonema adrianae* sp. n and two new species belonging to the Xyalidae: *Rhynchonema ronaldi* sp. n. and *Gonionchus ecuadoriensis* sp. n.

MATERIAL AND METHODS

Samples were collected with plastic cores (surface 10 cm^2) to 20 cm depth. The samples were fixed with hot (60°C) 4% formaldehyde seawater solution, neutralised with lithium carbonate ($LiCO_3$). Nematodes were extracted by decantation and centrifugation with Ludox HS 40 (Heip *et al.*, 1985), and collected on a 38 µm sieve. The nematodes were transferred to a series of glycerol-ethanol solutions (Vincx, 1996) and mounted on glass slides. Measurements and drawings were taken using a Leica microscope equipped with camera lucida. All measurements (not ratios) are in micrometers (µm) (ratios are given by De Man) and all curved structures are measured along the arc.

Abbreviations

a: body length divided by maximum body width

abd: anal body diameter

amph l: amphideal length

amph w: amphideal width

amph cbd: corresponding body diameter at level of the amphid

b: body length divided by pharyngeal length

c:	body length divided by tail length
c':	tail length divided by anal body diameter
cbd:	corresponding body diameter
cs:	length of cephalic setae
da:	distance from anterior end to anus
dexcp:	distance from anterior end to excretory pore
dsnr:	distance from base of stoma to nerve ring
gub:	length of gubernaculum
HD:	head diameter
L:	total body length
M:	maximum body diameter
ols:	outer labial seate
ph:	pharyngeal length
ph cbd:	corresponding body diameter at level of the pharynx
spic:	spicule length
t:	tail length
V:	position of vulva as percentage of total body length from anterior
V':	distance from the anterior end to vulva
SEM:	Scanning Electron Microscopy

Formula: distance from the anterior end to:

$$\frac{\text{cephalic seta} \quad \text{pharynx} \quad \text{M/vulva} \quad \text{anus}}{\text{cbd}} \qquad \text{L}$$

DESCRIPTIONS

Ceramonema adrianae sp. n.

Type material: Holotype ♂$_1$. Paratypes: ♂$_2$-♂$_6$ and ♀$_1$-♀$_5$.
Type locality: San Pedro de Manglaralto beach (1°56’30” S and 80°43’30” W) intertidal zone at low water mark, median grain size 245 μm, % silt= 0.40, % gravel= 0.46. Salinity= 33.8 PSU. Collected on 16 June, 2000.
Etymology: The species is dedicated to my daughter Adriana Cordero.

Measurements

Holotype

♂$_1$

$$\frac{10 \quad 160 \quad M \quad 313}{17 \quad 18 \quad 18 \quad 15} \quad 894\ \mu m$$

a= 50.7; b= 5.6; c= 9.0; c’= 6.4; spic= 21 μm

Paratype

♀$_1$

$$\frac{10 \quad 182 \quad 472 \quad 751}{20 \quad 20 \quad 21 \quad 18} \quad 868\ \mu m$$

a= 42.2; b= 4.8; c= 8.3; c’= 5.7; V= 54%

Other measurements see Table 6.1.

Description

Body elongated and clearly annulated. The cuticle is marked by coarse transverse ondulations, very obvious in SEM (Figure 6.1C). Each annule is divided by 8 longitudinal ridges into 8 longitudinal cuticular plates, which extend the entire length of the body; there are 2 lateral, 1 dorsal, 1 ventral and 4 sublateral plates. These ridges also extend into the head capsule. No subcuticular vacuolization. Cuticular annules are 5 µm wide, except for the tail, where the annules narrow from 3 µm (cloaca/anus) (males) to 2 µm (before the tail cone) (males). Total number of annules 153-209 (males) and 166-186 (females). Annule in the cloacal region not elongated. Somatic setae absent, except for 7 pairs of subventral setae (5-7 µm) present on the tail of males as well as a pair of 7 µm long lateral terminal setae situated on the distal cone of the male tail tip (Figures 6.2C, 6.1F). Cephalic capsule 22-24 µm long and 16-18 µm (females 22 µm) at the widest point. Six 'posterior' outer labial setae (12-13 µm long) and four cephalic setae (8-10 µm long), situated about 1-2 µm anteriorly from the outer labial setae (Figures 6.2A, 6.3B). Figure 6.1D shows the head cross-section of a juvenile, with the four cephalic setae posterior to the six outer labial setae. Inner labial setae are not visible. Amphids forming an oval loop (Figures 6.1A, 6.1B), in males: the amphids are dorsally wound, 10 µm long and 5 µm wide (at the widest point); in females the amphids are ventrally wound, 7 µm long and 4 µm wide (at the widest point). Buccal cavity small. Pharynx narrow, cylindrical and slightly wide posteriorly. Nerve ring is not distinct. Excretory gland clearly developed (Figures 6.2B, 6.3C) and with the excretory pore 5-8 annules anterior to pharynx intestinal junction, 129-158 µm from anterior end. Spicules curved, 21.3-26.5 µm long; gubernaculum 14-15.4 µm long (Figure 6.2D). Testes not clearly visible. Two opposed reflexed ovaries; although the specimens are not clearly developed the vulva is prominent (Figures 6.3A, 6.1E) and situated about 53-55% of the body length. Tail elongated; the terminal cone is 11-13 µm long males and 18-20 µm females. Caudal glands present but not clearly distinguishable.

	Males (n= 6)				**Females** (n= 5)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
L	875	1094	939	85.3	868	1034	963	67.1
a	49.6	62.0	53.2	4.8	42.2	50.2	46.4	3.5
b	4.8	5.8	5.5	0.4	4.8	5.5	5.1	0.3
c	9.0	11.1	9.7	0.9	8.3	9.5	8.9	0.5
c'	5.7	6.4	6.0	0.3	5.7	6.0	5.8	0.1
HD	15	18	16.5	1.0	19	20	19.7	0.3
cs	8	10	9.1	0.6	10	10	9.6	0.0
ols	12	13	12.5	0.7	12	13	11.9	0.3
amph l	10	10	9.7	0.3	7	7	7.2	0.3
amph w	5	5	5.1	0.2	4	4	4.2	0.2
amph cbd	16	18	17.3	0.8	20	21	20.4	0.6
dexcp	129	158	141.3	11.2	148	155	149.6	3.2
ph	154	195	171.9	15.2	182	196	188.4	6.0
ph cbd	18	18	17.8	0.3	20	21	20.0	0.3
M	18	18	17.6	0.0	21	21	20.7	0.3
da	310	343	318.4	12.3	751	913	855.8	68.8
V					472	553	517.4	32.8
V'					53	55	53.8	0.7
spic	21	26	24.0	2.0				
gub	14	15	14.7	0.7				
abd	15	17	16.3	0.6	18	19	18.5	0.3
t	96	99	98.0	1.7	104	110	107.5	2.0
# body annules	153	209	174	22	166	186	171	9

Table 6.1 Measurements of *Ceramonema adrianae* sp. n. from San Pedro de Manglaralto. Mean and standard deviation of the mean (SD).

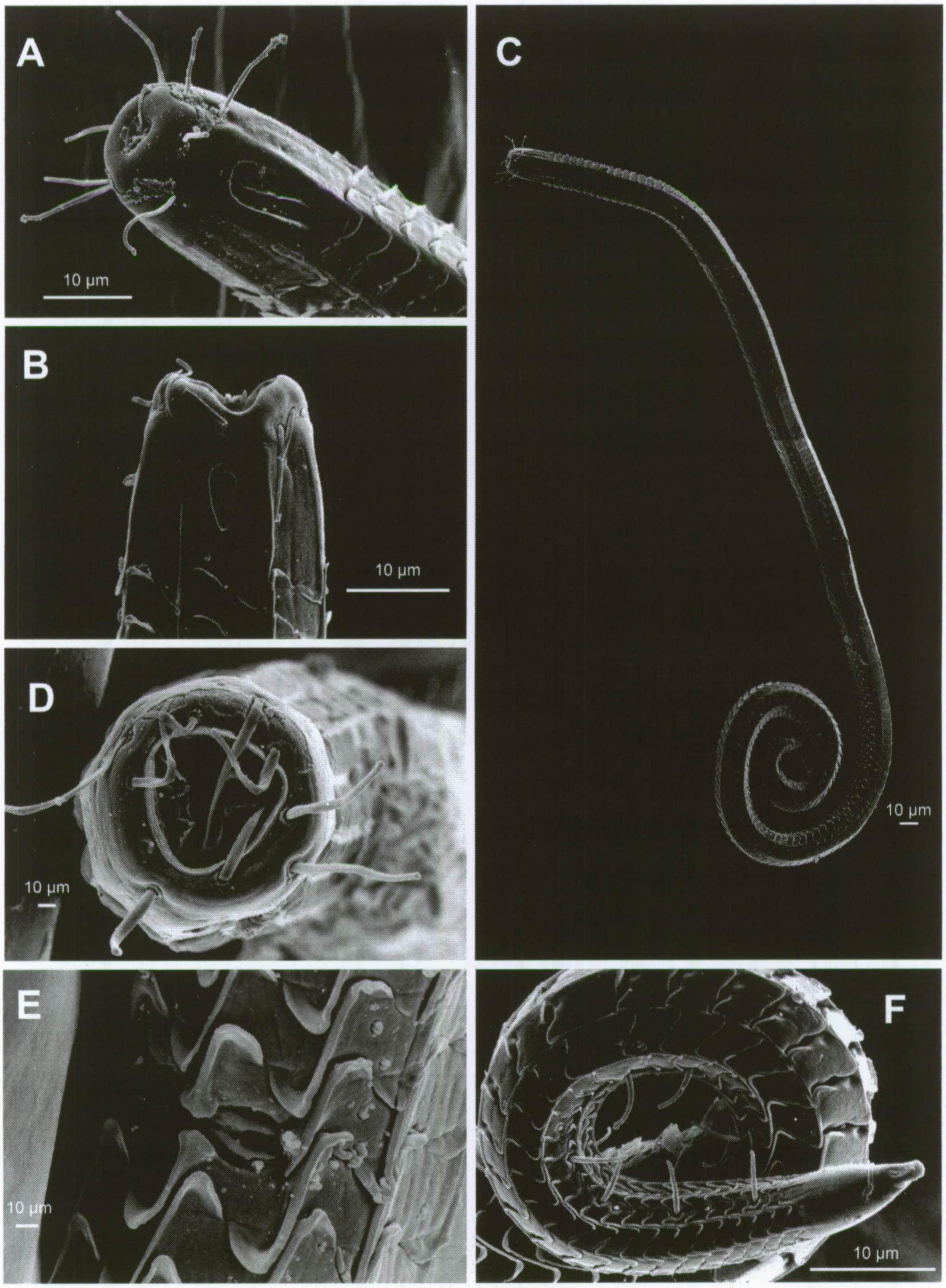


Figure 6.1 SEM photographs of *Ceramonema adrianae* sp. n.. A: Head of male; B: Head of female; C: Total view male; D: Face view head of juvenile; E: Vulva section; F: Tail of male showing the subventral setae.

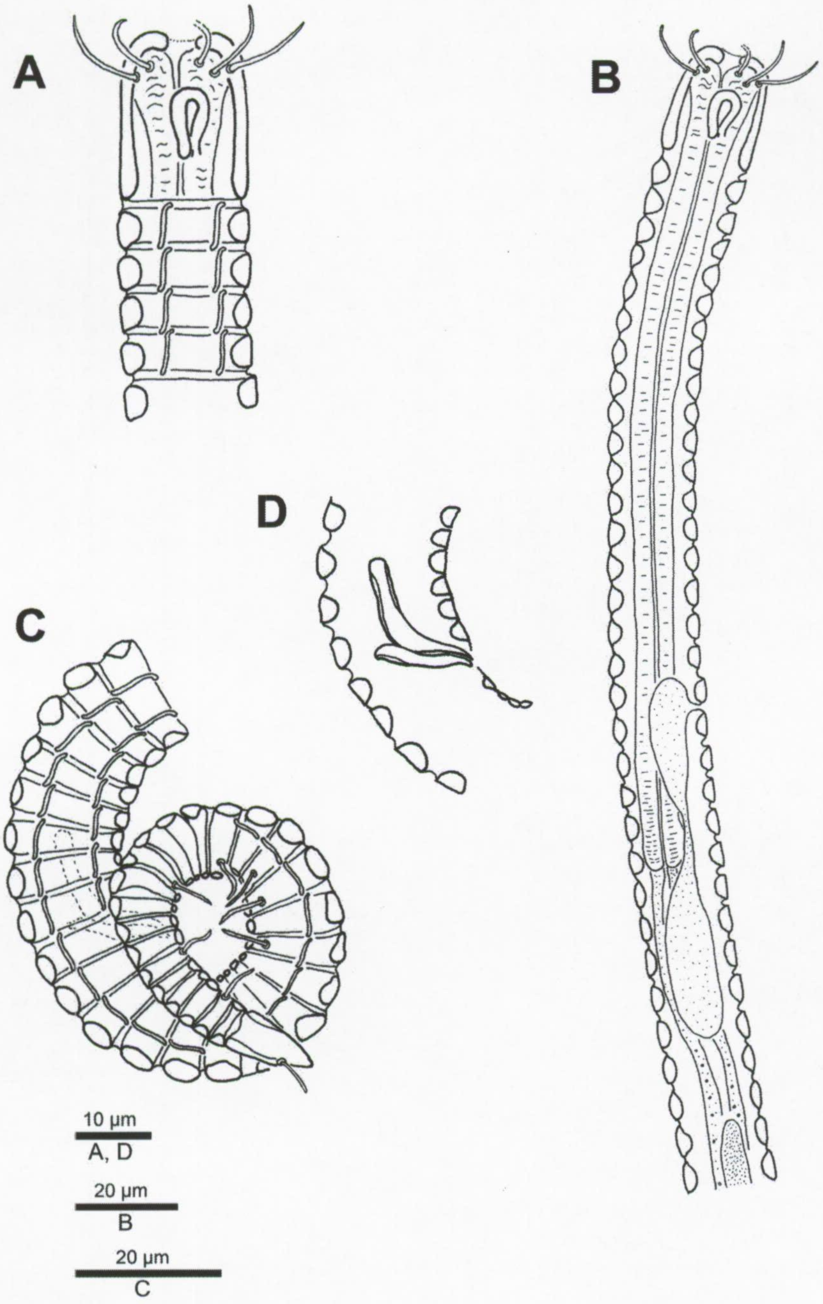


Figure 6.2 ***Ceramonema adrianae*** **sp. n. A: Anterior end of holotype ♂$_1$; B: Anterior region and position of excretory gland of holotype ♂$_1$; C: Tail view of holotype ♂$_1$; D: Spicule and gubernaculum holotype ♂$_1$.**

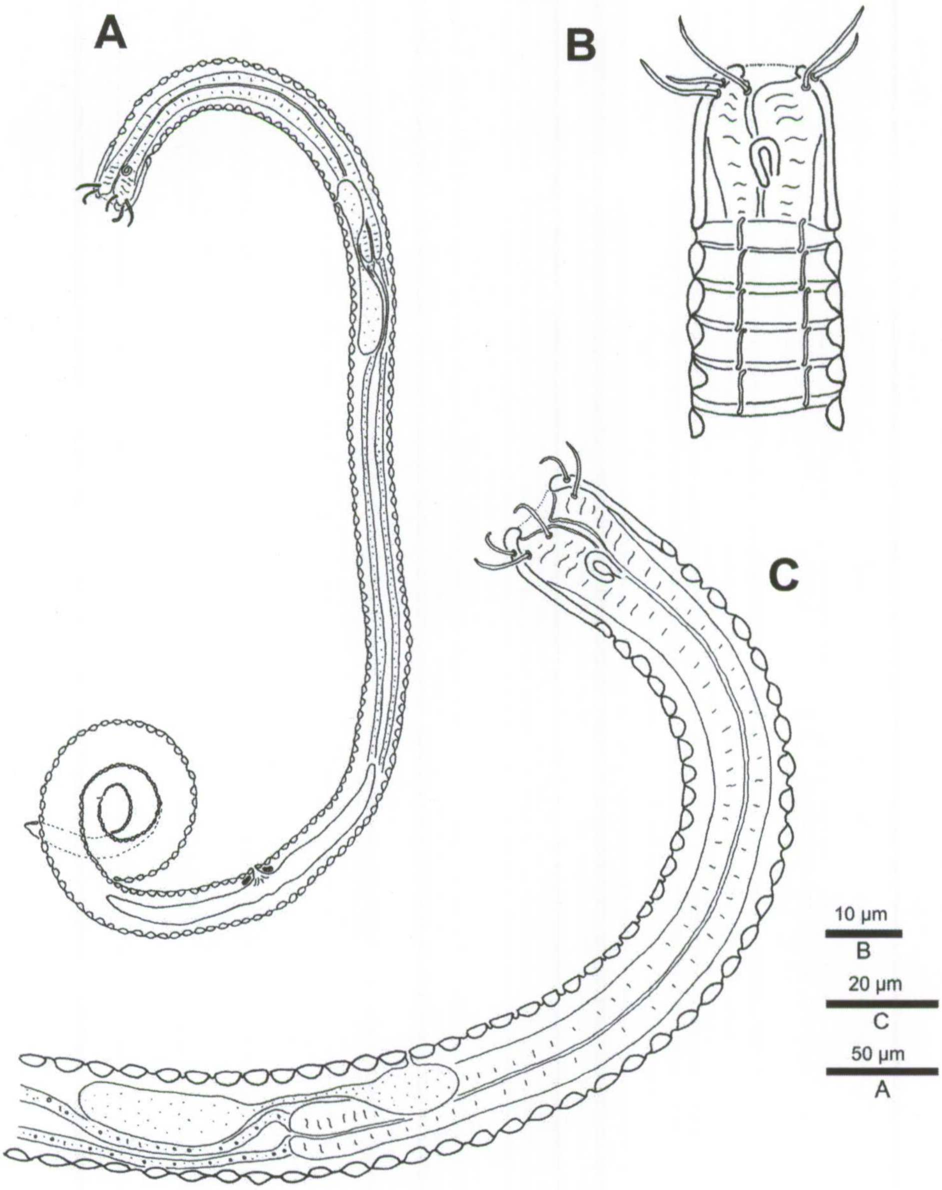


Figure 6.3 ***Ceramonema adrianae*** **sp. n. A: Total view of paratype ♀$_1$; B: Anterior end of paratype ♀$_2$; C: Anterior region and position of excretory gland of paratype ♀$_1$.**

Diagnosis and relationship

Ceramonema adrianae sp. n. is characterised by the following sexual dimorphism: amphids in the males are longer than in the females (10 µm vs. 7 µm) and dorsally wound in the males; the presence of a pair of terminal setae on the distal cone of the male tail and the position of the outer labial setae (situated at a 'posterior' circle) very close (1-2 µm) to the cephalic setae. The new species is closely related to *Ceramonema algoensis* FURSTENBERG & VINCX, 1993 because of the absence of a subcuticulal vacuolization and no elongated annule in the cloacal region. It differs from *C. algoensis* in having a lower number of annules (153-209 vs. 300-315), no elevated lip region and shorter spicule length (21-27 µm vs. 28-32 µm).

Key for identification of *Ceramonema* Species

1 Elongated cloacal annule in males 2

\- No elongated cloacal annule 6

2 Cephalic capsule shorter than wide or equal 3

\- Cephalic capsule longer than wide 4

3 Cephalic capsule 18 µm length and 28 µm wide ....*C. racovitzai* ANDRASSY, 1973

\- Cephalic capsule 24 µm length and 24 µm wide ....*C. kromensis* FURSTENBERG AND VINCX, 1993

4 Presence of 2 medial holes in the cephalic capsule .... *C. yunfengi* PLATT AND ZHANG, 1982

\- Cephalic capsule without holes 5

5 About 5 µm distance between the 2 circles of head setae ....*C. carinatum* WIESER, 1959

- About 7 µm distance between the 2 circles of head setae ....*C. africana* Furstenberg and Vincx, 1993

6 Buccal cavity with armature 7

- Buccal without armature 8

7 Subcuticular vacuolisation ....*C. chitwoodi* De Coninck, 1942

- No vacuolisation. .... *C. filipjevi* De Coninck, 1942

8 Longitudinal lines between the crests................*C. undulatum* De Coninck, 1942

- No longitudinal lines 9

9 Anterior end of cephalic capsule truncated ....*C. rectum* Gerlach, 1957

- Anterior end of cephalic capsule curved 10

10 Amphid hook like .... *C. attenuatum* Cobb, 1920

- Amphid oval loop like 11

11 Terminal setae on cone of tail male 12

- No terminal setae 13

12 More than 300 annules ....*C. algoensis* Furstenberg and Vincx, 1993

- About 153-209 annules ....*C. adrianae* sp. n.

13 Distance between the 2 circles of head setae 1/10 of the length capsule 14

- Distance between the 2 circles of head setae 3/10 of the length capsule .... *C. pisanum* Gerlach, 1953

14 Cephalic capsule about 40 µm length ....*C. salsicum* Gerlach, 1956

- Cephalic capsule about 30 µm length ....*C. reticulatum* Chitwood, 1936

- Cephalic capsule about 21 µm length ....*C. sculpturatum* Chitwood, 1936

Discussion

The anterior sensory organs of nematodes are arranged in three circles consisting of an outer circle of 4 cephalic setae, a middle circle of 6 outer labial setae and an inner circle of 6 inner labial setae (BIRD AND BIRD, 1991). The 14 *Ceramonema* species described until now have the 6 outer labial setae situated in front of the 4 cephalic setae. This arrangement differs in *Ceramonema adrianae* sp. n. with 6 outer labial setae situated in a posterior circle with the position of the 4 cephalic setae about 1-2 µm in front of the outer labial setae. Other Ceramonematidae genera as *Metadasynemoides* and *Metadasynemella* have the 6+4 cephalic setae in one common circle, while *Pselionema* and *Pterygonema* have only 4 cephalic setae (and papilliform or pore-like labial sensilla).

LORENZEN (1994) mentioned that the ventrally-spiral amphid is a common characteristic in Ceramonematidae (*f.i. Ceramonema africana*); nevertheless in *Ceramonema adrianae* sp. n. the amphids are dorsally wound in the males and ventrally wound in the females.

PLATT AND ZHANG (1982) showed a Pictorial key for 11 species of *Ceramonema*: *C. attenuatum* COBB, 1920; *C. carinatum* WIESER, 1959; *C. chitwoodi* DE CONINCK, 1942; *C. filipjevi* DE CONICK, 1942; *C. pisanum* GERLACH, 1952; *C. rectum* GERLACH, 1957, *C. reticulatum* CHITWOOD, 1936, *C. salsicum* GERLACH, 1956; *C. sculpturatum* CHITWOOD, 1936; *C. undulatum* DE CONINCK, 1942; and *C. yunfengi* PLATT AND ZHANG, 1982. The separation of these 11 species was based on the relative length of the cephalic capsule, the presence or absence of vacuolization, the cephalic setae length, the number of body annules, the presence of elongated anal annules and the presence of terminal setae.

The 16 *Ceramonema* species know to date, including *Ceramonema adrianae* sp. n., were separated on the base of the descriptions from adults specimens, except to *Ceramonema sculpturatum* CHITWOOD, 1936 which was described only from a juvenile.

Rhynchonema ronaldi **sp. n.**

Type material: Holotype ♂$_1$. Paratypes: ♂$_2$-♂$_6$ and ♀$_1$-♀$_5$

Type locality: San Pedro de Manglaralto beach (1°56'30" S and 80°43'30" W) intertidal zone at low water mark, median grain size 245 μm, % silt= 0.40, % gravel= 0.46. Salinity= 33.8 PSU. Collected on 16 June, 2000.

Etymology: The species is dedicated to my son Ronald Cordero.

Measurements

Holotype

♂$_1$

$$\frac{2 \quad 82 \quad M \quad 445}{4 \quad 16 \quad 17 \quad 15} \qquad 517\ \mu m$$

a= 30.6; b= 4.1; c= 7.3; c'= 33.5; spic= 23 μm

Paratype

♀$_1$

$$\frac{2 \quad 76 \quad 326 \quad 406}{4 \quad 18 \quad 18 \quad 17} \qquad 470\ \mu m$$

a= 25.6; b= 4.1; c= 7.9; c'= 27.8; V= 70%

Other measurements see Table 6.2.

Description

Cephalic region elongated forming beak-like neck region (Figures 6.4A, 6.5A and 6.6D). Head diameter is about 4 µm and 16-18 µm at the end of pharynx. Anal body diameter 15-16 µm in the males and 17-18 µm in the females. Cuticle strongly annulated, each annule 2 µm broad, annules being directed forward in the anterior part and backward in the posterior part (about 48% of body length) of the body in the males and posterior to the vulva in the females. Head bears six external labial setae (1.5-2.2 µm length) situated at the same level; they are difficult to distinguish at light microscope, but very obvious at SEM (Figure 6.6C). Stoma is 36-43 µm long in the males (Figure 6.4A) and 38-46 µm long in the females (Figure 6.5A). The amphids are circular, 4 µm diameter (52-61% cbd in females and males respectively) and situated at the level of the base of the stoma. 30-35 annules lie between the anterior end and anterior edge of amphids (Figures 6.4B, 6.6A, 6.6B). Cervical (4-5 µm long) and somatic setae (7-8 µm long) are located at regular intervals. Pharynx cylindrical and with a moderate bulb; cardia oval (Figures 6.4A, 6.5A). Nerve ring is between 39-43% of the pharynx measured from the base of the stoma. Excretory pore not observed. The female reproductive system is monodelphic, prodelphic and outstretched (Figure 6.5B). The vulva (Figure 6.6F) is situated about 69-71% of the body length. The testes are paired and opposed with the anterior one lying to the left and posterior one to the right side of the intestine. Spicules are protruded after fixation in the specimen examined (Figure 6.6G), 22-23 µm long, arcuate, at proximal cephalated; gubernaculum (10 µm long) is plate-like and has a dorsal apophysis (Figure 6.4C). Tail is conical (Figures 6.4D, 6.6E), about 67-71 µm long in the males and 56-60 µm long in the females.

	Males (n= 6)				**Females** (n= 5)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
L	496	517	503	7.9	419	479	452	28.1
a	29.3	30.6	29.8	0.5	23.7	26.5	25.2	1.2
b	4.1	4.9	4.3	0.3	3.7	4.1	3.9	0.2
c	7.1	7.5	7.3	0.2	7.5	8.3	7.9	0.4
c'	30.7	33.5	31.6	1.1	24.8	28.3	26.5	1.6
HD	4	4	3.8	0.3	4	4	4.0	0.0
stoma	36	43	41.2	2.9	38	46	40.7	3.6
cs	1	1	1.5	0.0	1	2	1.8	0.4
amph w	4	4	4.3	0.3	4	4	4.0	0.2
amph cbd	7	7	7.1	0.4	7	8	7.6	0.4
ph	65	82	76.1	5.9	68	77	74.1	3.4
ph cbd	16	16	16.2	0.0	18	18	18.4	0.0
dsnr	30	34	31.9	1.7	24	30	27.7	3.1
M	17	17	16.9	0.0	18	18	17.9	0.4
da	423	445	432.4	8.4	358	415	392.1	25.3
V					289	334	315.5	19.9
V'					69	71	69.8	0.7
spic	22	23	22.7	0.3				
gub	10	10	10.3	0.0				
abd	15	16	15.9	0.4	17	18	17.1	0.3
t	67	71	68.8	1.5	56	60	57.4	1.5

Table 6.2 Measurements of *Rhynchonema ronaldi* sp. n. from San Pedro de Manglaralto. Mean and standard deviation of the mean (SD).

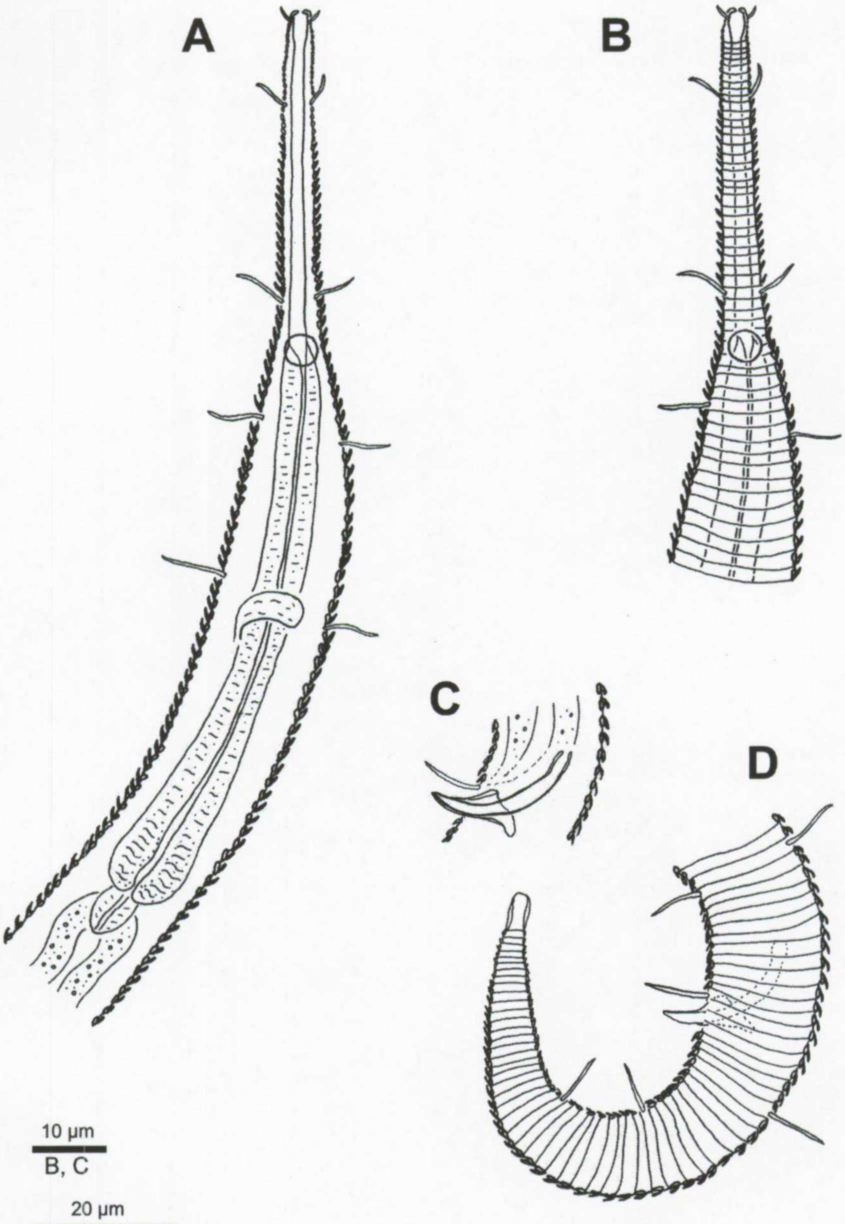


Figure 6.4 ***Rhynchonema ronaldi*** **sp. n. ♂₁. A: Anterior region; B: Head; C: Spicules and gubernaculum; D: Tail and cloacal region.**

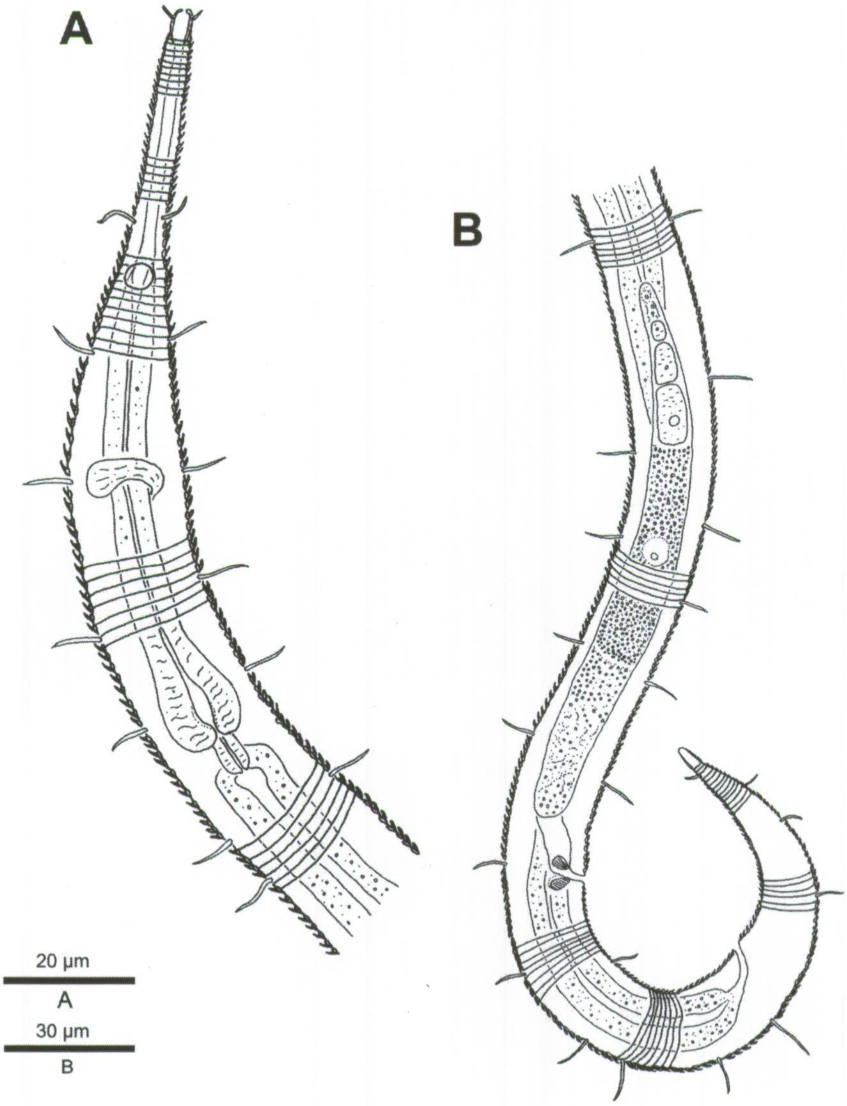


Figure 6.5 ***Rhynchonema ronaldi*** **sp. n. ♀$_1$. A: Anterior region; B: Reproductive system and tail region.**

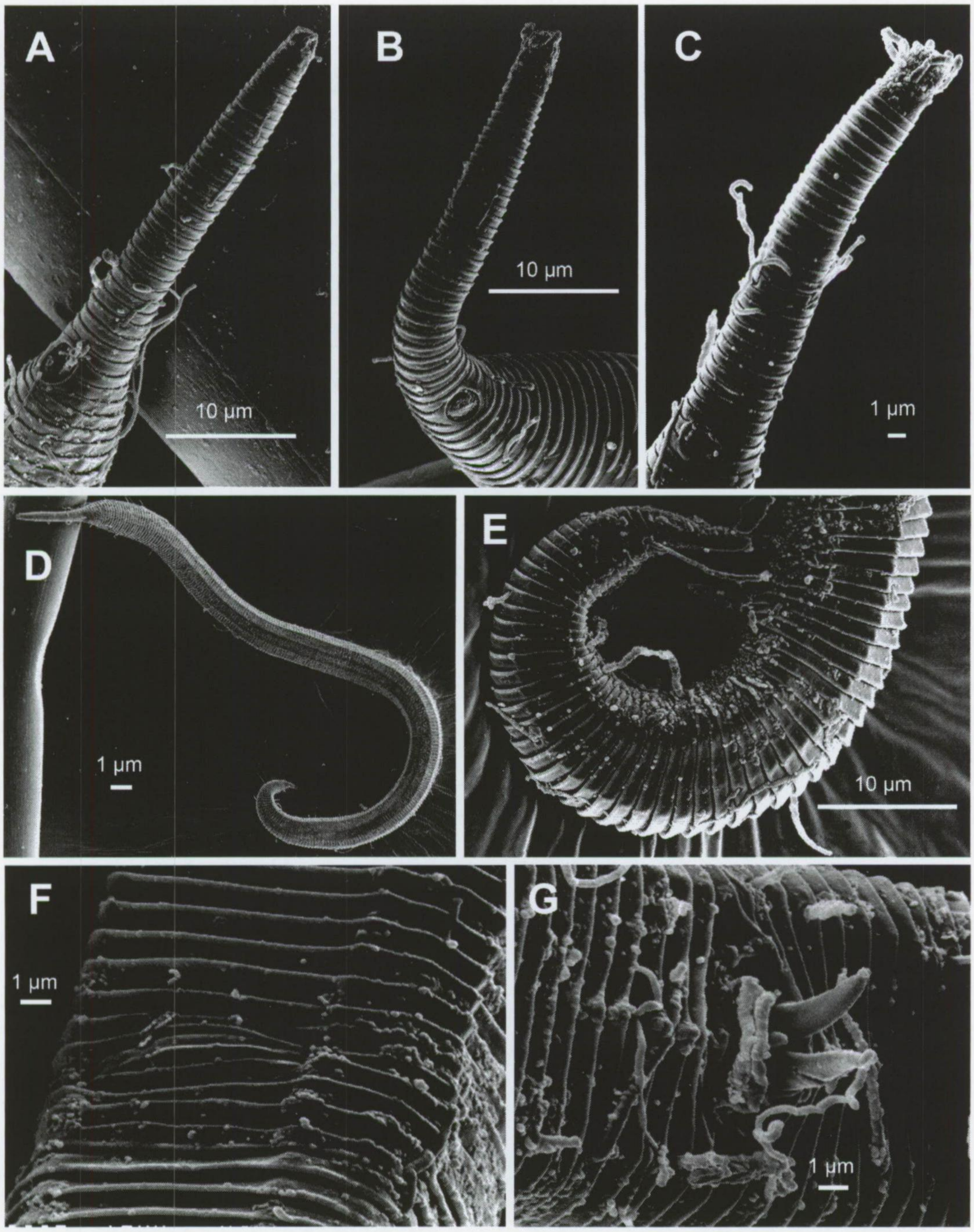


Figure 6.6 **SEM photographs of *Rhynchonema ronaldi* sp. n. A: Head of male; B: Head of female; C: Head of female showing the cephalic setae; D: Total view of male; E: Tail of male; F: Vulva section; G: Spicular apparatus.**

Diagnosis and relationship

Rhynchonema ronaldi sp. n. is characterised by the position of the amphids at the level of the base of the stoma (50-67% cbd) and the shape of the gubernaculum which is plate-like with a dorsal apophysis. The new species is closely related to *Rhynchonema hirsutum* Hopper, 1961 with the spicules equal, curved and the distal end pointed. However *R. hirsutum* has supplementary copulatory organs, which appear to be five openings in the hypodermis.

DISCUSSION

Up to now, the genus *Rhynchonema* contains twenty-eight species, which can be separated into five groups on the base of spicule shape and gubernaculum (except *Rhynchonema wieseri* HOPPER, 1961, only females specimens described):

A. Spicules slightly curved and the distal end is pointed, gubernaculum plate-like: *R. amakusanum* ARYUTHAKA, 1989; *R. chiloense* LORENZEN, 1975; *R. cinctum* COBB, 1920; *R. dispar* GOURBAULT, 1982; *R. fossum* LORENZEN, 1975; *R. hirsutum* HOPPER, 1961 (syn "*R. cinctum*" sensu GERLACH, 1955 and WIESER, 1956); *R. impar* LORENZEN, 1975; *R. kikuchii* ARYUTHAKA, 1989; *R. lyngei* GERLACH, 1953; *R. ornatum* LORENZEN, 1975; *R. ronaldi* sp. n.; *R. scutatum* LORENZEN, 1972; *R. sieverti* GOURBAULT, 1982; *R. subsetosum* MURPHY, 1964 and *R. tremendum* LORENZEN, 1975.

B. Spicules slightly curved and the distal end is pointed, gubernaculum with a distal hook: *R. brevituba* GERLACH, 1953; *R. ceramotos* BOUCHER, 1974; *R. falciferum* BOUCHER, 1974 and *R. longituba* GERLACH, 1953.

C. Spicules slightly curved and the distal end is claw-like: *R. megamphida* BOUCHER, 1974; *R. ambianorum* BOUCHER 1974; *R. deconincki* VITIELLO, 1967 and *R. quemer* BOUCHER, 1974.

D. Spicules slightly curved and the distal end is bifid: *R. gerlachi* VITIELLO, 1967 and *R. moorea* BOUCHER, 1974.

E. Spicules sharply curved as "L-shaped": *R. semiserratum* LORENZEN, 1975, *R. separatum* LORENZEN, 1975.

The fifteen *Rhynchonema* species belonging to group A can be separated into species with equal spicules: *R. amakusanum* ARYUTHAKA, 1989; *R. chiloense* LORENZEN, 1975; *R. cinctum* COBB, 1920; *R. hirsutum* HOPPER, 1961; *R. lyngei* GERLACH, 1953; *R. ornatum* LORENZEN, 1975; *R. ronaldi* sp. n.; *R. scutatum* LORENZEN, 1972; *R. sieverti* GOURBAULT, 1982 and *R. subsetosum* MURPHY, 1964; and species with unequal spicules: *R. dispar* GOURBAULT, 1982; *R. fossum* LORENZEN, 1975; *R. impar* LORENZEN, 1975; *R. kikuchii* ARYUTHAKA, 1989; and *R. tremendum* LORENZEN, 1975.

The new species belongs to group A, with spicules equal; which contains the type species of the genus as well, *Rhynchonema cinctum* COBB, 1920 which has a problem of classification because the author did not provide a drawing of the copulatory apparatus. He described: "Spicules of the male, about as wide as one of the adjacent annules, are slender, rather frail, and sub-acute, and when seen in profile appear to have their proximal ends about opposite or little dorsal from the body axis". This lack of information causes on the species a certain number of confusions that HOPPER (1961) has tried to overcome by creating the new species *Rhynchonema hirsutum* HOPPER, 1961, which has spicules equal (26 µm long), arcuate, cephalated proximally, gubernaculum with caudally directed apophysis and presence of supplementary copulatory organs, which appear to be five openings in the hypodermis. COBB (1920) also described the presence of three papilloid supplementary copulatory organs for *R. cinctum*. Despite of the absence of supplementary copulatory organs, *Rhynchonema ronaldi* sp. n. is related to *R. cinctum* and *R. hirsutum* by the position of the amphid, it is situated at the level of the base of the stoma. Table 6.3 shows the measurements and geographical distribution of the preceding species. The new species differs principally by its smaller dimensions of the stoma length, amphid width and body diameter in the male.

Rhynchonema ronaldi sp. n. differs from the other species with spicules equal (Group A) as follows: in R. *amakusanum*, *R. ornatum* and *R. subsetosum*, the amphid is situated above the posterior end of the stoma; while in *R. chiloense*, *R. lyngei*, *R. scutatum and R. sieverti*, the amphid is situated posterior to the stoma.

Rhynchonema wieseri HOPPER, 1961 (pro "R. cinctum" sensu WIESER 1956) is closely related to *R. cinctum* COBB, 1920, but differs by the size dimensions of the stoma (44 µm vs 36-37 µm long respectively) and the number of the annules (25 vs 30-35 respectively) at the stoma region. Nevertheless only female specimens of *R. wieseri* were observed.

	R. ronaldi sp. n.		*R. cinctum* COBB, 1920		*R. hirsutum* HOPPER, 1961	
n	♂(6)	♀(5)	♂(1)	♀(2)	♂(1)	♀(5)
L	496-517	419-479	596	474-554	533	525-550
a	29.3-30.6	23.7-26.5	27	25	21.3	21-22
b	4.1-4.9	3.7-4.1	3.6	3.6	4.1	3.8-4.0
c	7.1-7.5	7.5-8.3	7.2	7.4	6.7	6.1-6.8
Spic	22-23		21		26	
Stoma	36-46	38-46	54-60		53-55	
amph w	4	4	5	4-5	6	4
V		69-71%		66%		60-67%
Abd	15-16	17-18			21	
Distribution:	Ecuador		Perú, El Salvador, Chile		Gulf of Mexico	

Table 6.3 Measurements and distribution of *Rhynchonema ronaldi* sp. n.; *Rhynchonema cinctum* COBB, 1920 and *Rhynchonema hirsutum* HOPPER, 1961.

Gonionchus ecuadoriensis sp. n.

Paper prepared as

CALLES A, VINCX M
(submitted)

Description of *Gonionchus ecuadoriensis* sp. n., (Nematoda: Xyalidae) a dominant species on Ecuadorian sandy beaches.

Summary

Gonionchus ecuadoriensis sp. n. is described from intertidal zone of an Ecuadorian sandy beach, and is characterised by the longitudinal ornamentations starting at the cervical region and continuing throughout the body to the tip tail; unarmed buccal cavity; equal spicules and the gubernaculum with a small dorsal apophysis. *Gonionchus ecuadoriensis* sp. n. closely resembles *Gonionchus longicaudatus* (Ward, 1972). *Gonionchus ecuadoriensis* sp. n., however has a smaller amphid diameter (2-3 vs 9 µm) in the males and 3-4 vs 7 µm in the females; a shorter tail length (77-104 µm) in the males compared to *G. longicaudatus* (179 µm). A dichotomons identification key of the genus *Gonionchus* is provided to separate the thirteen species into two groups, principally on the presence or absence of longitudinal ornamentations.

KEYWORDS - free-living marine nematodes, new species, identification key, Ecuador.

INTRODUCTION

The Xyalidae, together with the Monhysteridae and Sphaerolaimidae, constitute the Monhysteroidea (LORENZEN, 1978), and are consistent in possessing a single outstretched ovary. LORENZEN (1994), in his phylogenetic analysis of the Adenophorea, established the monophyly of the Xyalidae species by the constant location of the anterior testis on the left and the posterior testis when present on the right side of the intestine.

In the Xyalidae the cuticle is always annulated; the six outer labial and the four cephalic setae are situated at the same level, sometimes with additional cephalic setae in the same crown. Occasionally eight groups of subcephalic setae develop. There may be one or two testes, the anterior one lying to the left of the intestine, the posterior (if present) to the right, but the single anterior outstretched ovary is positioned on the left side of the intestine. The secretory-excretory system is absent in most cases.

Gonionchus species have the cuticle annulated and may have longitudinal ridges; anteriorly extended hyaline lips with the labial setae appearing as pointed extensions; buccal cavity spacious, and can have two ventrosublateral teeth; tail long and conical, without terminal setae.

Gonionchus ecuadoriensis sp. n. is described as a part of the project on environmental management in the Ecuadorian sandy beaches. The main diagnostic features of the new species are related to the cuticle; cephalic region, amphideal fovea; pharyngeal and tail region in male and female. A dichotomons identification key of the genus *Gonionchus* is provided to separate the thirteen species into two groups, principally on the presence or absence of longitudinal ornamentations.

Materials and Methods

Samples were collected at low tide level of the intertidal zone of San Pedro de Manglaralto beach at the Ecuadorian coast (1°56'30" S and 80°43'30" W); plastic cores (surface 10 cm^2) were used to a depth of 10 cm in the sediment. The samples were fixed with hot (60°C) 4% formaldehyde seawater solution, neutralised with lithium carbonate ($LiCO_3$). Nematodes were extracted by decantation and centrifugation with Ludox HS 40 (Heip *et al.*, 1985), and collected on a 38 μm sieve. The organisms were stained with 1% Rose Bengal. The nematodes were transferred through a series of glycerol-ethanol solutions (De Grisse, 1969 & Vincx, 1996) and mounted on aluminum Cobb slides. Measurements and drawings were taken using a camera lucida microscope Olympus CH30RF200. All measurements (not ratios) are in micrometers (μm) (ratios are given by De Man) and all curved structures are measured along the arc. Type material is deposited in the Zoology Museum voor Dierkunde of Ghent University, Belgium (UGMD 104055, 104056 and 104057).

***Gonionchus ecuadoriensis*[1] sp. n.**

(Figures 6.7-6.9)

Measurements

See Table 6.4.

Description

Male: Body elongated and cylindrical; tail tapering with cylindrical end part. Cuticle prominently annulated; annules *ca* 2 µm broad. Longitudinal ornamentation (as rod-like structures) starting at *ca* 24 longitudinal ridges in cervical region and decreasing in number to *ca* 12 in the anal region; ridges present until tail tip.

Six lips very high, weakly cuticularised. Each lip consisting of a basal part, which is separated from an apical part by a rather well pronounced boundary. Apical part ending in a flap-like protrusion. Six internal labial setae 6-8 µm long, projecting from outer anterior wall of basal part of lips. Six external labial setae 10 µm long and not segmented; four cephalic setae (6-8 µm length) at same level of former. Subcephalic setae absent. Somatic setae scarce.

Amphideal fovea circular (2-3 µm diam. or 11-17% of cbd) situated between 9-14 µm from anterior end.

Buccal cavity unarmed, short and conical. Pharynx cylindrical and muscular throughout its length and partly surrounding buccal cavity; lumen of pharynx is well cuticularised. Cardia 10 µm long. Nerve ring at 28-29% of pharyngeal length from anterior end. Ventral gland and pore not observed.

Diorchic with anterior testis on left side of intestine and posterior testis on right side of intestine. Sperm cells amoeboid (6 µm diameter) with round, dense nucleus. Spicules equal (22-33 µm), slightly curved, cephalated proximally; partly protruded after fixation in the specimens examined. Gubernaculum (11 µm) surrounding distal part of spicules

---

[1] Etymology: the species are dedicated to Ecuador the country of the type locality.

and with small dorsal apophysis. Tail 77-104 µm long, conical at first, then cylindrical and with longitudinal ornamentations. Three caudal gland cells observed. No terminal setae.

Female: External morphology similar to male. Only differences from male are mentioned. Amphideal fovea (3-4 µm diam.), situated between 4-5 µm from anterior end, occupying about 14-18% of corresponding body diam. Reproductive system monodelphic with outstretched anterior ovary situated to left side of intestine. Two pre vaginal gland cells observed. Tail with 72-91 µm long.

	Holotype	Males		Females	
n		7		4	
L	1012	1050.3 ± 17.6	(1005-1120)	1119.0 ± 32.6	(1043-1192)
a	44.0	47.0 ± 1.3	(44.0-52.5)	39.6 ± 0.9	(38.4-42.2)
b	3.6	3.8 ± 0.1	(3.6-3.9)	3.1 ± 0.1	(2.9-3.2)
c	11.8	11.8 ± 0.4	(10.7-13.1)	13.3 ± 0.4	(12.6-14.5)
c'	4.1	4.0 ± 0.2	(3.4-4.9)	3.7 ± 0.1	(3.4-3.9)
Spic	22	27.2 ± 1.8	(22-33)		
V				85.1 ± 0.8	(84-87)

Table 6.4 Measurements of *Gonionchus ecuadoriensis* sp. n. (all measurements in µm).

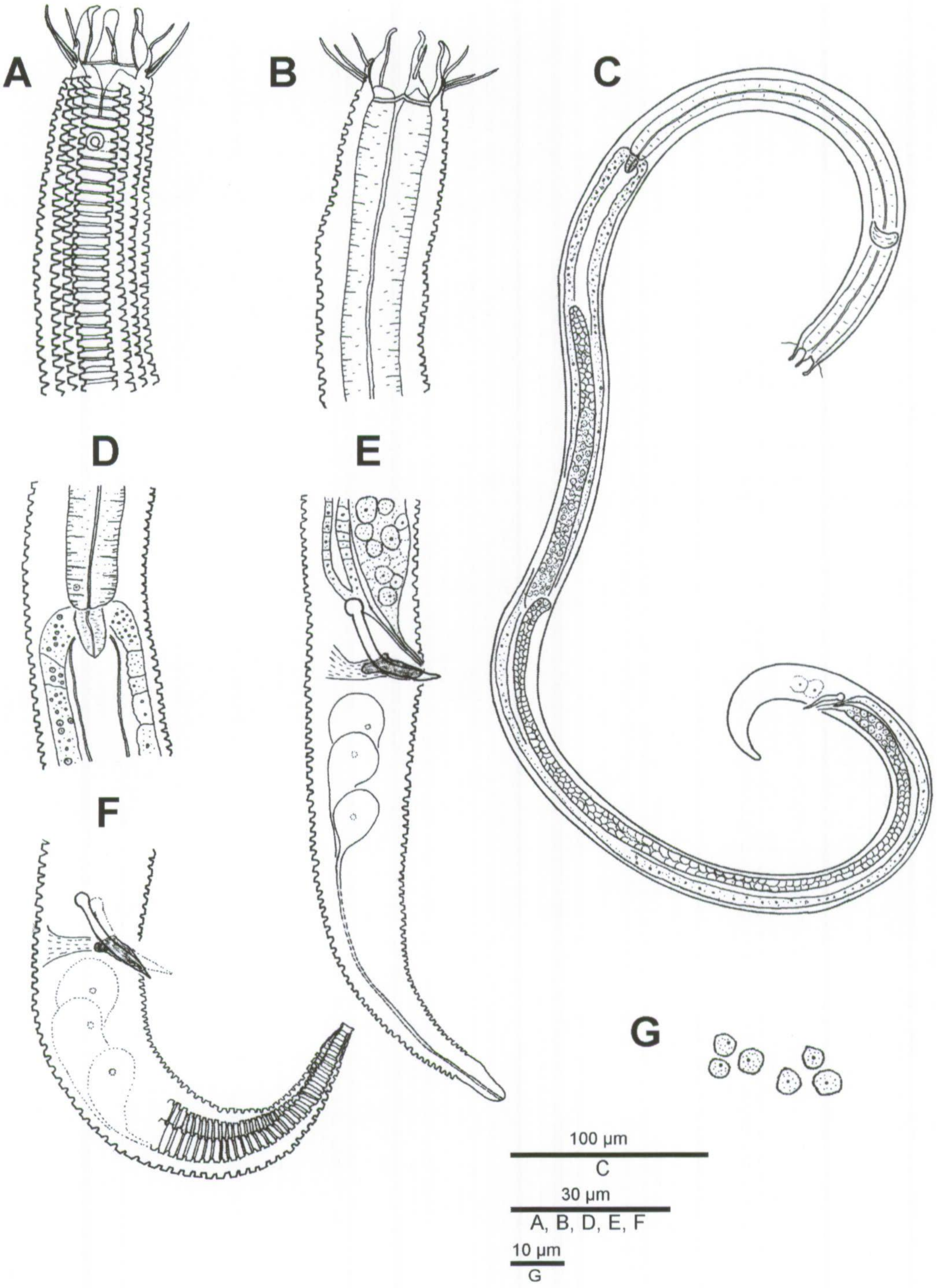


Figure 6.7 ***Gonionchus ecuadoriensis*** **sp. n. Male. A: Head end holotype ♂$_1$; B: Buccal cavity holotype ♂$_1$; C: Total view holotype ♂$_1$; D: Cardial region holotype ♂$_1$; E: Coppulatory apparatus paratype ♂$_2$; F: Tail region holotype ♂$_1$; G: Sperm cells holotype ♂$_1$. Arrows indicate the position of the sperm cell in the testis.**

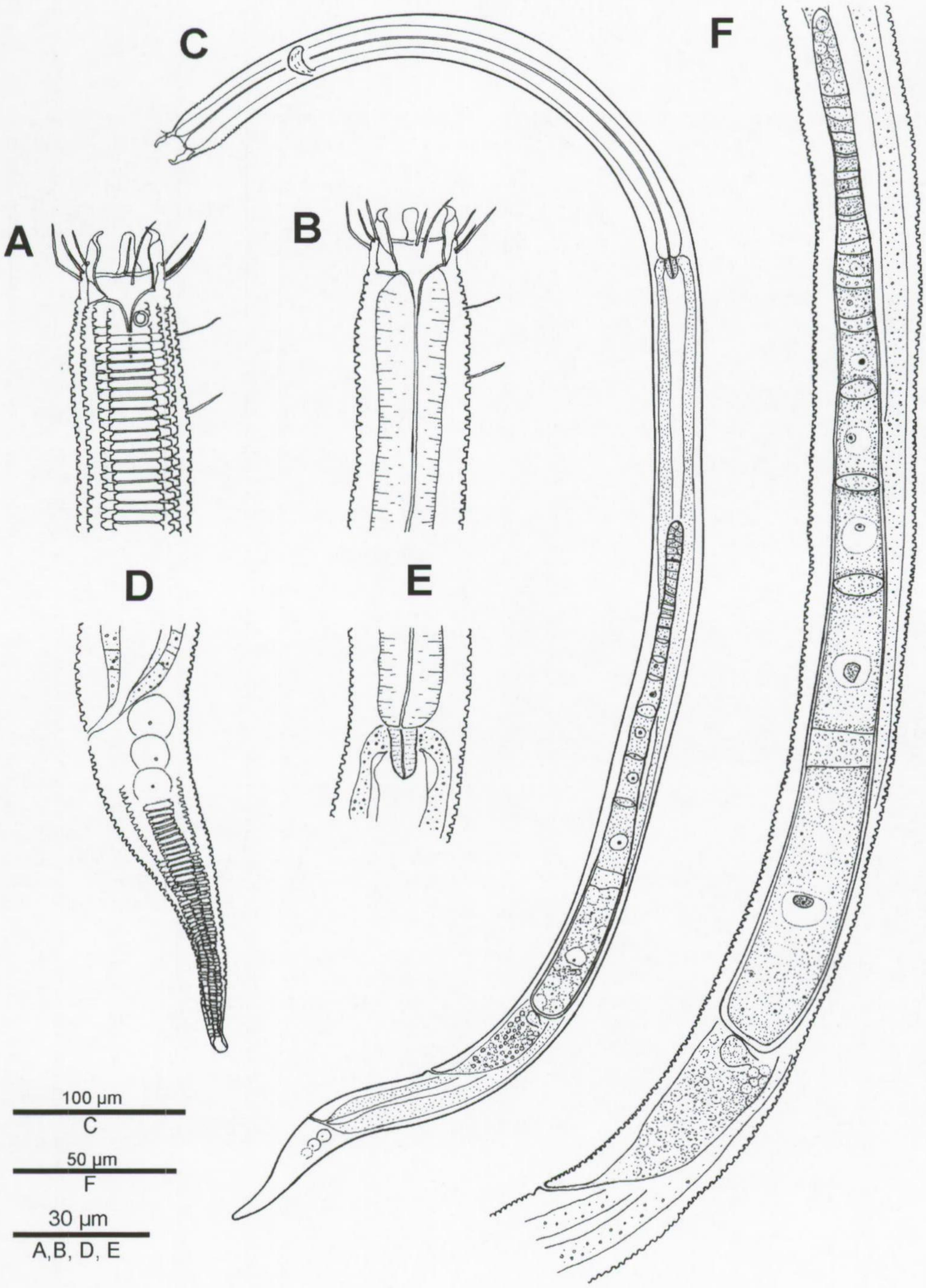


Figure 6.8 ***Gonionchus ecuadoriensis*** **sp. n. Female. A: Head end; B: Buccal cavity; C: Total view; D: Tail region; E: Cardial region; F: Vulva region.**

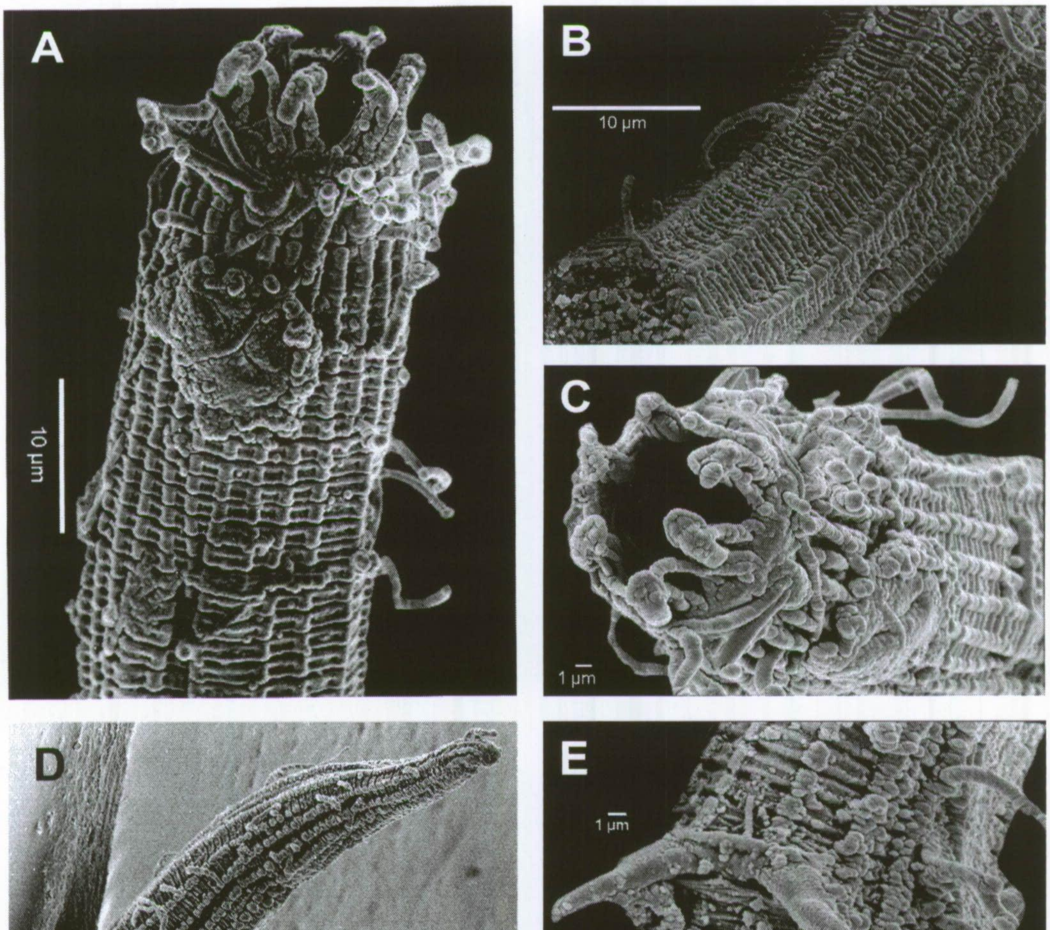


Figure 6.9 *Gonionchus ecuadoriensis* sp. n. A: Head; B: Cuticle ornamentations; C: Buccal cavity and lips; D: Spicular apparatus; E: Tail region.

Diagnosis and relationships

Gonionchus ecuadoriensis sp. n. is characterised by longitudinal ornamentations (as rod-like structures) starting in the cervical region and continuing throughout the body to the tail tip, spicules equal and cephalated and the gubernaculum with a small dorsal apophysis.

Gonionchus ecuadoriensis sp. n. closely resembles *Gonionchus longicaudatus* (Ward, 1972) because the cuticle with longitudinal ornamentations and the absence of ventrosublateral teeth in the buccal cavity. However the size of the amphideal fovea of *G. ecuadoriensis* sp. n. is smaller (diameter= 2-3 µm in the males and 3-4 µm in the females) compared to *G. longicaudatus* (diameter= 9 µm in the males and 7 µm in the females). *Gonionchus ecuadoriensis* sp. n. has a shorter tail (77-104 µm) in the males, compared to *G. longicaudatus* (179 µm).

Type host and locality

Low zone of the intertidal of San Pedro de Manglaralto beach (1°56'30" S and 80°43'30" W) in front of the CENAIM (Centro Nacional de Acuicultura e Investigaciones Marinas) at the Guayas province of the Ecuadorian coast. Fine to medium sand with median particle diameter of the sand fraction= 201 µm; % silt= 1.6; no gravel. Collected on 25 August 1999.

Type material

Seven males and four females. Holotype ♂$_1$ (slide No. UGMD 104055) Paratypes: ♂$_{2\text{-}7}$ (slides No. UGMD 104055 and UGMD 104057), ♀$_{1\text{-}4}$ (slides No. UGMD 104056 and UGMD 104057).

Key for identification of *Gonionchus* Species

1 Cuticle with longitudinal ornamentations 2

\- Cuticle without ornamentations 6

2 Buccal cavity with 2 ventrosublateral teeth 3

\- Buccal cavity unarmed 4

3 Circa 12 ridges in cervical region, tip tail lacking ornamentations ....*G. heipi* VINCX, 1986

\- Circa 24-28 ridges in cervical region and decreasing to ca 12 to anal region and continuous to tip tail...........................*G. alastairi* STEWART AND NICHOLAS, 1994

4 Amphideal fovea *ca* 50% cbd in males and 25% cbd in females ....*G. sensibilis* LORENZEN, 1977

\- Amphideal fovea 11-30% cbd in males and 14-23% in females 5

5 Amphideal fovea 2-3 µm diam. .. ..*G. ecuadoriensis* sp. n.

\- Amphideal fovea 7-9 µm diam .... *G. longicaudatus* (WARD, 1972)

6 Spicules equal 6

\- Spicules unequal ....*G. inaequalis* WARWICK AND PLATT, 1973

7 Gubernaculum with apophysis 8

\- Gubernaculum inconspicuous or without apophysis 11

8 Spicules distally bifid 9

\- Spicules not bifid 10

9 Tail long and filiform ....*G. cumbraensis* BENWELL, 1981

\- Tail short and conical ....*G. africanus* VINCX AND FURSTENBERG, 1988

10 Circa 28 µm between anterior end and amphid ....*G. intermedius* JENSEN, 1986

\- Circa 18 µm between anterior end and amphid ……………………………………………*G. australis* STEWART AND NICHOLAS, 1994

\- Circa 8 µm between anterior end and amphid ………………………………………………………………*G. latentis* FADEEVA, 1984

11 Cephalic setae *ca* 50% of length of external labial setae …………………………………………………………*G. paravillosus* BLOME, 1982

\- Cephalic setae *ca* 75% of length of external labial setae ………………………………………………………………*G. villosus* COBB, 1920

DISCUSSION

Up to now, the genus *Gonionchus* contains thirteen species (including *Gonionchus ecuadoriensis* sp. n.) which can be separated into two groups: a group of eight species without longitudinal ornamentations, *i.e.*, *G. africanus* VINCX AND FURSTENBERG, 1988; *G. australis* STEWART AND NICHOLAS, 1994; *G. cumbraensis* BENWELL, 1981; *G. inaequalis* WARWICK AND PLATT, 1973; *G. intermedius* JENSEN, 1986; *G. latentis* FADEEVA, 1984; *G. paravillosus* BLOME, 1982 and *G. villosus* COBB, 1920 and an other group with five species having longitudinal ornamentations: *G. alastairi* STEWART AND NICHOLAS, 1994; *G. ecuadoriensis* sp. n.; *G. heipi* VINCX, 1986; *G. longicaudatus* (WARD, 1972) and *G. sensibilis* LORENZEN, 1977.

The similarity of the eight species of the first group (excluding *G. inaequalis* which has unequal spicules) is striking. *Gonionchus cumbraensis* and *G. africanus* differ from *G. villosus* by the bifid distal end of the spicules and by the possession of a gubernacular apophysis. *Gonionchus villosus* differs from G. paravillosus by the length of the cephalic setae to the external labial setae (75% vs 50%).

Gonionchus villosus sensu VINCX, 1981, from specimens of the Southern Bight of the North Sea, was synonymised with *G. cumbraensis* by the presence of an obvious gubernacular apophysis (which indicates the difference with the original description of *G. villosus* COBB, 1920).

The presence or absence of marginal tubes in the pharynx in *G. intermedius* was not used in this paper to distinguish them from the other *Gonionchus* species, because probably this structure was not observed nor mentioned in some of the descriptions. *Gonionchus intermedius* differs from *G. latentis* and *G. australis* in the distance between the anterior end and the amphid (28, 18 and 8 µm respectively).

Gonionchus ecuadoriensis sp. n. differs from the species included in the second group as follows: in *Gonionchus heipi* and *G. alastairi* with buccal cavity having two ventrosublateral teeth, also in *G. heipi* the longitudinal ornamentation starts at irregular levels anteriorly and does not continue in the tail tip and the anterior border of the cervical annules cover the posterior border of the preceding annules; *G. alastairi* has longer spicule length than *G. ecuadoriensis* sp. n. (60 µm vs. 22-33 µm); *G. sensibilis* shows sexual dimorphism in the size of amphideal fovea (50% cbd in

the males and 25% cbd in the females) and *G. longicaudatus* with amphideal fovea having longer diam. (9 vs 2-3 µm in the males and 7 vs 3-4 µm in the females).

Acknowledgements

This study was made possible by financial support for VLIR-ESPOL program. We are greatly indebted to the CENAIM foundation for their logistic facilities. Thanks to Rita Van Driessche for the preparation of SEM photos.

CHAPTER VII

General discussion and conclusions

COMPARISON BETWEEN INTERTIDAL ECUADORIAN SANDY BEACHES AND OTHER AREAS.

ZONATION PATTERNS OF THE MEIOFAUNA

Faunal zonation is a distinctive and well described feature of interidal zones and has been much studied by ecologists (reviewed by MCLACHLAN AND JARAMILLO, 1995). Community structure and zonation of the intertidal meiofauna are highly affected by sediment (HICKS AND COULL, 1983; GIERE, 1993) and beach characteristics (MCLACHLAN, 1980; MCLACHLAN *et al.*, 1981). According to COULL (1988) and HEIP *et al.* (1985), the density and diversity of the meiofauna is primary influenced by the median grain size of the sediment. The general zonation scheme for sandy shores was proposed by SALVAT (1964) on the basis of macrobenthic distribution. Based entirely on physical factors, it was subsequently ratified by POLLOCK AND HUMMON (1971) and MCLACHLAN (1980) for the interstitial environment of sandy beaches, in terms of water content the zonation along the beach can be described from the top of the shore downwards into four zones:

- a zone of dry sand above neap high tides which loses capillary and pendular moisture during the low tide and at neap tides. This zone undergoes strong thermal fluctuations and is immersed irregularly. It supports a sparse interstitial meiofauna, typically small nematodes, but dependent on granulometry;
- a next zone is a stratum of retention, which wetted by all tides, but loses capillary water and retains only pendular moisture during low tide. On the surface, most water input here occurs on the mid and later part of the incoming tide. This zone supports the richest interstitial fauna, with harpacticoids and nematodes usually the dominant groups, dependent on granulometry;
- a zone of resurgence consists of wet sand including capillary moisture and marked by intense circulation of interstitial water;
- a zone of saturation at and below the permanent water table, where percolation is slow and marked by groundwater discharge.

The interstitial fauna of beaches is extremely difficult to compare over different geographic areas (cf. MCLACHLAN AND TURNER, 1994). Since very high variability is present in the morphodynamics of the beaches (gradients from reflective over dissipative), the tidal regime level (macro-micro tidal), the nature of the substrate (volcanic, quartz), the seasonality (polar, temperate, tropical) and the anthropogenic influence on the substrate.

In general, the studies of the meiofauna composition in sandy beaches focusing on cross-shore variability show different patterns (MCINTYRE, 1968; GRAY AND RIEGER, 1971; HARRIS, 1972; ANSARI *et al.*, 1984, 1990; OLAFSSON, 1991; RODRÍGUEZ *et al.*, 2001; GHESKIERE *et al.*, 2002, 2005; URBAN-MALINGA *et al.*, 2004 AND KOTWICKI *et al.*, 2005). Table 7.1 summarizes the marine meiofauna densities and major taxon composition on intertidal sandy beaches according to beach type classification*. Total meiofauna densities at the sheltered beaches usually showed highest densities compared with exposed beaches (968-2502 ind./10 cm^2 vs. 7-2131 ind./10 cm^2); the nematodes usually are the dominant taxon in sheltered beaches ranging from 48% to 73% at high tide level and from 25-80% at low tide level; while at exposed beaches meiofauna composition showed larger variability. At exposed beaches the nematodes are represented between 56 and 75% at the high tide level, nevertheless copepods can become dominant (copepods represented 48% of the total meiofauna at the N-E England beach and 70% at the S-W Iceland beach). At low tide level, the exposed beaches showed dominance of nematodes, turbellarians and gastrotrichs. In Ecuador the exposed beach studied showed a dominance of nematodes at both tide levels, representing 61-83% of the total meiofauna density respectively, followed by dominance of copepods at the upper station (29%).

MCLACHLAN AND TURNER (1994) predicted that optimum conditions for the development of a diverse and abundant meiofauna are likely to occur in intermediate beaches; their prediction was based upon the fact that beaches with intermediate morphodynamic characteristics represent an equilibrium state between organic inputs (which increases towards the dissipative beach state) and aerobic interstitial conditions (which increase towards the reflective beach state). Both factors are the most favorable for the presence on meiofauna in intertidal habitats (e.g., GIERE, 1993). In contrast with that

---

* Only those studies were included with detailed information on cross-shore gradients (High Water/Low Water difference). Also See Figure 7.1.

statement, the results of intertidal meiofauna of sandy beaches located in southern Chile (reflective, intermediate and dissipative beaches) (RODRÍGUEZ *et al.*, 2001) showed that the highest meiofauna density occurs at the reflective beach (6172 ind./10 cm^2) as compared with the intermediate beach (3390 ind./10 cm^2) and the dissipative beach (3667 ind./10 cm^2). Also the highest meiofaunal densities occurred at the upper shore level of the reflective and intermediate beaches (4939 ind./10 cm^2 and 5500 ind./10 cm^2 respectively). The meiofauna composition of an intermediate/reflective sandy beach in Ecuador showed a clear cross-shore difference based on the densities of the meiofauna taxa; the differences were caused by highest densities of copepods at the upper station (275 ind./10 cm^2) and highest densities of nematodes at the lower station (738 ind./10 cm^2). The average value of the total meiofauna densities decreased from high water level (963±167ind./10 cm^2) to low water level (890±69 ind./10 cm^2).

GHESKIERE *et al.*, (2005) showed that reflective Italian beaches registered highest meiofauna densities compared with dissipative beaches in Poland (250-950 ind./10 cm^2 vs. 140-190 ind./10 cm^2 respectively), with the highest values at the low water level on both beaches. Nematoda was the dominant meiofauna taxon at each station level (>75%).

Despite the different geographically location of the study sites, it is observed that dissipative beaches registered the highest densities at low water level; while intermediate and reflective beaches (including Ecuadorian beach) showed highest densities at high water level (except in Italy beach).

KOTWICKI *et al.* (2005) investigated two dissipative beaches along the Belgian coast with clear morphodynamic differences: a highly exposed beach and a little exposed beach; at both beaches the different trends of meiofauna densities were observed at the mid-tide zone. The general intertidal zonation of major meiofauna taxa showed that density peaks of nematodes are found at the high water level at both beaches. Also the distribution of turbellarians increased from high water level to low water level.

GRAY AND RIEGER (1971) showed that the high water station of an exposed sandy beach at the north-east coast of England was quantitatively the richest area (162 ind. /10 cm^2) and the low water station was the poorest (81 ind./10 cm^2) in total meiofauna. Harpacticoida were dominant at high level station and represented 48% of the total meiofauna density while Nematoda was dominant at low level station and represented 47% of the total meiofauna density.

The meiofauna assemblage on the southwest coast of Iceland varied considerably both between and within the beaches (OLAFSSON, 1991). The beaches were different in substrate ranging from exposed coarse volcanic sands to sheltered sandy beaches. At the sheltered beach nematodes were dominant at both shore levels (48 and 36% at upper and lower station respectively). At a very exposed beach consisting of very coarse volcanic sediment, the number of turbellarians was highest (up to 699 ind./10 cm^2 or 92 % of the meiofauna at the low water level) and the nematodes increased towards the high water station, from 25 ind./10 cm^2 (5%) to 257 ind./10 cm^2 (59%). At another beach, classified as rather exposed and consisting of medium fine shell sand, the Gastrotricha dominated the low water station (89%), while nematodes dominated the high water station (69%). Copepoda reached 70% of the meiofauna at the high water station of the beach consisting of extremely coarse volcanic sands (highly exposed).

At a sheltered sandy beach in Mombasa, Kenya (ANSARI *et al.*, 1984) the highest number of meiofauna occurred around the high water mark (2502 ind./10 cm^2) and the number dropped gradually (1268 ind./10 cm^2) to the low water level, while at an exposed sandy beach the meiofauna was aggregated downshore and highest numbers were recorded at the low water mark (1717 ind./10 cm^2 and 2131 ind./10 cm^2 respectively). On both beaches, the meiofauna was dominated by nematodes (48-62%) followed by copepods. Along the Belgian coast, a macrotidal, dissipative and little exposed sandy beach (GHESKIERE *et al.*, 2002), Nematoda were dominant (76-97%) followed by Turbellaria. The total meiofauna densities increased from high tide (56±13 ind./10 cm^2) towards the low water mark (1470±303 ind./10 cm^2).

In Ecuador, at the lower station the total meiofauna and nematode densities showed a significant correlation with the distance (as a proxy for elevation); the densities decreased towards the subtidal level (963±167 ind./10 cm^2 at the upper station and 890±69 ind./10 cm^2 at the lower station). Nematodes and meiofaunal densities were significantly positively correlated with rainfall, but only at the low water level. MCLACHLAN *et al.* (1977) found that rain lowered salinities of interstitial water in only the top 5 cm at higher tide levels on a Californian beach has a slight effect on the meiofauna.

The hydrodynamics of each area could influence the infaunal densities by producing differential responses of meiofauna assemblages to physical disturbance. The extent of disturbance is also very important: frequent or continuous, strong/or large-scale disturbance will have a negative effect on the diversity of the meiobenthos, whereas sporadic, less vigorous and small-scale disturbance will have the opposite effect (OLAFSSON *et al.*, 1995).

The meiofauna studied quarterly from August 1999 until February 2001, at a sheltered (highly tourist visited) and an exposed (fisheries activities developed) Ecuadorian sandy beaches at low tide level (CALLES *et al*, 2005) showed highest meiofauna densities at the exposed beach (376-2388 ind./10 cm^2) and the lowest at the sheltered beach (461-1848 ind./10 cm^2). Nematodes dominated at the exposed (76-95%) beach, while at the sheltered beach, nematodes represented 22-81% of the total meiofauna density, followed by the turbellarians (7-76%). SCHRATZBERGER AND WARWICK (1999) reported that in treatments of physical and biological disturbance, the nematodes show most extreme changes as a result of organic enrichment. In our study the turbellarians were more abundant in Salinas (waste water is deposited directly into the bay) during warm months (249-1097 ind./10 cm^2). Turbellarians have been demonstrated being very common in wave-protected areas with little mixing of the sediments (CANNON AND FAUBEL, 1988).

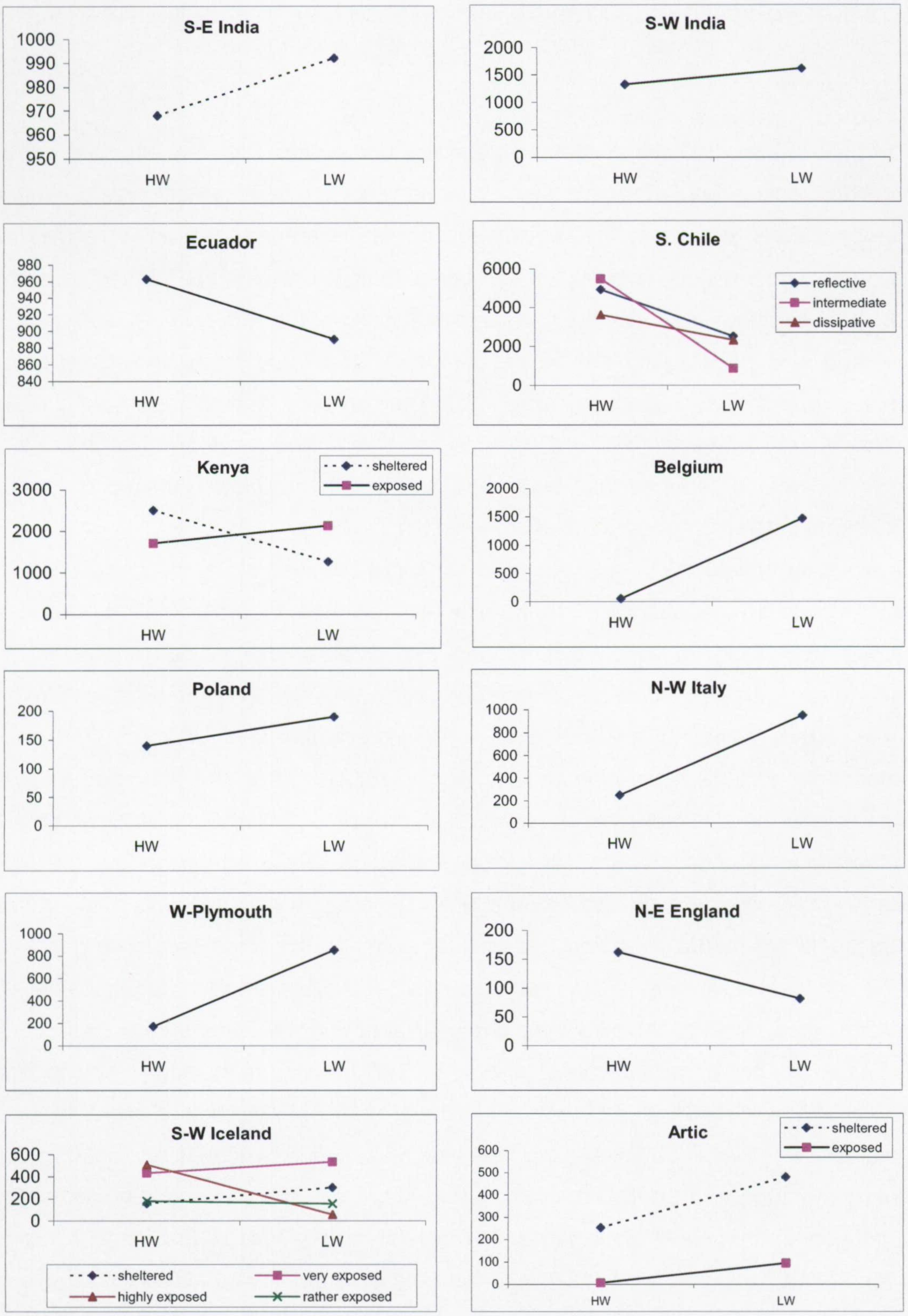
Human trampling (*i.e.* tourism activity) primarily taking place at the upper beach, possible influences the meiobenthic environment. GHESKIERE (2005) found significant differences between tourist and non-tourist beaches at the upper station in the Mediterranean region mainly to a complete loss of Insecta, Harpacticoida, Oligochaeta, terrestrial nematodes and marine Ironidae nematode species. The Baltic region is characterized by the absence of Oligochaeta, Tardigrada, Insecta and terrestrial nematode species. The absence of terrestrial nematodes is most likely due to the destruction of the dunes and probably also a disruption of sub-terranean freshwater connections from the hinterland which terrestrial nematodes use to invade on the beach (GHESKIERE *et al.*, 2004).

Compared with other cross-shore patterns illustrated in literature, the nature of the meiofauna data from the Ecuadorian beach increase the high spatial and temporal variability of the interstitial meiofauna present in sandy beaches world wide.

Therefore, there is not something like a 'typical' sandy beach meiofauna.

Reference	**Locality**	depth (cm)	**Beach type**		**median grain size (µm)**	**HW meio ind/10 cm^2**	**LW meio ind/10 cm^2**	**% NEMAT HW/LW**	**% COPEP HW/LW**	**% TURBEL HW/LW**	**% GASTR HW/LW**
McIntyre, 1968	**S-E India**	20-30	sheltered	fine sand	220-240	968	992	61/80	19/2	<19/14	<19/<1
Gray & Rieger, 1971	**N-E England**	10	exposed	fine sand	191-196	162	81	30/47	48/26	7/23	<1/1
Harris, 1972	**U.K**	50	exposed	medium sand	328	173	852	56/50	28/33	6/2	<1/1
Ansari *et al*., 1984	**Kenya**	15	sheltered	medium sand	300	2502	1268	75/25	3/43	-	-
		15	exposed	fine sand	160	1717	2131	75/63	3/9	-	-
Ansari *et al*., 1990	**S-W India**	10	exposed	medium-coarse coralline sand	270-550	1329	1618	63/46	14/23	10/9	-
Olafsson, 1991	**S-W Iceland**	100	sheltered	coarse shell sand	1255	159	304	48/33	1/7	0/27	0/0
		100	very exposed	coarse volcanic sand	1170	434	537	59/5	0/0	24/92	0/0
		100	highly exposed	extremely coarse volcanic and	2340	509	57	14/26	70/30	8/40	0/0
		100	rather exposed	medium shell sand	355	182	157	69/2	0/0	1/9	1/89
Rodríguez *et al.,* 2001	**S. Chile**	120	reflective	coarse and very coarse sand	1000	4939	2515	50/33	13/50	<1/2	<1/0
		120	intermediate	medium sand	400	5500	868	60/32	30/20	1/5	0/<1
		120	dissipative	fine sand	200	3619	2315	70/66	10/3	1/4	2/4
Urban-Malinga *et al*., 2004	**Artic**	10	sheltered	coarse sand-gravel	900-3800	254	481	73/<1	<1/27	25/72	-
		10	exposed	medium-coarse sand	375-750	7	95	27/8	0/0	55/88	-
Gheskiere *et al*., 2002	**Belgium**	15	dissipative	fine-medium sand	125-250	56	1470	96/97	0/<1	0/1	0/0
Gheskiere *et al*., 2005	**N-W Italy**	15	Intermediate-reflective	coarse sand sand	509	250	950	>75	-	-	-
	Poland	15	Intermediate-dissipative	medium sand	385	140	190	>75	-	-	-
Kotwicki *et al*., 2005	**Belgium**	10	highly exposed-dissipative	fine-medium sand	125-250	52	399	73/41	4/35	17/22	2/0
		10	little exposed-dissipative	fine-medium sand	125-251	83	3385	98/98	0/<1	0/1	0/0
Calles *et al*., 2005	**Ecuador**	20	sheltered	fine sand	184-224	-	461-1848	22-81	0-1	7-76%	0-11%
Present study	**Ecuador**	20	exposed, intermediate-reflective	fine-medium sand	191-301	186-3907	417-1940	61/83	29/<1	1/6	0/9

Table 7.1 Meiofauna densities (ind./10 cm^2) from marine sandy beaches, and the relative abundances of the dominant taxa at high (HW) and low (LW) water level respectively. NEMAT= Nematoda, COPEP= Copepoda, TURBEL= Turbellaria, GASTR= Gastrotricha.



S-E India

S-W India

Ecuador

S. Chile

Kenya

Belgium

Poland

N-W Italy

W-Plymouth

N-E England

S-W Iceland

Artic

Figure 7.1 **Zonation of meiofauna of some sandy beaches. The vertical scale indicated the number of individuals (ind./10 cm^2).**

DISTRIBUTION, SEASONAL PATTERNS AND DIVERSITY OF THE FREE-LIVING MARINE NEMATODES

BLOME (1983) studied the nematode species composition from an intertidal sandy beach on the Island of Sylt (North Sea) over one year. The beach profile was divided in different regions, with dominant species showing a preference for a particular region. The upper and middle regions of the beach slope showed the highest density. *Leptolaimus ampullaceus* and *Enoploides spiculohamatus* were important species here, and also on the sand-flat before the beach slope. Over the whole shore, the dominant species was *Viscosia franzii* (27%) followed by *Microlaimus nanus* (8%), *Metepsilonema emersum* (6%) and *Paracanthonchus longus* (6%). The beach slope is poorer in nematode species than the sand-flat. *Enoplolaimus litoralis* follows horizontal fluctuations of the high-water level over the year.

The intertidal meiofauna from exposed to sheltered beaches along the coast of North Carolina was studied by OTT (1972). He distinguished four associations along a transect from high to low water. These faunal assemblages were affected by temperature, salinity, pore water content and redox potential. In these beaches closely related species, mainly of the genera *Ptycholaimellus*, *Microlaimus*, *Theristus*, *Pomponema* and *Terschellingia* co-exist (OTT, 1972). Within the first four genera, differences in the size of trophic structures (*e.g.* size of teeth in the mouth cavity) exist, so that food partitioning seems to be important. The distribution of the two *Terschellingia* species suggested competition for the same resources. *T. brevicaudata* is limited to the mid-tidal region and out-competes in this area the closely related species *T. longicaudata*, a species that occurs under a wider range of conditions.

The nematode density variability over one-year period in the intermediate Ecuadorian sandy beach ranged between 359 and 1170 ind./10 cm^2 at the lower station and between 188 and 1488 ind./10 cm^2 at the upper station, nevertheless the nematode densities in Ecuador is 50% lower than the Italian and North Sea beaches, but *ca*. 90% higher comparing with the Baltic coast. Cross-shore differences were detected at the Ecuadorian sandy beach, explained by the highest abundances of *Enoplolaimus* sp. 1 (14%), *Metachromadora* sp. 1 (13%) and *Viscosia* sp. 2 (11%) at the upper station, and the highest abundances of *Ceramonema* sp. 1 (19%) and *Ceramonema* sp. 2 (8%) at the lower station. Figure 7.2 shows the distribution of the dominant nematode species on the beach profile along the Ecuadorian beach.

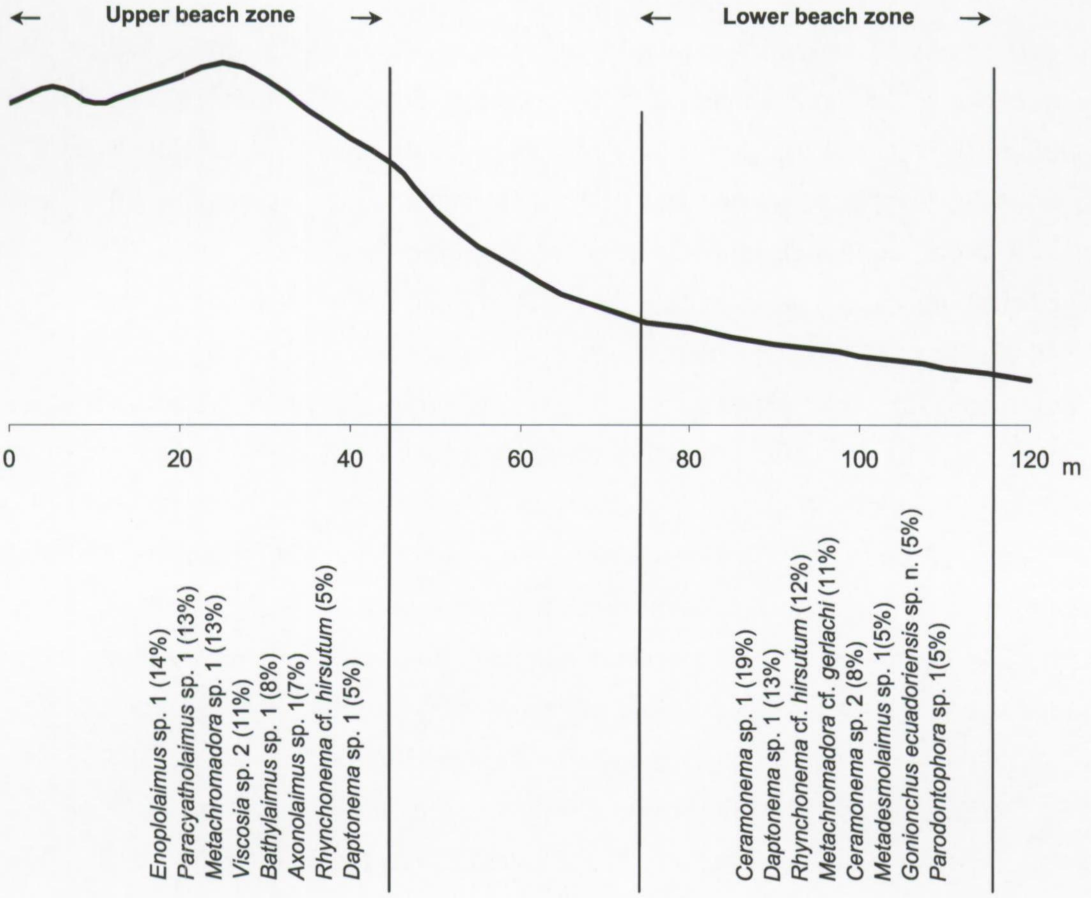


Figure 7.2 Scheme of the species distribution on the profile of an Ecuadorian exposed sandy beach.

TIETJEN (1991) found evidence of differences in species composition on a temporal scale (summer vs spring) at the NE Australian beaches. The genera *Spirinia*, *Molgolaimus* and *Paracanthonchus* were more abundant in January (summer), while *Sabatieria*, *Paracomesoma* and *Metacomesoma* were more abundant in October (spring). Strikingly, the former three genera are epigrowth feeders, while the latter three are non-selective deposit feeders. This observation provides evidence for the hypothesis that community composition is also structured by changes in trophic composition, which is in turn determined by the amount of phytodetritus. Nevertheless, TIETJEN (1991) refuted the existence of seasonal changes in nematode trophic composition and attributed the irregular, short-term fluctuations to changes in sediment temperature.

At the exposed Ecuadorian beaches, at the low tide level the non-selective deposit feeders were the most abundant feeding group of the nematode community (43%), although with fluctuating dominance (4-90%). Three nematode sample groups were found, reflecting seasonal periods: (I) June-December, (II) January and (III) February-May, with the highest dissimilarity between the species groups II and III (71%). These significant differences were largely the result of high abundances of *Daptonema* sp. 1 (490±197 ind./10 cm^2), *Rhynchonema* cf. *hirsutum* (163±18 ind./10 cm^2), and *Paramonohystera* sp. (56±19 ind./10 cm^2) in group II; while *Ceramonema* sp. 1 (208±50 ind./10 cm^2), *Ceramonema* sp. 2 (75±15 ind./10 cm^2), *Metachromadora* cf. *gerlachi* (51±24 ind./10 cm^2), *Microlaimus* sp. (50±9 ind./10 cm^2), *Parodontophora* sp. 1 (43±9 ind./10 cm^2) and *Paracyatholaimus* sp. 1 (21±6 ind./10 cm^2) were abundant in group III. At the high tide level predators/omnivores were dominant (47%) in the nematode community but also with fluctuating dominance (20-80%). Two temporal nematode species associations were observed: May-September and October-April; the separation is explained for the highest abundances of *Axonolaimus* sp. (223±74 ind./10 cm^2) *Bathylaimus* sp. 1 (137±66 ind./10 cm^2), *Metachromadora* sp. 1 (155±6 ind./10 cm^2), *Rhynchonema* cf. *hirsutum* (213±14 ind./10 cm^2) and *Viscosia* sp. 2 (380±132 ind./10 cm^2) found between June and September, followed by a sharp density decline. The presence of different feeding types in the same microhabitat at the same time reflects the ability of nematodes species to partition the available food (LEE *et al.*, 1977). The peak abundance of several nematode species at the upper beach was associated with the presence of a large number of juveniles (654±156 ind./10 cm^2), ranging between 26% (July 2001) and 56% (March 2001) (See Chapter V). This is also the case in the studies of SHARMA AND WEBSTER (1983), describing peak abundance of *Paralinhomoeus buculentus*, *Linhomoeus undulates* and *Sabatieria pulchra* associated with large number of juveniles.

The abilities of free-living species of nematodes to survive short term salinity fluctuations were investigated by FORSTER (1998) in two sites on the east coast of England; throughout the year the salinity ranges between 33 and 35 PSU. *Axonolaimus paraspinosus* and *Cervonema tenuicauda* from the upper intertidal zone; *Daptonema* *oxycerca* from lower intertidal zone and *Sabatieria punctata* from subtidal zone, were studied to assess their ability to osmoregulate under various conditions (3.3, 16.6, 33.3 and 66.6 PSU) of osmotic stress. The results demonstrated that all species were able, to differing extents, to regulate water content. In general, in hypotonic solutions, an initial influx or loss of water was followed by a gradual recovery to water content values approaching those of nematodes in 33.3 PSU. However specific differences in the rate and efficiency of osmoregulation were distinct ranged from no change in body diameter content (*A. paraspinosus*; hypotonic solutions) to extreme expansion and rupture of the cuticle (*D. oxycerca*; hypotonic solutions). The species from the upper shore demonstrated the greatest capacity to osmoregulate and/or tolerate periods of raised body water content. Those results suggested that ability to overcome salinity fluctuations is a factor in determining horizontal distribution of nematode assemblages in littoral habitats. It would be expected that species found at the upper intertidal sites will be able to tolerate osmotic changes and resist the effects of the associated stress more effectively than species from lower intertidal or subtidal sites. In the natural environment, loss of motility during periods of osmotic stress will result in the cessation of normal activities such as feeding. This may be an important negative selection factor for it will undoubtedly have an effect on the long term survival of nematode species in intertidal habitats.

At an exposed sandy beach (S-E Australian), NICHOLAS AND HODDA (1999) found predators (20-63%) and deposit feeders (7-68%) as dominant nematode feeding groups; the total abundance of nematodes was lower at low tide level than at mid or high tide level; this suggested that the results may represent a trend between the tidal levels, or it could be a result of vertical movement. Some species were found more frequently at the upper beach station such as: *Praeacanthonchus* sp., *Comesa* sp. and *Microlaimus* sp. which represented more than 30% of the nematode composition, while *Theristus* sp., *Nicascolaimus punctatus*, *Oxyonchus* sp. and *Gonionchus australis* represented 40% of the nematode composition at the lower beach station. *Onyx* sp. was found on both levels (12% at upper and 20% at lower level).

ALONGI (1986) found that epigrowth-feeding species belonging to genera *Oncholaimus**, *Neochromadora* and *Microlaimus* were numerically dominant in medium to coarse sandy beaches because they possess teeth capable of rasping food particles

---

* ALONGI (1986) on pag. 614 considered Oncholaimus as a 2A-species (although WIESER, 1953 considered it as a 2B).

off large sand grains, while taxa associated with strong hydrodynamic disturbance were *Viscosia*, *Metoncholaimus, Paracyatholaimus, Neochromadora, Paracomesoma and Metalinhomoeus*. Epsilonematidae and the related Draconematidae were indicated as typical outer reef taxa in the study of NETTO *et al.* (1999), who attributed their success in the high-energy environment of the outer reef subtidal to adaptations to high substratum instability. Although all authors stress the existence of distinct communities, the composition of these communities is seldom discussed and preferences are difficult to discover.

Physical disturbance is one of the factors controlling the spatial and temporal composition of marine soft sediment communities (HALL, 1994), which are subjected to a range of natural (NEIRA *et al.*, 2001) and anthropogenic perturbations (GHESKIERE *et al.* 2005). Biological disturbances occur as a result of processes such as foraging by predators (MENN AND ARMONIES, 1999 and MENN, 2002), bioturbation (SCHRATZBERGER AND WARWICK, 1999) and other biotic interactions that cause changes to habitat properties such as sediment stability and permeability. Nevertheless SCHRATZBERGER *et al.* (2002) found under experimental condition that the impacts due to trawling were minor in relation to seasonal changes in the meiofaunal communities, detecting a 50% change in species richness and a 65% change in biomass.

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 these shores the "small food web" (meiofauna) of agile organisms dominates, while organic storage and the "large food web" (macrofauna, epifauna, fish and shorebirds) is important on stable, dissipative and accreting shores (MENN, 2002).

The presence of El Niño and La Niña events in the Ecuadorian coast causes fluctuating climatic conditions, which can have an effect on the meiofauna composition, but more studies will be necessary to compare the temporal patterns under normal and anomalous conditions. The nematode *Daptonema* sp. 1 could be studied as an indicator of the pluviosity fluctuations at the Ecuadorian coast. Nevertheless, the species that occur in estuary habitats are well adapted, not only to low or high salinities, but especially to fluctuations (HEIP *et al.*, 1985). In the paper of HEIP *et al* (1985) it has been recorded nematodes such as *Daptonema oxycerca* and *Metachromadora remanei*, can survive in low salinity conditions up to 35 PSU. During August 1999 (after the 1997-98 El Niño phase) Ecuadorian beaches (CALLES *et al.*,

2005) showed some evidence that ENSO has a substantial influence on nematode species; the most abundant genera *Neochromadora*, *Daptonema* and *Rhynchonema* registered highest densities at the exposed beach and lowest densities at the sheltered beach (63±8.2 vs. 28±0.6, 388±4.2 vs. 55±16.2 and 509±180 vs. 2±0.2 ind./10 cm^2 respectively). Sea Surface Temperature (SST) from the last 13 years for El Pelado station, near our beach of investigation (refer to the page 46 in the thesis) are plotted in the figure 7.3.

VANAGT (2006) found that total macrobenthos densities of Ecuadorian coast were lower during the La Niña phase compared with equal months in the normal phase. *Daptonema* sp. 1 was a dominant nematode species at the lower station and registered highest densities in January 2001 (490±197 ind./10 cm^2); it was related with the pluviosity fluctuations (Figure 7.4), a period also characterized also by lowest salinity concentrations; while at the upper station *Metachromadora* sp. 1, *Viscosia* sp. 2, *Bathylaimus* sp. 1, *Axonolaimus* sp. 1 and *Rhynchonema* cf. *hirsutum* showed the highest densities from June 2000 to September 2000 and a subsequently density decline between October 2000 and April 2001.

Daptonema sp. 1 was found at both stations on the beach; nevertheless at the upper station showed lowest densities (maximum density was in August 2000 with 156±15 ind./10 cm^2). It could be expected that at the upper beach the environmental conditions are extreme and the abundance and distribution of organisms are controlled by physical factors such as extremes of temperature and desiccation (See also KNOX, 2001).

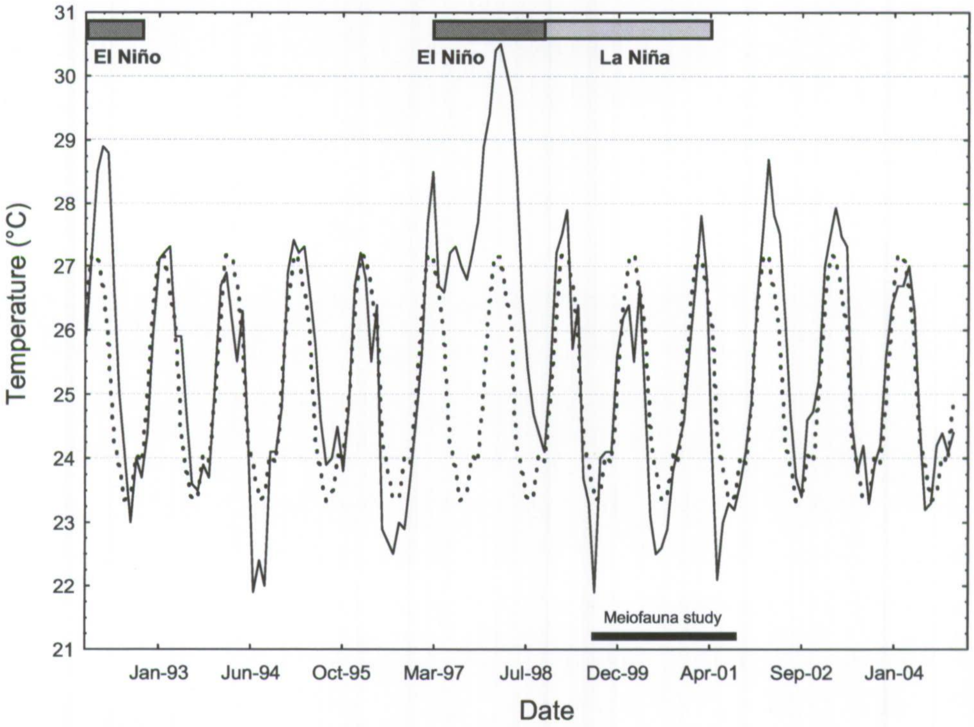


Figure 7.3 SST values from the last 13 years for El Pelado station (full line: actual values; dotted line: long-term average). El Niño and La Niña events are marked at the top of the graph.

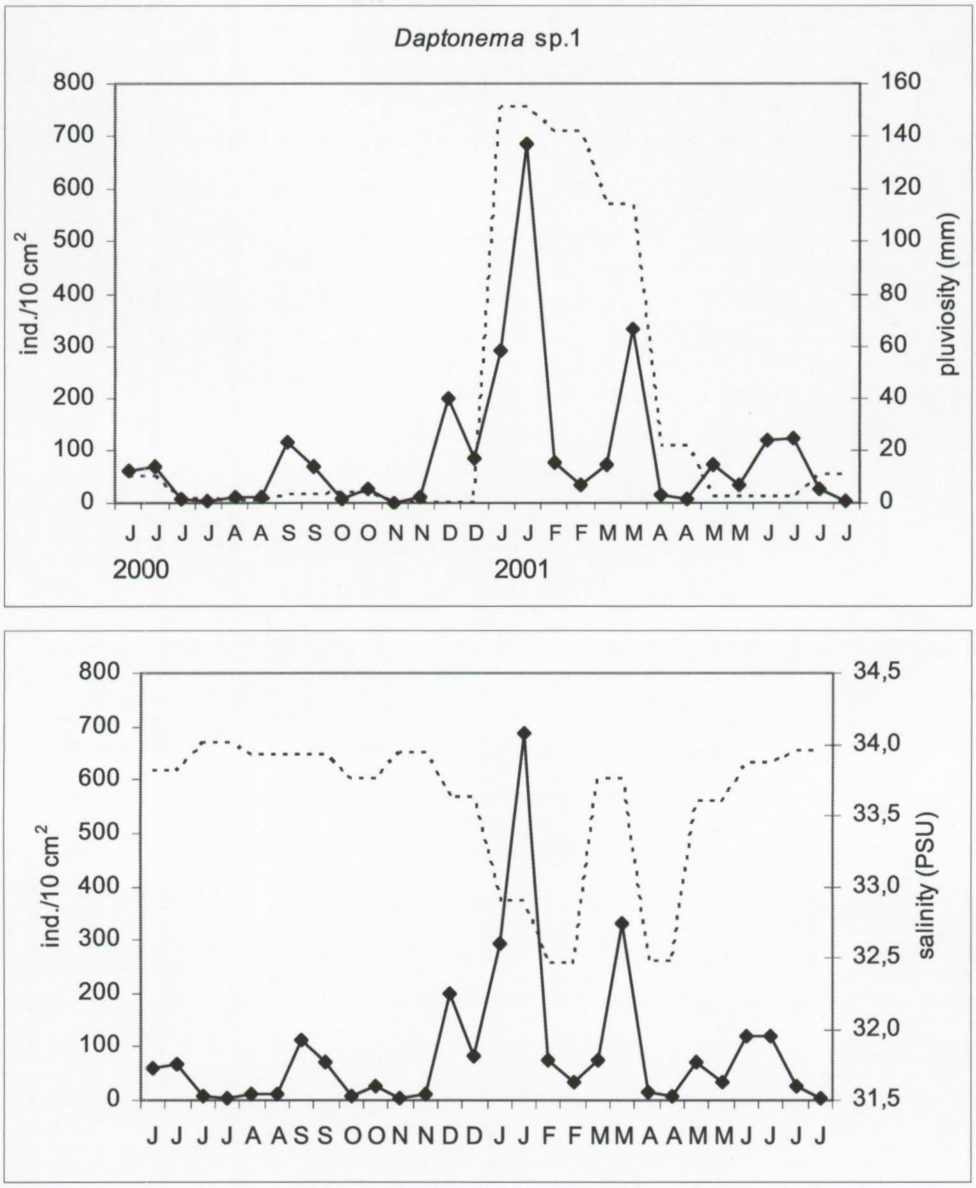


Figure 7.4 **Temporal fluctuations of *Daptonema* sp. 1 at the low tide level, from June 2000 until July 2001 (continuous lines) and salinity and pluviosity values (discontinuous lines).**

Nematoda species richness

The intertidal environment of marine beaches has a particular brackish-water fauna which lives in the coastal subsoil water. This environment is a transition zone between sublittoral, truly marine bottoms and the continental subterranean waters with their phreatic freshwater fauna (HEIP *et al.*, 1985). The nematode species community along the Ecuadorian beach is more an 'estuarine' community (with dominance of *Daptonema* and *Metachromadora*) (See Chapter IV).

Tables 7.2-7.4 shows the percentage of family dominance, number of genera and species of the Ecuadorian marine community (exposed and sheltered beaches) and other nematode sandy beaches studied. We only used the number of species/genera as a value of diversity since from many studies it was possible to calculate the diversity indices. The information present in tables 2-4 has been originally recalculated.

Striking factor on the Ecuadorian beach is the lack of Epsilonematidae and Draconematidae typical for Guadeloupe (12% and 10% respectively), Brasil (Epsilonematidae with more than 50%), Italy (42 and 4% respectively), Australia (only Epsilonematidae with less to 5%), Kenya (RAES, *et al.*, submitted) (6 and 10% respectively) and Zanzibar (RAES, *et al.*, submitted) (2 and 8% respectively); while Xyalidae was the dominant family on Ecuadorian (35%), Belgium (30%), Australian (21%) and Poland (22%) sandy beaches.

A total of 72 species belonging to 48 genera and 20 families were registered at the Ecuadorian sandy beaches (sheltered and exposed); while the study in Australia NICHOLAS AND HODDA (1999) registered 58 species belonging to 48 genera at exposed beaches, in Brasil at an exposed beach (BEZERRA, 2001) 32 species and 28 genera were found, in Guadeloupe island at sheltered and exposed beaches (GOURBAULT *et al.*, 1998) 122 species belonging to 112 genera were found, in Belgium at the dissipative beach (GHESKIERE *et al*, 2004) 88 species belonging to 65 genera occur, in Italy at very exposed beaches (GHESKIERE *et al.*, 2005) 70 species belonging to 49 genera were found, in Poland also at very exposed beaches (GHESKIERE *et al.*, 2005) 67 species belonging to 46 genera and the Canadian Pacific beaches (SHARMA AND WEBSTER, 1983) with medium to coarse grain size (268-813 µm) registered 70 species belonging to 60 genera.

	Family % dominance							
	Ecuador	Australia	Brasil	Guadeloupe	Belgium	Italy	Poland	Canada
Aegiolaimidae					4.70			
Anoplostomatidae	0.07	1.19			0.96		1.86	<1
Anticomidae	1.76					0.01	0.07	<1
Aponchidae								<1
Axonolaimidae	4.25	5.21	0.69		8.36	4.17	9.1	3.7
Ceramonematidae	11.58	0.46					0.07	
Chromadoridae	4.64	5.57	1.08	5.5	8.70	0.41	9.89	2-5
Comesomatidae	0.13		0.24		0.51		0.2	0.07-52
Coninckiidae					0.02			
Cyatholaimidae	9.03	11.53	15.94	2.00	8.40	0.15	0.46	0.97-13
Desmodoridae	16.24	15.14	8.07	3.70	5.25	0.13	3.59	
Desmoscolecidae		<5		3.90				
Diplopeltidae					0.34	0.01	0.6	1.9
Dorylaimidae				1.70		0.75	6.18	
Draconematidae				10.20		3.79		
Enchelidiidae	0.11	0.83	0.09	0.80		0.05	0.13	<1
Enoplidae		5.87						
Epsilonematidae		<5	54.44	11.60		41.62		
Ethmolaimidae		4.43						2-12
Haliplectidae		1.54		4.10		0.02		
Ironidae	0.65	1.24		1.00	0.38	0.53	12.75	
Lauratonematidae				<5		0.18		<1
Leptolaimidae	0.25	1.45		4.30	1.55	0.61	2.86	<1
Leptosomatidae						0.31		
Linhomoeidae	0.18				2.37	0.01	0.73	29.5
Microlaimidae	1.69	5.29	9.25	8.00	2.38	0.1	2.19	<1
Monhysteridae						0.01	2.26	<1
Monoposthiidae					3.60	0.01		<1
Neotonchidae					0.06			
Oncholaimidae	5.6	<5	0.15	2.40	10.28	0.17	2.79	3-4
Oxystominidae	0.25	<5	0.30	2.50		0.03		<1
Paramicrolaimidae							0.13	
Peresianidae							0.13	
Phanodermatidae					0.03			
Rhabditidae		1.78		2.10	3.29	0.47	0.93	<1
Rhabdodemaniidae					0.03	0.18		
Selachinematidae	0.02	<5	0.30	5.80	1.61		0.27	<1
Sipholaimidae					0.18			<1
Sphaerolaimidae	0.004		0.60				0.07	<1
Tarvaiidae					0.54	0.02		
Thoracostomopsidae	5.87	7.78	3.25	2.70	5.77	9.95	6.44	<1
Trefusiidae					0.17			<1
Tripyloididae	3.11	4.3	0.66	2.10	0.81	0.13	14.41	0.2-5
Xyalidae	34.58	21.39	4.91	5.00	29.72	36.19	21.91	0.8-5
TOTAL	100	100	100	79.4	100	100	100	77-81

Table 7.2 **Comparison of relative abundance of nematode families between the Ecuadorian beaches and temperate and tropical areas.**

	Number of genera							
	Ecuador	Australia	Brasil	Guadeloupe*	Belgium	Italy	Poland	Canada**
Aegiolaimidae					2			
Anoplostomatidae	1	2			1		1	1
Anticomidae	2					1	1	1
Aponchidae								1
Axonolaimidae	3	2	1		3	2	1	3
Ceramonematidae	2	2					1	
Chromadoridae	2	5	2	4	5	2	5	6
Comesomatidae	1		1		2		2	1
Coninckiidae					1			
Cyatholaimidae	2	2	4	2	4	1	3	6
Desmodoridae	3	2	3	4	5	4	1	
Desmoscolecidae		1		2				
Diplopeltidae					1	1	1	1
Dorylaimidae				1		2	2	
Draconematidae				2		1		
Enchelidiidae	3	1	1	1		2	1	3
Enoplidae		1						
Epsilonematidae		2	2	5		1		
Ethmolaimidae		1						1
Haliplectidae		1		1		2		
Ironidae	2	3		1	1	2	2	
Lauratonema				1		1		1
Leptolaimidae	2	2		3	2	3	2	1
Leptosomatidae						1		
Linhomoeidae	4				5	1	2	7
Microlaimidae	1	1	2	2	2	2	3	1
Monhysteridae						1	2	2
Monoposthiidae					1	1		1
Neotonchidae					1			
Oncholaimidae	4	2	1	2	4	3	2	2
Oxystominidae	3	1	1	2		2		2
Paramicrolaimidae							1	
Peresianidae							1	
Phanodermatidae					1			
Rhabditidae		1		1	1	1	1	1
Rhabdodemaniidae					1	1		
Selachinematidae	1	1	1	1	4		2	1
Sipholaimidae					1			3
Sphaerolaimidae	1		1				1	1
Tarvaiidae					1	1		
Thoracostomopsidae	1	7	2	1	2	4	1	2
Trefusiidae					2			1
Tripyloididae	1	1	1	1	1	1	2	3
Xyalidae	9	7	5	4	11	5	5	7
TOTAL	48	48	28	41	65	49	46	60

* Number of genera provided from the Table 3 in the publication (Gourbault *et al*., 1998)

** Number of genera provided from the Table 3 in the publication (Sharma & Webster, 1983)

Table 7.3 Comparison of nematode genera number between the Ecuadorian beaches and temperate and tropical areas.

	Number of species							
	Ecuador	Australia	Brasil	Guadeloupe*	Belgium	Italy	Poland	Canada**
Aegiolaimidae					2			
Anoplostomatidae	1	2			1		1	1
Anticomidae	3					1	1	1
Aponchidae								1
Axonolaimidae	5	2	1		6	2	3	3
Ceramonematidae	4	2					1	
Chromadoridae	2	6	2		8	3	8	7
Comesomatidae	1		1		3		2	3
Coninckiidae					1			
Cyatholaimidae	5	2	5		6	2	3	7
Desmodoridae	5	3	3		5	4	1	
Desmoscolecidae		1						
Diplopeltidae					1	1	1	2
Dorylaimidae						3	3	
Draconematidae						1		
Enchelidiidae	3	1	1			2	1	3
Enoplidae		1						
Epsilonematidae		2	3			1		
Ethmolaimidae		1						1
Haliplectidae		1				2		
Ironidae	2	3			1	4	2	
Lauratonematidae						2		1
Leptolaimidae	2	2			3	3	5	1
Leptosomatidae						2		
Linhomoeidae	4				4	1	2	8
Microlaimidae	1	2	2		4	3	4	2
Monhysteridae						1	2	2
Monoposthiidae					2	1		1
Neotonchidae					1			
Oncholaimidae	7	2	1		4	4	3	4
Oxystominidae	3	1	1			2		2
Paramicrolaimidae							1	
Peresianidae							1	
Phanodermatidae					1			
Rhabditidae		1			1	1	1	1
Rhabdodemaniidae					1	1		
Selachinematidae	1	1	1		4		2	1
Sipholaimidae					1			3
Sphaerolaimidae	1		1				1	1
Tarvaiidae					1	1		
Thoracostomopsidae	4	9	3		4	8	4	2
Trefusiidae					2			1
Tripyloididae	2	2	1		1	1	5	3
Xyalidae	16	11	6		20	13	9	8
TOTAL	72	58	32		88	70	67	70

* Number of species (122) is not complete in the publication (Gourbault *et al*., 1998).

** Number of species provided from the Table 3 in the publication (Sharma & Webster, 1983)

Table 7.4 **Comparison of nematode species number between the Ecuadorian beaches and temperate and tropical areas (for references see text).**

CONCLUSIONS

The ecological survey of the meiofauna of Ecuadorian sandy beaches, with emphasis on the species distribution of free-living marine nematodes, revealed that:

- Meiofauna and nematode community differences were found between tourist and non-tourist beaches respectively situated in a sheltered and in an exposed site. Differences with regard to the temporal variation were observed as well: so each beach, clearly different in sediment texture, does have an own meiofauna and nematode composition. The maximum total meiofauna densities at the sheltered beach were 22% lower than the exposed one. Although Nematoda was the dominant taxon, at the sheltered beach turbellarians became dominant in May 2000 and February 2001 (during the warm period and most visited month for the tourists). At both beaches lowest diversity occurred in August 1999 (influenced by “La Niña” event), while at the sheltered beach the highest diversity ocurred in February 2001 and at the exposed beach the highest diversity ocurred in February and November 2000.

- Meiofauna cross-shore pattern were observed and explained by differences between the high water level (upper station) (with dominance of nematodes and copepods) and the low water level (lower station) (mainly dominance of nematodes) and with the season (densities increased during rainy season at the lower station). The average total meiofauna densities decreased from high water level towards low water level, nevertheless no significant differences were detected.

- Nematoda assemblages were associated with the seasonal period (dry versus rainy). Highest dominance of nematode species was found during January 2001 (maximum rainfall month); at the same time lowest diversity was registered. Interesting correlations are detected between rainfall and nematode species composition, in such a way that *Daptonema* sp.1 can be considered as a bio-indicator for excess in rainfall (although not very much reflected in a decrease of salinity of the overlying sea water).

- Nematode cross-shore differences were detected, explained by the highest abundances of *Enoplolaimus* sp. 1, *Viscosia* sp. 2 and *Metachromadora* sp. 1 (predatory nematodes) at the upper station, and the highest abundances of *Ceramonema* sp. 1 and *Ceramonema* sp. 2 (deposit feeders) at the lower station.

RELEVANCE AND FUTURE PERSPECTIVES

This research is the first scientific contribution to the study of meiofauna and free-living marine nematodes on the coastal Ecuadorian beaches related with spatial and temporal patterns.

The Ecuadorian coast is strongly influenced by anomalous El Niño and La Niña events every 2-8 years (Santos, 2006). During the strong anomalous conditions (La Niña 1999) several of the most abundant genera collected, such as *Neochromadora, Daptonema* and *Rhynchonema* registered highest densities, especially at the exposed beach; while at the sheltered beach this period attained lowest densities. Unfortunately the no information on the impacts that ENSO can produce on the biota in our coasts is scarce. Thus, further studies on meiofauna (especially nematodes) during and after an ENSO event are necessarily to evaluate de effects in the sandy beach environment.

The positive correlation between the pluviosity and *Daptonema* sp. 1 at the low water level showed that there is an evidence to use the nematode community structure (dominant species) as a bioindicator in environmental monitoring. This study will provide a basis for future environmental management and legal decision making.

Sediment environmental factors such as temperature, salinity, photosynthetic pigment concentrations and organic matter were not investigated in this study. The missing values must be considered for future sampling campaigns; perhaps, they also could explain the spatial as well as the temporal variability in the abundance of the meiofauna.

During the ecological surveys, many nematode species could not be named and will be probably new to science. The taxonomic descriptions are important to extend the geographical distribution of the species around the world.

REFERENCES

A

AARNIO, K., 2001. The role of meiofauna in benthic food webs of the Northern Baltic Sea. *Acta Academiae Aboensis, Series B* 61, 1-37.

AERTS K., VANAGT, T., DEGRAER, S., GUARTATANGA, S., WITTOECK, J., FOCKEDEY, N., CORNEJO-RODRÍGUEZ, M.P., CALDERÓN, J. & VINCX, M., 2004. Macrofaunal community structure and zonation of an Ecuadorian sandy beach (Bay of Valdivia). *Belgian Journal of Zoology* 134(1): 17-24.

ALONGI, D.M., 1986. Population structure and trophic composition of the free-living nematodes inhabiting carbonate sands of Davies reef, Great Barrier Reef, Australia. *Australian Journal of Marine and Freshwater Research* 37, 609-619.

AMBROSE, W.G., 1984. Role of predatory infana in structuring marine soft-bottom communities. *Marine Ecology Progress Series* 17, 109-115.

ANDRASSY, I., 1973. Nematoden aus Strand- und Höhlenbiotopen von Kuba. *Acta Zoologica Hungarica* 19: 233-270.

ANSARI, A. A., INGOLE, B.S. & PARULEKAR, A.H., 1984. Macrofauna and Meiofauna of two sandy beaches at Mombasa, Kenya. *Indian Journal of Marine Sciences* 13: 187-189.

ANSARI, Z., RAMANI, P., RIVONKER, C.U. & PARULEKAR, A.H., 1990. Macro and meiofaunal abundance in six sandy beaches of Lakzhadweep island. *Indian Journal of Marine Sciences* 19, 159-164.

ARYUTHAKA, C. 1989. Two new species of the genus Rhynchonema (Nematoda, Xyalidae) from Amakusa, south Japan. *Hydrobiologia* 17: 3-10.

AYÓN, H., 1987. Grandes rasgos geomorfologicos de la costa ecuatoriana. *Programa de Manejo de Recursos Costeros* (*PMRC*), Ecuador, 128 pp.

B

BENWELL, M.P., 1981. A new species of *Gonionchus* (Nematoda, Xyalidae) from the Firth of Clyde, with a redescription of *Enoploides spiculohamatus* Schulz (Nematoda, Enoplidae). *Cahiers de Biologie Marine* 22, 177-184.

BEZERRA, T.N., 2001. Nematofauna de uma praia arenosa tropical: Istmo de Olinda-Pernambuco- Brasil. RECIFE. Tesis Universidade Federal de Pernambuco.100 pp.

BIRD, A. & BIRD, J., 1991. The structure of nematodes. Academic Press Inc., 316 pp.

BLOME, D., 1982. Systematik der Nematoda eines Sandstrandes der Nordseeinsel Sylt. *Mikrofauna des Meeresbodens* 86, 1-194.

BLOME, D., 1983. Oekologie der Nematoda eines sandstrandes der Nordseeinsel Sylt. *Mikrofauna Meeresboden* 88, 517-590.

BONGERS, T., ALKEMADE, R. & YEATES, G., 1991. Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. *Marine Ecology Progress Series* 76: 135-142.

BONGERS, T. & FERRIS, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution*, Elsevier Science 14(6), 224-228.

BOUCHER, G., 1974. Six espèces nouvelles du genre *Rhynchonema* (Rhynchonematinae-Nematoda). *Cahiers de Biologie Marine* 15: 447-463.

BUCHANAN, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds), Methods for the study of marine benthos. *Blackwell Scientific Publications*, Oxford, pp. 41-65.

C

CALLES, A., CORNEJO, M.P., DEGRAER, S. & VINCX, M. Temporal variability in the composition and biodiversity of free-living marine nematodes in a tropical beach (Ecuador), submitted.

CALLES, A., DEGRAER, S., VANAGT, T., GHESKIERE, T., CORNEJO, M.P. & VINCX, M. Tropical sandy beach meiofauna: a case study on cross-shore and seasonal patterns in Ecuador, submitted.

CALLES, A., VINCX, M., CORNEJO, P. &, CALDERÓN, J., 2005. Patterns of meiofauna (especially nematodes) in physical disturbed Ecuadorian sandy beaches. *Meiofauna Marina* 14, 121-129.

CANNON, L. & FAUBEL, A., 1988. Turbellaria. In: *Introduction to the study of meiofauna*, Higgins & Thiel (Eds), Smithsonian Institution Press, Washington D.C, 273-282 pp.

CHITWOOD, B. G., 1936. Some marine nematodes from North Carolina. . *Proceedings of Helminthological Society of Washington* 31(1): 1-16.

CLARKE, K. R., 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117-143.

CLARKE, K. R. & GORLEY, R.N., 2001. PRIMER v5: User manual/tutorial. PRIMER-E, Plymouth, UK., 91 pp.

CLARKE, K.R. & WARWICK, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* 216, 265-278.

COBB, N.A., 1920. One hundred new nemas. *Contributions to a Science of Nematology* 9, 217-343.

CORNEJO, M., 1976. Estudio preliminar de los Eufáusidos en el mar ecuatorino. *Instituto Oceanográfico e la Armada* (*INOCAR*), Guayaquil, Ecuador, 1-46 pp.

CORNEJO, M., 1998. Variaciones climáticas: Impacto del Fenómeno de El Niño/Oscilación Sur en la Acuicultura de Ecuador, Boletín CENAIM, in press.

CORNEJO, M.P., 1999. Reporte del proyecto "Variaciones estacionales e interanuales de la climatología de la zona costera ecuatoriana". CONUEP, Ecuador, 154 pp.

COULL, B. C., 1988. Ecology of the marine meiofauna. In: Higgins R.H. & Thiel, H. (Eds) *Introduction to the study of meiofauna*. Smithsonian Institution Press Washington D.C., 18-38 pp.

COVAZZI, A., PUSCEDDU, A., DELLA CROCE, N., & DANOVARO, R., 2000. Spatial and temporal changes in beach meiofaunal communities of the Ligurian Sea (NW Mediterranean). *Revista de Biología Marina y Oceanografía* 35 (1): 57-64.

CRUZ, M., 1983a. Bivalvos del Golfo de Guayaquil. *Acta Oceanográfica del Pacífico* 2(2), 735-819.

CRUZ, M., 1998. Estudio del meiobentos en el Golfo de Guayaquil, (Río Guayas, Canal Cascajal y Estero Salado), Ecuador, en Agosto de 1996. *Acta Oceanográfica del Pacífico*, INOCAR, Ecuador 9 (1), 177-185.

CRUZ, M., GABOR, N., MORA, E., JIMÉNEZ, R. & MAIR, J., 2003. The known and unknown about marine biodiversity in Ecuador (Continental and Insular). *Gayana* 67 (2), 232-260.

CUCALÓN, E., 1986b. Variabilidad oceanográfica frente a la costa de Ecuador durante el período 1981-86. Boletín ERFEN, CPPS 19, 11-26.

CUCALÓN, E., 1989. Oceanographic characteristics of the coast of Ecuador. In: Establishing a Sustainable shrimp Mariculture Industry in Ecuador. Olsen & Arriaga (ed). Technnical report E-6, URI-AID-DIGEMA, 185-194.

D

DAUER, D., EWING, R.M., TOURTELLOTE, G.H., HARLAN, W.T., SOURBEER, J.W. & BARKER, H.R., 1982. Predation, resourse limitation and the structure of benthic infaunal communities of the Lower Chesapeake Bay. *International Review of Gesamten Hydrobiologic* 67 (4), 477-489.

DAVIES, J.L., 1964. A morphogenic approach to world shore-lines. *Zeitschrift fur Geomorphologie* 8, Mortensen Sonderheft, 127-142.

DAVIES, J.L., 1980. Geographical Variation in Coastal Development, 2nd Edition. *Longman*, London, 212 pp.

DAVIES, J.L., 1982a. High-latitude coasts. In Schwartz, M. L (Ed). Encyclopedia of Beaches and Coastal Environments. *Hutchinson Ross*, Stroudsburg, 462-463.

DAVIES, J.L., 1982b. Low-latitude coasts. In Schwartz, M. L (Ed). Encyclopedia of Beaches and Coastal Environments. *Hutchinson Ross*, Stroudsburg, 522-524.

DAVIES, J.L., 1982c. Mid-latitude coasts. In Schwartz, M. L (Ed). Encyclopedia of Beaches and Coastal Environments. *Hutchinson Ross*, Stroudsburg, 543-544.

DAVIS, R.A. & HAYES, M.O., 1984. What is a wave-dominated coast?. *Marine Geology* 60, 313-329.

DE CONICK, L.A.P., 1942. Sur quelques espèces de Nématodes libres (Ceramonematinae Cobb, 1933), avec quelques remarques de systématique. *Bulletin du Museum National d'Histoire Naturelle de Belgique* 18(22), 1-37.

DE GRISSE, A.T., 1969. Redescription ou modification de quelques techniques utilisées dans l'étude des nématodes phytoparasitaires. Mededelingen Rijksfakulteit Landbouwwetenschappen Gent 34, 351-369.

DOMÍNGUEZ, L., FOCKEDEY, N., DE MEY, M., BEYST, B., CORNEJO, M., CALDERON, J. & VINCX, M., 2004. Spatial patterns of the surf zone hyperbenthic fauna of Valdivia Bay (Ecuador). *Hydrobiologia* 529, 205-224.

E

ENFIELD, D., 1976. Oceanografía de la región norte del Frente Ecuatorial: aspectos físicos. FAO Fish Report 185, 299-334.

ESPINOZA, J., 1996. El Niño y sus implicaciones sobre el medio ambiente. Acta Oceanográfica del Pacífico. INOCAR 8 (1), 115-134.

F

FADEEVA, N.P., 1984. The morphology of two new species of free-living nematodes - *Gonionchus latentis* n. sp. and *Amphimonhystera galea* n. sp. from the Sea of Japan. *Nauchnye Doklady Vysshei Shkoly, Biologicheskie Nauki* 7, 44-48.

FIEDLER, P.C., 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Marine Ecology Progress Series* 244, 256-283.

FORSTER, S.J., 1998. Osmotic stress tolerance and osmoregulation of intertidal and subtidal nematodes. *Journal of Experimental Marine Biology and Ecology* 224, 109-125.

FURSTENBERG, J. P. & VINCX, M., 1993. Five new species of the Family Ceramonematidae (Nematoda: Order Chromadorida) from South Africa. *Nematologica* 39, 141-149.

G

Galluci, F., Steyaert, M. & Moens, T. 2005. Can field distributions of marine predacious nematodes be explained by sediment constraints on their foraging success?. *Marine Ecology Progress Series* 304, 167-178.

GEE, J.M., 1989. An ecological and economic review of meiofauna as food for fish. *Zoological Journal of the Linnean Society* 96: 243-261.

genres *Rhynchonema* Cobb et *Prorhynchonema* nov. gen. *Bulletin du Muséum National d'Histoire Naturelle Paris* 4 (4), 75-87.

GERLACH, S.A., 1953. Die Nematodenbesiedlung des Sandstrandes und des Küstengrungwassers an der italienischen Küste. I. Systematischer Teil. *Archivio Zoologico Italiano* 37, 517-640.

GERLACH, S.A., 1953. Die Nematodenfauna der Uferz onen und des Küstengrundwassers am Finnisc hen Meerbusen. *Acta Zoologica Fennica* 73, 1-32.

GERLACH, S.A., 1955. Zur Kenntnis der Freilebenden marinen Namatoden von San Salvador. *Zeitschrift für Wissenschaftliche Zoologie* 158, 249-303.

GERLACH, S.A., 1956. Neue Nematoden aus dem Küstengrundwasser des Golfes de Gascogne (Biskaya). *Vie et Milieu* 6(3), 426-434.

GERLACH, S.A., 1957. Die Nematodenfauna des Sandstrandes an der Küste von Mittel Brasilien (Brasilianische Meeres-Nematoden IV). *Mitteilungen aus dem Zoologischen Museum in Berlin* 33(2), 411-459.

GHESKIERE, T., HOSTE, E., KOTWICKI, L., DEGRAER, S., VANAVERBEKE, J. & VINCX, M., 2002. The sandy beach meiofauna and free-living nematodes from De Panne (Belgium). *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique*, *Biologie* 72, 43-49.

GHESKIERE, T., HOSTE, E., VANAVERBEKE, J., VINCX, M. & DEGRAER, S., 2004. Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium). *Journal of Sea Research* 52, 211-226.

GHESKIERE, T., VINCX, M., URBAN-MALINGA, B., ROSSANO, C., SCAPINI, F., DEGRAER, S., 2005. Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. *Estuarine, Coastal and Shelf Science* 62, 365-375.

GHESKIERE, T., VINCX, M., WESLAWSKI, J.M., SCAPINI, F. & DEGRAER, S., 2005. Meiofauna as descriptor of tourism-induced changes at sandy beaches. *Marine Environmental Research* 60, 245-265.

GIBBS, R. J., MATTHEWS, M.D. & LINK, D.A., 1971. The relationship between sphere size and settling velocity. *Journal of Sedimentary Petrology* 41, 7-19.

GIERE, O., 1993. Meiobenthology: The microscopic fauna in aquatic sediments. *Springer-Verlag*, Berlin, Germany, 325 pp.

GORDON, R.B., 1987. The value of benthic infauna in marine pollution monitoring studies. Marine Pollution Bulletin 18(11), 581-585.

GOURBAULT, N. 1982. Nématodes marins de Guadeloupe. I. Xyalidae nouveaux des genres *Rhynchonema* Cobb et *Prorhynchonema* nov. gen. *Bulletin du Muséum National d'Histoire Naturelle Paris* 4(4), 75-87.

GOURBAULT, N. & WARWICK, R.M., 1994. Is the determination of meiobenthic diversity affected by the sampling method in sandy beaches?. *Marine Ecology* 15, 267-279.

GOURBAULT, N., WARWICK, R.M. & HELLÉOUET, M.N., 1995. A survey of intertidal meiobenthos (especially Nematoda) in coral sandy beaches of Moorea (French Polynesia. *Bulletin of Marine Science*, 57(2), 476-488.

GOURBAULT, N., WARWICK, R.M. & HELLÉOUET, M.N., 1998. Spatial and temporal variability in the composition and structure of meiobenthic assemblages (especially nematodes) in tropical beaches (Guadeloupe, FWI). *Cahiers de Biologie Marine* 39, 29-39.

GOURLAY, M.R., 1968. Beach and Dune Erosion Tests. Delft Hydraulics Laboratory, Report No. M935/M936.

GRAY, J. & R. RIEGER, 1971. A quantitative study of the meiofauna of an exposed sandy beach, at Robin Hood's bay, Yorkshire. *Journal of Marine Biology Association U.K.* 51: 1-19.

GUALANCAÑAY, E., 1983. Foraminíferos bentónicos del Golfo de Guayaquil. *Acta Oceanográfica del Pacífico* 2 (2), 589-657.

H

HALL, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: an Annual Review* 32: 179-239.

HAMELS, I., MOENS, T., MUYLAERT, K., VYVERMAN, W., 2001. Trophic interactions between ciliates and nematodes from an intertidal flat. *Aquatic Microbial Ecology* 26, 61-72.

HARRIS, R.P., 1972. The distribution and ecology of the interstitial meiofauna of a sandy beach at Withsand Bay, East Cornwall. *Journal of the Marine Biology Association of the United Kingdom* 52,1-18.

HAYES, M.O., 1979. Barrier island morphology as a function of tidal and wave regime. In Leatherman, S. P (ed). Barrier Islands. *Academic Press*, New York, 1-27.

Heip, C., 1980. Meiobenthos as a tool in the assessment of marine environmental quality. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 179, 182-187.

HEIP, C., VINCX, M. & VRANKEN, G., 1985. The ecology of marine nematodes. *Oceanography and Marine Biology Annual Review* 23, 399-489.

HICKS, G.R. & COULL, B.C., 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology Annual Review* 21: 67-175.

HIGGINS R.P. & THIEL, H., 1988. Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC, USA.

HILL, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427-432.

HOOGE, M.D., 1999. Abundance and horizontal distribution of meiofauna on a Northern California beach. Pacific Science 53 (3), 305-315.

HOPPER, B.E., 1961. Marine nematodes from the coast line of the Gulf of Mexico, II. *Canadian Journal of Zoology* 39, 359-365.

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

J

JENSEN, P., 1986. The nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. II. Monhysterida. *Zoologica Scripta* 15, 1-11.

JIMÉMEZ, R., 1983. Diatomeas y silicoflagelados del fitoplancton del Golfo de Guayaquil. Instituto Ocenaográfico de la Armada 2(2), 193-281.

K

KOTWICKI, L., DE TROCH, M., URBAN-MALINGA, B., GHESKIERE, T. & WESLAWSKI, J.M., 2005. Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France). *Helgoland Marine Research* 59, 255-264.

KRUSKAL, J.B., 1964. Non-metric multidimensional scaling, a numerical method. *Psychometrika* 29, 115-129.

KENNEDY, A.D., 1994. Predation within meiofaunal commuities: description and results of a rapid-freezing method of investigation. *Marine Ecology Progress Series* 5, 215-221.

KENNEDY, A.D. & JACOBY, C.A., 1999. Biological indicators of marine environmental health: meiofauna – a neglected benthic component?. *Environmental Monitoring and Assessment* 54, 47-68

KNOX, G.A., 2001. The Ecology of Seashores. *CRC Press*, Boca Raton, 557 pp.

L

LAMBSHEAD, P.J.D., PLATT, H.M. & SHAW, K.M., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* 17, 859-874.

LEE, J.J., TIETJEN, J.H., MASTROPAOLO, C. & RUBIN, H., 1977. Food quality and the heterogenous spatial distribution of meiofauna. Helgoländer Wissenschaften Meeresuntersuchungen 30, 272-282.

LORENZEN, S., 1972. Die Nematodenfauna im Verklappungsgebiet für Industrieabwässer norwestlich von Helgoland I. Araeolaimida und Monhysterida. Zoologischer Anzeiger 187, 223-248.

LORENZEN, S., 1975. Rhynchonema Arten (Nematodes, Monhysteridae) aus Südamerika und Europa. Mikrofauna Meeresboden 55, 1-29.

LORENZEN, S., 1977. Revision der Xyalidae (freilebende Nematoden) aus der Grundlage einer kritischen Analyse von 56 Arten aus Nord – und Ostsee. *Veröffentlichungen Institut für Meeresforschung in Bremerhaven* 16, 197-261.

LORENZEN, S., 1978. The system of the Monhysteroidea (Nematodes) - a new approach. *Zoologische Jahrbücher Systematik* 105, 515-536.

LORENZEN, S., 1994. The Phylogenetic Systematics of Freeliving Nematodes. *The Ray Society*, London, 383 pp.

M

MARE, M.F., 1942. A study of a marine benthic community with special reference to the micro-organisms. *Journal of the Marine Biological Association of the United Kingdom* 25, 517-554.

MARTENS, P.M. & SCHOCKAERT, E.R. 1986. The importance of turbellarians in the marine meiobenthos: a review. *Hydrobiologia* 123, 295-303.

MASSAY, S., 1983. Revisión de la lista de los peces marinos del Ecuador. Boletín Científico Técnico. *Instituto Nacional de Pesca*, Guayaquil, Ecuador 6(1), 113 pp.

MASSELINK, G., 1993. Simulating the effects of tides on beach morphodynamics. *Journal of Coastal Research*, Special Issue 15, 180-197.

Mazzola, A., Mirto, S., La Rosa, T., Fabiano, M. & Danovaro, R., 2000. Fish-farming effects on benthic community structure in coastal sediments: analysis of meiofaunal recovery. *Journal of Marine Science* 57, 1454-1461.

MCCUNE, B. & MEFFORT M.J., 1999. Multivariate Analysis of Ecological Data Version 4. MjM Software Design, Gleneden Beach, Oregon.

MCPHADEN, M.J., 1999. Genesis and evolution of the 1997-98 El Niño. *Science*, 950-954.

MCLACHLAN, A., ERASMUS, T. & FURSTENBERG, J.P., 1977. Migrations of sandy beach meiofauna. *Zoologica Africana* 12(2), 257-277.

MCLACHLAN, A., 1980. Intertidal zonation of macrofauna and stratification of meiofauna on high energy sandy beaches in the Eastern Cape, South Africa. *Transactions of the Royal Society of South Africa* 44, 2213-2230.

MCLACHLAN, A., 1981. Exposed sandy beaches as semi-closed ecosystems. *Marine Environmental Research* 4: 59-63.

MCLACHLAN, A., WOOLDRIDGE, T. & DYE, A.H., 1981. The ecology of sandy beaches in Southern Africa. *South African Journal of Zoology* 16, 219-231.

McLachlan, A., Jaramillo, E., Donn, T.E. & Wessels, F., 1993. Sandy beach macrofauna communities and their control by physical environment: a geographical comparison. *Journal of Coastal Research* 15, 27-38.

McLachlan, A. & Turner, I., 1994. The interstitial environment of sandy beaches. *Marine Ecology* 15, 177-211.

McLachlan, A. & Jaramillo, E., 1995. Zonation on sandy beaches. *Oceanography and Marine Biology: an Annual Review* 33, 305-335.

Menn, I. & Armonies, W., 1999. Predatory *Promesostoma* species (Plathelminthes, Rhabdocoela) in the Wadden Sea. *Journal of Sea Research* 41, 309-320.

Menn, I., 2002. Beach morphology and food web structure: comparison of an eroding and an accreting sandy shore in the North Sea. *Helgoland Marine Research* 56, 177-189.

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

Moens, T., Herman, P, Verbeeck, L., Steyaert, M. & Vincx, M., 2000. Predation rates and prey selectivity in two predacious estuarine nematode species. *Marine Ecology Progress Series* 205, 185-193.

Moore, C. & Bett, B., 1989. The use of meiofauna in marine pollution impact assessment. *Zoological Journal of the Linnean Society 96,* 263-280.

Mora, E., 1990. Catálogo de Bivalvos Marinos del Ecuador. Boletín Científico Técnico. *Instituto Nacional de Pesca*, Guayaquil, Ecuador 10(1), 136 pp.

Murphy, D.G., 1964. Rhynchonema subsetosa, a new species of marine nematode, with a note on the genus Phylolaimus Murphy, 1963. Proceedings of Helminthological Society of Washington 31(1), 26-28.

N

Neira, C., Sellanes J., Soto, A., Gutiérrez, D. & Gallardo, V., 2001. Meiofauna and sedimentary organic matter off Central Chile: response to changes caused by the 1997-1998 El Niño. *Oceanologica Acta* 24, 313-327.

Netto, S.A, Attrill, M.J. & Warwick, R.M., 1999. The effect of a natural water-movement related disturbance on the structure of meiofauna and macrofauna communities in the intertidal sand flat of Rocas Atoll (NE Brazil). *Journal of Sea Research* 42, 291-302.

NICHOLAS, W.L. & HODDA, M., 1999. The free-living nematodes of a temperate, high energy, sandy beach: faunal composition and variation over space and time. *Hydrobiologia* 394, 113-127.

NICHOLAS, W.L., 2001. Seasonal variations in nematode assemblages on an Australian temperate beach; the effect of heavy seas and unusually high tides. *Hydrobiologia* 464, 17-26.

NORDSTROM, K.F., 1992. Estuarine Beaches. *Elsevier*, Barking, 255 pp.

NORUSIS, M.J., 1992. SPSS for Windows. Professional Statistics. Release 5.0 SPSS Inc., Chicago.

O

OLAFSSON, E., 1991. Intertidal meiofauna of four sandy beaches in Iceland. *Ophelia* 33(1), 55-65.

OLAFSSON, E., JOHNSTONE, R.W., NDARO, S.G.M., 1995. Effects of intensive seaweed farming on the meiobenthos in a tropical lagoon. Journal of Experimental Marine Biology and Ecology 191, 101-117.

OTT, J.,1972. Studies on the nematode fauna in intertidal sediments. 5th. European Marine Biology Symposium, Piccin, Padua, pp 275-285.

OTVOS, E.G., 1982a. Barrier beaches. In Schwartz, M.L (ed.). Encyclopedia of Beaches and Coastal Environments, *Hutchinson Ross*, Stroudsburg, 123 pp.

OTVOS, E.G., 1982b. High-energy coasts. In Schwartz, M.L (ed.). Encyclopedia of Beaches and Coastal Environments, *Hutchinson Ross*, Stroudsburg, 461 pp.

P

PARSONS, T., MAITA, Y. & LALLI, C., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. *Pergamon Press*, Oxford, England, 173 pp.

PATRA, 1996. Sistemas Biofísicos en el Golfo de Guayaquil. CREARIMAGEN. 223 pp.

PLATT, H., 1984. Classify worms and spot pollution. Marine nematodes may reveal the "health" of the oceans-but only if we are able to distinguish one species from another. *New Scientist Newspaper*, p 28.

PLATT, H.M. & WARWICK, R.M., 1980. The significance of free-living nematode of the littoral ecosystem. In: Price J.H., Irvine, D.E.G. & Farnham, W.F. (eds.). The shore environment, Vol. 2. Ecosystems. *Academic Press*, London, pp. 729-759.

PLATT, H.M. & ZHANG, Z.N., 1982. New species of marine nematodes from Loch Ewe, Scotland. Bulletin of the British Museum of Natural History (Zoology) 42: 227–246.

PMRC (Programa de Manejo de Recursos Pesqueros), 1993. Plan de Manejo de la ZEM San Pedro-Valdivia-Manglaralto, 65 pp.

PLATT, H.M. & WARWICK, R.M., 1983. Free-living Marine Nematodes. Part I British Enoplids. *Cambridge University Press*, Cambridge, 307 pp.

PLATT, H.M. & WARWICK, R.M., 1988. Free-living Marine Nematodes. Part II British Chromadorids. *E. J. Brill and Dr. W. Backhuys*, New York, 502 pp.

POLLOCK, L. & HUMMON, W.D.,1971. Cyclic changes in interstitial water content, atmospheric exposure and temperature in marine beach. *Limnology and Oceanography* 16, 522-535.

R

RAES, M., DE TROCH, M., NDARO, S.G.M., MUTHUMBI, A., GUILINI, K & VANREUSEL, A. The structuring role of microhabitat type in coral degradation zones: a case study with marine nematodes from Kenya and Zanzibar, submitted.

RODRÍGUEZ, J.G., LÓPEZ, J. & JARAMILLO, E., 2001. Community estructure of the intertidal meiofauna along a gradient of morphodynamic sandy beach types in southern Chile. *Revista Chilena de Historia Natural* 74(4), 885-897.

S

SALVAT, B.,1964. Les conditions hydrodynamiques interstitielles des sediment meubles intertidaux et la repartition verticale des la fauna endogee. Academie des Sciences (Paris), *Comptes Rendus* 259, 1576-1579.

SANDERS, H.L., 1968. Marine benthic diversity: a comparative study. *The American Naturalist* 102, 243-282.

SANDULLI, R. & NICOLLA, M., 1991. Response of meiobenthic communities along a gradient of seawage pollution. *Marine Pollution Bulletin* 22, 463-467.

SANTOS, J., 1999. El Niño and La Niña: A Climate Oscillation. In: El Niño event in Ecuador: From disaster to prevention. Comitate Internationazionale per lo Sviluppo dei Popoli, 205 pp.

SANTOS, J., 2006. The impact of El Niño-Southern Oscillation Events on South America. *Advances in Geosciences* 6, 221-225.

SCHRATZBERGER, M. & WARWICK, R.M. 1999. Differential effects of various types of disturbances on the structure of nematode assemblages: an experimental approach. *Marine Ecology Progress Series* 181, 227-236.

SCHRATZBERGER, M, GEE, J.M, REES, H.L., BOYD, S.E. & WALL, C.M., 2000. The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments. *Marine Biology Association of the United Kingdom* 80, 969-980.

SCHRATZBERGER, M., DINMORE, T.A. & JENNINGS, S. 2002. Impacts of trwling on the diversity, biomass and structure of meiofauna assemblages. *Marine Biology* 140, 83-93.

SHARMA, J. & WEBSTER, J.M., 1983. The abundance and distribution of free-living nematodes from two Canadian Pacific beaches. *Estuarine, Coastal and Shelf Science*, 16, 217-227.

SHAW, K.M., LAMBSHEAD, P.J.D. & PLATT, H.M., 1983. Detection of pullution-induced disturbance in marine benthic assemblages with special reference to nematodes. *Marine Ecology Progress Series* 11, 195-202.

SHORT, A. D., 1999. Handbook of beach and Shoreface Morphodynamics. *John Wiley & Sons, Ltd, Chichester*, West Sussex, 379 pp.

STATSOFT, INC., 2001. STATISTICA Data Analysis Software System, Version 6. StatSoft, Inc., Tulsa, OK, USA.

STEWART, A.C. & NICHOLAS, W., 1994. New species of Xyalidae (Nematoda: Monhysterida) from Australian Ocean Beaches. *Invertebrate Taxonomy* 8, 91-115.

T

THRUSH, S.F., 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: Implications of changes in spatial scale for experimental studies. *Australian Journal of Ecology* 24, 344-354.

TIETJEN, J.H., 1991. Ecology of Free-living Nematodes from the Continental Shelf of the Central Great Barrier Reef Province. *Estuarine, Coastal and Shelf Science* 32, 421-438.

U

URBAN-MALINGA, B., KOTWICKI, L., GHESKIERE, T., JANKOWSKA, K., OPALIŃSKI, K. & MALINGA, M., 2004. Composition and distribution of meiofauna, including nematode genera, in two contrasting Artic beaches. *Polar Biology* 27, 447-457.

V

VANAGT, T., BEEKMAN, E., VINCX, M. & DEGRAER, S., 2006. ENSO and sandy beach macrobenthos of the tropical East Pacific: some speculations. *Advances in Geosciences* 6, 57-61.

VILLAMAR, F. 1989. Poliquetos bentónicos del Golfo de Guayaquil. *Acta Oceanográfica del Pacífico* 2(2), 659-733.

VINCX, M., 1981. New and little known nematodes from the North Sea. *Cahiers de Biologie Marine* 22, 431-451.

VINCX, M., 1986. Free-living marine nematodes from the Southern Bight of the North Sea. I. Notes on species of the genera *Gonionchus* Cobb, 1920, *Neochromadora* Micoletzky, 1924 and *Sabatieria* Rouville, 1903. *Hydrobiologia* 140, 255-286.

VINCX, M. & FURSTENBERG, J., 1988. Three new Xyalidae species (Nematoda) from South Africa, with a redefinition of the genus *Xyala* Cobb, 1920. *Cahiers de Biologie Marine* 29, 497-512.

VINCX, M. & HEIP, C., 1991. The use of meiobenthos in pollution monitoring studies: a review. Benthic Communities: Use in Monitoring Point-source Discharges (*Techniques in Marine Environmental Sciences*, No. 16). 50-67.

VINCX, M., 1996. Meiofauna in Marine and Freshwater Sediments. In: Hall, G.S. (Ed.), Methods for the examination of organismal diversity in soils and sediments. *CAB International*, Wallingford, pp. 187-195.

VINCX, M., 1996. The role of meiofauna in marine and freshwater ecosystems. CAB International. Methods for the examination of organismal diversity in soil and sediments (Ed. Hall, G.S.). 195-197.

VITIELLO, P., 1967. Deux nouvelles spèces du genre *Rhynchonema* (Nematoda, Monhysteridae). *Bulletin de la Societe Zoologique de France* 92(1), 113-121.

W

WARD, A.R., 1972. Two new species of *Xyala* (Nematoda, Monhysteroidea) from sublittoral sediments in Liverpool Bay. *Marine Biology* 13, 176-178.

WARWICK, R.M. & PLATT H.M., 1973. New and little known marine nematodes from a Scottish sandy beach. *Cahiers de Biologie Marine* 14, 135-158.

WARWICK, R.M., 1987. Meiofauna: their role in marine detrital systems. In: Moriarty, D.J.W. & Pullin R.S.V. (Eds), *Detritus and microbial ecology in aquaculture*. International Center for Living Aquatic Resources Management, Manila, pp. 282-295.

WARWICK, R.M. & CLARKE, K.R., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* 129, 301-305.

WARWICK, R.M., PLATT, H.M. & SOMERFIELD, P.J., 1998. Free-living Marine Nematodes. Part III Monhysterids. *Field Studies Council*, Shrewsbury, 296 pp.

WARWICK, R.M., PLATT, H.M., CLARKE, K.R., AGARD, J. & GOBIN, J., 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology* 138, 119-142.

WATZIN, M.C., 1983. The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. *Oecologia* 59, 163-166.

WIESER, W., 1953. Die beziehung zwischen Mundhöhlengestalt, Ernährungswiese und Vorkommen bei freilebenden marinen Nematoden. Eine ökologisch-morphologische Studie. *Arkiv für Zoology* 4, 439-483.

WIESER, W., 1956. Free-living marine nematodes. III Axonolaimoidea and Monhysteroidea. *Acta Universitatis Lundensis*, N.F, Avd 2, 52(13), 115 pp.

WIESER, W., 1959. Free-living nematodes and other small invertebrates of Puget Sound beaches. University of Washington. *Publications in Biology*, 19, 1-179.

WILSON, W.H., 1991. Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics* 21, 221-241.

Z

ZAMBRANO, E., 1996. El Niño. Acta Oceanográfica del Pacífico. INOCAR 8 (1), 109-114.

ANNEXES

ANNEX 1

Systematic list of the free-living marine nematodes in the Ecuadorian Sandy beaches based in Lorenzen (1981) classification.

Class ADENOPHOREA (von Linstow, 1905)
Subclass ENOPLIA Pearse, 1942
Order ENOPLIDA Filipjev, 1929
Suborder ENOPLINA Chitwood and Chitwood, 1937
Superfamily ENOPLACEA Dujardin, 1937

Family Thoracostomopsidae Filipjev, 1927
Subfamily Enoplolaiminae de Conink, 1965
Enoplolaimus de Man, 1893
Enoplolaimus sp.
Enoplolaimus sp. 1
Enoplolaimus sp. 2
Family Anoplostomatidae Gerlach and Rieman 1974
Subfamily Anoplostomatinae Gerlach and Rieman 1974
Anoplostoma Bütschli 1874
Anoplostoma sp.
Family Anticomidae Filipjev 1918
Anticoma Bastian, 1865
Odontanticoma Platonova 1976
Odontanticoma sp. 1
Family Ironidae de Man, 1876
Subfamily Thalassironinae Andrassy, 1976
Syringolaimus de Man, 1888
Syringolaimus sp.
Trissonchulus Cobb 1920
Trissonchulus sp.
Family Oxystominidae Chitwood, 1935
Subfamily Oxystomininae Chitwood, 1935
Nemanema Cobb 1920
Wieseria Gerlach 1956
Wieseria sp.
Subfamily Halalaiminae de Coninck, 1965
Halalaimus de Man, 1888
Halalaimus sp.

Superfamily ONCHOLAIMACEA Filipjev, 1916
Family Oncholaimidae Filipjev, 1916
Subfamily Oncholaimellinae de Coninck, 1965
Oncholaimellus de Man, 1890
Viscosia de Man, 1890
Viscosia sp. 1
Viscosia sp. 2
Viscosia sp. 3
Family Oncholaiminae Filipjev, 1916
Metoncholaimus Filipjev, 1918
Oncholaimus Dujardin 1845

Family Enchelidiidae Filipjev, 1918
    Ditlevsenella, Filipjev, 1927
    Ditlevsenella sp.
    Eurystomina Filipjev, 1921
    Eurystomina sp.
    Pareurystomina Micoletzky 1930
    Pareurystomina sp.

Suborder TRIPYLOIDINA de Conick, 1965
  Family Tripyloididae Filipjev 1928
    Bathylaimus Cobb 1864
    Bathylaimus sp.
    Bathylaimus sp. 1

Subclass CHROMADORIA Peare, 1942
  Order CHROMADORIDA Filipjev 1929
   Suborder CHROMADORINA Filipjev 1929
    Superfamily CHROMADOROIDEA Filipjev, 1917

  Family Chromadoridae Filipjev, 1937
   Subfamily Hypodontolaiminae de Coninck, 1965
     Dichromadora Kreis, 1929
     Dichromadora sp.
     Neochromadora Micolettzky, 1924
     Neochromadora sp.
  Family Comesomatidae, Filipjev 1918
   Subfamily Sabatieriinae Filipjev 1934
     Sabatieria Rouville 1903
  Family Cyatholaimidae Filipjev, 1918
   Subfamily Pomponematinae Gerlach and Riemmann, 1973
     Pomponema Cobb, 1917
     Pomponema sp.
   Subfamily Paracanthonchinae de Coninck, 1965
     Paracyatholaimus Micoletzky, 1924
     Paracyatholaimus sp. 1
     Paracyatholaimus sp. 2
     Paracyatholaimus sp. 3
  Family Selachinematidae Cobb, 1915
     Synonchiella Cobb, 1920
     Synonchiella sp.

Superfamily DESMODOROIDEA Filipjev, 1922
  Family Desmodoridae Filipjev, 1922
   Subfamily Molgolaiminae Jensen, 1978
     Molgolaimus Ditlevsen, 1921
     Molgolaimus sp.
   Subfamily Spiriniinae Gerlach and Murphy, 1965
     Metachromadora Filipjev, 1918
     Metachromadora sp. 1

Metachromadora cf. *gerlachi* Gerlach, 1955
Spirinia Gerlach, 1963

Superfamily MICROLAIMOIDEA Micoletzky, 1922
Family Microlaimidae Micoletzky, 1922
Microlaimus de Mann, 1880
Microlaimus sp.

Order LEPTOLAIMINA Lorenzen 1981
Family Leptolaimidae Örley, 1880
Subfamily Leptolaiminae Örley, 1880
Leptolaimus de Man, 1867
Leptolaimus sp.
Subfamily Camacolaiminae Micoletzky, 1924
Camacolaimus de Man, 1889
Camacolaimus sp.
Family Ceramonematidae Cobb 1933
Cermonema Cobb 1920
Ceramonema adrianae sp. n.
Ceramonema sp. 1
Ceramonema sp. 2
Dasynemoides Chitwood 1936
Dasynemoides sp.

Order MONHYSTERIDA Filipjev, 1929
Superfamily MONHYSTEROIDEA de Mann, 1876
Family Xyalidae Chitwood, 1951
Cobbia de Man, 1907
Cobbia sp.
Daptonema Cobb, 1920
Daptonema sp.
Daptonema sp. 1
Daptonema sp. 2
Daptonema sp. 3
Elzalia Gerlach 1957
Gonionchus Cobb, 1920
Gonionchus ecuadoriensis sp. n.
Metadesmolaimus Stekhoven, 1935
Metadesmolaimus sp. 1
Metadesmolaimus sp. 2
Omicronema Cobb, 1920
Omicronema sp. 1
Paramonohystera Steiner, 1916
Paramonohystera sp.
Pseudosteineria Wieser 1956
Rhynchonema Cobb, 1920
Rhynchonema cf. *hirsutum* Hopper 1961

Superfamily SIPHONOAEROMOIDEA Filipjev, 1918
  Family Sphaerolaimidae Filipjev, 1918
    Subfamily Sphaerolaiminae Filipjev, 1918
      Sphaerolaimus Bastian, 1865
  Family Linhomoeidae Filipjev, 1922
    Subfamily Desmolaiminae Schneider, 1926
      Metalinhomoeus de Man, 1907
    Subfamily Eleutherolaiminae Gerlach and Riemann, 1973
      Eumorpholaimus Schulz, 1932
      Eumorpholaimus sp.
    Subfamily Linhomoeinae Filipjev, 1922
      Linhomoeus Bastian, 1865
      Linhomoeus sp.
      Paralinhomoeus de Man, 1907

Superfamily AXONOLAIMOIDEA Filipjev, 1918
  Family Axonolaimidae Filipjev, 1918
      Axonolaimus de Man, 1889
      Axonolaimus sp. 1
      Odontophora Bütschli, 1874
      Parodontophora Timm, 1963
      Parodontophora sp. 1

Beach	Sampling date	Temperature (°C)	Salinity (PSU)	Chlorophyll *a* (mg/l)	SPM (mg/l)	POM (mg/l)	m.g.s (µm)
Salinas	Aug-99	22,5	34	1,1	16,6	4,5	188
	Nov-99	25,5	34	1,1	10,1	5,0	204
	Feb-00	26,5	35	3,7	34,2	8,2	186
	May-00	22,0	36	1,7	20,1	3,2	199
	Aug-00	23,0	36	0,8	290,2	53,5	224
	Nov-00	23,5	35	0,1	61,9	12,7	200
	Feb-01	29,0	35	1,6	66,3	24,5	184
San Pedro	Aug-99	23,0	34	3,2	371,2	40,8	201
	Nov-99	25,5	35	1,3	218,7	20,7	228
	Feb-00	27,0	35	3,3	367,1	20,0	260
	May-00	26,5	36	2,5	639,3	33,9	211
	Aug-00	24,0	36	1,8	50,5	195,4	219
	Nov-00	23,0	36	1,2	1392,4	78,3	223
	Feb-01	28,5	34	3,4	1331,2	70,1	238

ANNEX 2. Environmental variables from Salinas and San Pedro de Manglaralto (August 1999-February 2001); SPM (Suspended Particular Matter); POM (Particular Organic Matter), m.g.s (median grain size).

MEIOFAUNA	Aug-99	Nov-99	Feb-00	May-00	Aug-00	Nov-00	Feb-01
	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE
Nematoda	373,5 ± 61,5	434,0 ± 36,0	799,0 ± 35,0	695,0 ± 38,0	222,5 ± 32,5	850,5 ± 38,5	247,5 ± 19,5
Gastrotricha	52,5 ± 18,5	3,0 ± 1,0	26,5 ± 12,5	30,5 ± 20,5	5,5 ± 1,5	4,0 ± 3,0	2,5 ± 0,5
Turbellaria	30,5 ± 19,5	241,5 ± 7,5	248,5 ± 1,5	1096,5 ± 55,5	232,5 ± 36,5	301,0 ± 20,0	868,5 ± 200,5
Copepoda	1,5 ± 0,5	9,0 ± 2,0	5,0 ± 1,0	1,5 ± 1,5	3,5 ± 0,5	1,5 ± 0,5	0,0 ± 0,0
Nauplii	2,0 ± 2,0	2,0 ± 1,0	4,5 ± 3,5	1,5 ± 0,5	3,0 ± 1,0	1,5 ± 1,5	0,0 ± 0,0
Polychaeta	0,5 ± 0,5	0,0 ± 0,0	0,5 ± 0,5	2,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,0 ± 1,0
Rotifera	0,0 ± 0,0	6,0 ± 1,0	10,0 ± 4,0	3,5 ± 1,5	2,5 ± 1,5	2,0 ± 0,0	0,0 ± 0,0
Ostracoda	0,0 ± 0,0	4,5 ± 3,5	7,0 ± 4,0	2,0 ± 2,0	1,5 ± 0,5	6,0 ± 6,0	0,0 ± 0,0
Isopoda	0,0 ± 0,0	12,0 ± 1,0	63,0 ± 11,0	15,5 ± 2,5	3,0 ± 1,0	1,0 ± 0,0	25,5 ± 4,5
Tardigrada	0,0 ± 0,0	1,0 ± 1,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0

ANNEX 3. Average meiofauna densities (ind./10 cm^2) at Salinas beach from August 1999 to February 2001 (n= 2)

MEIOFAUNA	Aug-99	Nov-99	Feb-00	May-00	Aug-00	Nov-00	Feb-01
	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE
Nematoda	2272,5 ± 125,5	1874,5 ± 206,5	868,0 ± 138,0	811,0 ± 2,0	705,5 ± 14,5	320,5 ± 29,5	649,5 ± 108,5
Gastrotricha	49,0 ± 11,0	19,5 ± 9,5	3,0 ± 1,0	128,5 ± 0,5	38,5 ± 9,5	35,0 ± 4,0	80,0 ± 31,0
Turbellaria	61,5 ± 22,5	26,0 ± 1,0	9,5 ± 7,5	11,5 ± 2,5	48,0 ± 9,0	16,5 ± 4,5	51,5 ± 15,5
Copeppoda	1,0 ± 0,0	2,0 ± 1,0	8,5 ± 0,5	2,0 ± 0,0	1,5 ± 0,5	2,0 ± 0,0	2,5 ± 0,5
Nauplii	2,5 ± 2,5	47,5 ± 7,5	38,5 ± 4,5	4,5 ± 0,5	0,0 ± 0,0	0,5 ± 0,5	7,0 ± 6,0
Polychaeta	1,0 ± 0,0	5,5 ± 0,5	2,5 ± 0,5	4,5 ± 1,5	3,5 ± 0,5	0,5 ± 0,5	2,5 ± 1,5
Rotifera	0,0 ± 0,0	13,5 ± 1,5	13,5 ± 2,5	1,5 ± 0,5	0,0 ± 0,0	0,5 ± 0,5	64,5 ± 6,5
Ostracoda	0,0 ± 0,0	58,5 ± 51,5	5,5 ± 2,5	1,0 ± 1,0	0,0 ± 0,0	0,0 ± 0,0	1,5 ± 0,5
Isopoda	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,5 ± 1,5
Tardigrada	0,0 ± 0,0	3,5 ± 0,5	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Bivalvia	0,0 ± 0,0	0,0 ± 0,0	0,5 ± 0,5	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Cnidaria	0,0 ± 0,0	0,0 ± 0,0	0,5 ± 0,5	0,5 ± 0,5	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0

ANNEX 4. Average meiofauna densities (ind./10 cm^2) at San Pedro de Manglaralto beach from August 1999 to February 2001(n= 2)

Genera	Aug-99	Nov-99	Feb-00	May-00	Aug-00	Nov-00	Feb-01
	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE
Anoplostoma	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,8 ± 0,8
Camacolaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,8 ± 1,8	0,6 ± 0,6	0,0 ± 0,0	0,0 ± 0,0
Ceramonema	0,0 ± 0,0	1,0 ± 1,0	2,2 ± 2,2	1,7 ± 1,7	0,0 ± 0,0	0,0 ± 0,0	0,6 ± 0,6
Daptonema	54,6 ± 16,2	32,7 ± 2,1	142,8 ± 19,2	238,4 ± 11,5	35,9 ± 10,0	115,5 ± 5,5	79,1 ± 22,8
Dichromadora	0,0 ± 0,0	1,4 ± 1,4	5,7 ± 1,3	1,7 ± 1,7	0,0 ± 0,0	23,0 ± 23,0	7,3 ± 2,1
Enoplolaimus	0,0 ± 0,0	7,2 ± 1,1	0,0 ± 0,0	0,0 ± 0,0	12,7 ± 4,7	8,0 ± 0,4	0,8 ± 0,8
Eumorpholaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	10,5 ± 10,5	0,0 ± 0,0	0,0 ± 0,0	0,6 ± 0,6
Halalaimus	3,4 ± 0,8	0,0 ± 0,0	1,8 ± 1,8	0,0 ± 0,0	1,6 ± 0,4	0,0 ± 0,0	0,0 ± 0,0
Metachromadora	2,1 ± 2,1	98,6 ± 4,3	335,0 ± 71,0	10,6 ± 3,4	63,2 ± 8,5	61,5 ± 38,7	38,5 ± 11,4
Metadesmolaimus	203,9 ± 41,7	55,8 ± 5,7	20,3 ± 6,2	29,8 ± 15,5	9,8 ± 6,1	96,4 ± 20,5	23,0 ± 10,5
Metoncholaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,7 ± 1,7	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Neochromadora	27,6 ± 0,6	3,4 ± 0,7	63,4 ± 10,5	273,7 ± 11,9	10,2 ± 2,2	318,7 ± 68,3	28,8 ± 2,2
Oncholaimellus	0,0 ± 0,0	3,8 ± 1,8	0,0 ± 0,0	0,0 ± 0,0	3,0 ± 3,0	12,1 ± 4,6	0,0 ± 0,0
Odontanticoma	0,0 ± 0,0	6,2 ± 2,1	4,0 ± 0,4	0,0 ± 0,0	1,9 ± 1,9	0,0 ± 0,0	0,8 ± 0,8
Odontophora	1,0 ± 1,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Omicronema	9,3 ± 1,0	91,5 ± 11,4	31,7 ± 3,6	29,9 ± 8,5	18,4 ± 3,5	51,4 ± 5,5	17,1 ± 1,6
Oncholaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,6 ± 0,6	0,0 ± 0,0	0,0 ± 0,0
Paracyatholaimus	31,7 ± 29,7	2,1 ± 2,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,6 ± 1,6
Paralinhomoeus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,4 ± 0,1
Paramonohystera	0,0 ± 0,0	30,3 ± 2,5	126,0 ± 6,3	28,2 ± 6,7	5,2 ± 2,7	8,2 ± 4,4	4,7 ± 3,1
Parodontophora	14,2 ± 6,6	6,9 ± 1,3	12,3 ± 5,3	5,3 ± 1,8	9,1 ± 2,9	47,6 ± 1,7	9,1 ± 1,3
Pomponema	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	3,8 ± 3,8	0,0 ± 0,0
Pseudosteineria	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	13,8 ± 1,3	1,6 ± 1,6
Rhynchonema	2,3 ± 0,2	36,5 ± 0,4	34,3 ± 25,5	40,4 ± 15,4	30,1 ± 17,7	22,2 ± 7,0	17,8 ± 1,0
Sabatieria	2,6 ± 2,6	0,0 ± 0,0	0,0 ± 0,0	1,7 ± 1,7	0,0 ± 0,0	21,4 ± 8,9	10,5 ± 1,1
Sphaerolaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,0 ± 1,0	0,0 ± 0,0	0,0 ± 0,0
Spirinia	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,6 ± 0,6	0,0 ± 0,0	0,0 ± 0,0
Synonchiela	1,3 ± 1,3	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Viscosia	19,5 ± 11,2	56,4 ± 29,8	19,4 ± 1,7	19,4 ± 2,0	18,5 ± 7,4	46,9 ± 24,1	3,6 ± 1,1

ANNEX 5. Average nematode densities (ind./10 cm^2) at Salinas beach from August 1999 to February 2001 (n= 2)

Genera	Aug-99	Nov-99	Feb-00	May-00	Aug-00	Nov-00	Feb01
	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE	Av SE
Anticoma	0,0 ± 0,0	5,2 ± 5,2	2,0 ± 0,0	0,0 ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,5 ± 0,0
Axonolaimus	0,0 ± 0,0	3,8 ± 3,8	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Bathylaimus	56,6 ± 9,1	19,2 ± 11,7	27,0 ± 3,6	4,1 ± 0,1	8,8 ± 5,0	0,0 ± 0,0	0,0 ± 0,0
Camacolaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,8 ± 1,8
Ceramonema	125,1 ± 6,4	54,7 ± 13,5	101,5 ± 31,3	173,8 ± 12,8	66,0 ± 31,5	140,4 ± 35,5	209,4 ± 111,1
Cobbia	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,5 ± 1,5	0,0 ± 0,0
Daptonema	387,6 ± 4,2	69,4 ± 54,2	119,1 ± 13,7	111,9 ± 33,0	14,4 ± 0,6	7,6 ± 5,7	55,3 ± 21,9
Dichromadora	0,0 ± 0,0	17,9 ± 2,7	0,0 ± 0,0	0,0 ± 0,0	3,6 ± 0,1	0,7 ± 0,7	0,0 ± 0,0
Ditlevsenella	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	3,0 ± 0,5
Enoplolaimus	0,0 ± 0,0	5,2 ± 5,2	5,1 ± 5,1	2,1 ± 2,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Eurystomina	0,0 ± 0,0	0,0 ± 0,0	4,5 ± 0,6	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Gonionchus	194,9 ± 30,6	120,0 ± 13,9	60,8 ± 25,1	20,5 ± 4,4	93,4 ± 3,4	12,0 ± 4,6	71,5 ± 68,9
Halalaimus	0,0 ± 0,0	0,0 ± 0,0	4,5 ± 0,6	0,0 ± 0,0	1,7 ± 1,7	3,9 ± 2,0	0,0 ± 0,0
Leptolaimus	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,3 ± 1,3
Metachromadora	477,5 ± 116,0	649,2 ± 10,4	116,8 ± 46,6	96,6 ± 36,2	203,6 ± 34,8	45,1 ± 6,7	44,2 ± 36,5
Metadesmolaimus	110,9 ± 75,3	220,0 ± 68,4	11,6 ± 3,8	57,2 ± 0,9	53,7 ± 5,0	15,9 ± 4,8	20,1 ± 15,0
Microlaimus	0,0 ± 0,0	0,0 ± 0,0	11,6 ± 3,8	28,2 ± 24,1	5,6 ± 5,6	6,8 ± 5,0	17,1 ± 13,6
Nemanema	0,0 ± 0,0	0,0 ± 0,0	2,0 ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Neochromadora	63,0 ± 8,2	5,2 ± 5,2	2,0 ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,9 ± 0,9	0,0 ± 0,0
Odontanticoma	51,1 ± 3,6	64,7 ± 33,8	58,6 ± 7,8	20,6 ± 12,6	41,4 ± 0,1	11,1 ± 3,7	15,3 ± 12,8
Omicronema	56,1 ± 20,5	26,8 ± 4,1	18,2 ± 13,1	14,2 ± 5,9	43,2 ± 1,8	0,9 ± 0,9	15,7 ± 5,4
Paracyatholaimus	235,1 ± 104,5	410,0 ± 53,6	118,3 ± 24,6	34,5 ± 17,9	51,9 ± 6,9	13,3 ± 1,5	28,4 ± 20,7
Paramonohystera	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	6,1 ± 4,2	7,4 ± 0,3
Pareurystomina	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,7 ± 0,7	0,0 ± 0,0
Parodontophora	0,0 ± 0,0	3,8 ± 3,8	0,0 ± 0,0	54,6 ± 33,9	25,5 ± 8,2	13,3 ± 1,5	29,6 ± 9,0
Pomponema	0,0 ± 0,0	0,0 ± 0,0	11,6 ± 3,8	16,4 ± 4,3	7,2 ± 0,3	6,3 ± 2,6	9,6 ± 4,5
Rhynchonema	508,6 ± 180,0	175,0 ± 31,0	191,0 ± 38,8	172,2 ± 43,4	76,5 ± 24,7	32,2 ± 1,2	108,3 ± 39,1
Viscosia	5,9 ± 5,9	24,4 ± 16,8	3,9 ± 3,9	2,1 ± 2,1	8,9 ± 1,4	1,7 ± 0,2	11,7 ± 1,1

ANNEX 6. Average nematode densities (ind./10 cm^2) at San Pedro de Manglaralto beach from August 1999 to February 2001 (n= 2)

	Sediment							Water		
Sampling Date	m.g.s (µm)	63 – 125 µm	125 – 250 µm	250 – 500 µm	500-1000 µm	> 1000 µm	distance (m)	SST (°C)	Salinity (PSU)	Pluviosity (mm)
june00fm	244	3	50	41	5	1	37,5	23,6	34	9,9
jul00nm1	290	1	34	54	10	1	31,0	22,1	34	9,9
jul00fm	215	5	62	31	2	0	41,7	22,0	34	1,5
jul00nm2	265	1	42	52	5	0	33,6	23,1	34	1,5
aug00fm	247	2	50	46	3	0	37,9	22,7	34	1,0
aug00nm	263	2	43	48	7	1	38,6	22,5	34	1,0
sep00fm	258	2	45	49	4	0	40,0	22,6	34	3,3
sep00nm	267	1	42	49	7	1	35,9	23,2	34	3,3
oct00fm	246	2	50	46	2	0	36,7	24,0	34	3,5
oct00nm	257	2	46	48	3	0	34,1	23,8	34	3,5
nov00fm	258	1	46	47	6	1	40,3	22,5	34	0,0
nov00nm	263	1	44	45	8	1	41,6	25,0	34	0,0
dec00fm	265	2	42	49	7	1	37,6	25,1	34	0,0
dec00nm	282	2	39	40	16	4	46,7	24,5	34	0,0
jan01fm	251	2	48	48	3	0	39,3	25,3	33	150,9
jan01nm	245	2	50	45	3	0	39,3	24,6	33	150,9
feb01fm	266	1	42	54	3	0	38,6	27,5	32	141,6
feb01nm	258	2	45	43	9	1	53,5	25,6	33	141,6
mar01fm	261	1	44	53	2	0	38,8	27,5	34	113,8
mar01nm	254	2	46	49	3	0	43,4	27,4	34	113,8
abr01fm	240	2	53	44	1	0	42,9	27,4	32	21,1
abr01nm	263	1	44	50	5	0	38,2	25,0	33	21,1
may01fm	283	2	37	54	8	1	38,7	25,4	34	2,2
may01nm	267	0	43	50	7	0	39,7	23,1	34	2,2
jun01fm	257	1	46	50	3	0	37,3	23,1	34	1,9
jun01nm	249	1	49	47	2	0	38,9	21,4	34	1,9
jul01fm	270	2	42	44	11	1	41,7	22,4	34	10,5
jul01nm	227	3	58	37	2	0	38,2	23,3	34	10,5

ANNEX 7. Environmental variables from San Pedro de Manglaralto at high water level (June 2000-July 2001); fm= full moon, nm= new moon; m.g.s (median grain size); SST (Sea Surface Temperature).

	Sediment								Water					
Sampling Date	m.g.s (µm)	< 63 µm	63 – 125 µm	125 – 250 µm	250 – 500 µm	500-1000 µm	> 1000 µm	distance	SST (°C)	Salinity (PSU)	Pluviosity (mm)	Chlorophyll *a* (mg/l)	SPM (mg/l)	POM (mg/l)
june00fm	245	0	6	46	37	10	2	84,0	23,6	34	9,9	-	-	-
jul00nm1	293	0	5	36	36	20	4	102,0	22,1	34	9,9	3,0	781,7	69,8
jul00fm	212	1	11	47	23	14	3	89,8	22,0	34	1,5	3,4	111,8	10,5
jul00nm2	222	0	9	50	31	9	1	94,8	23,1	34	1,5	1,2	-	17,0
aug00fm	219	1	7	53	26	11	3	75,8	22,7	34	1,0	1,8	-	-
aug00nm	213	1	12	47	27	11	2	104,5	22,5	34	1,0	3,6	290,1	25,4
sep00fm	244	1	7	44	40	15	4	90,0	22,6	34	3,3	2,0	478,4	249,0
sep00nm	221	2	1	41	25	16	3	110,0	23,2	34	3,3	2,9	744,0	46,5
oct00fm	260	1	8	50	43	17	3	102,4	24,0	34	3,5	2,9	483,2	23,9
oct00nm	279	1	9	36	24	24	6	100,7	23,8	34	3,5	1,3	1410,1	76,4
nov00fm	223	1	8	49	21	17	6	102,0	22,5	34	0,0	1,2	1392,4	78,3
nov00nm	198	-	3	52	15	15	5	91,1	25,0	34	0,0	2,7	1432,5	66,0
dec00fm	211	1	11	48	21	14	4	105,3	25,1	34	0,0	3,5	4368,0	147,7
dec00nm	202	1	1	57	23	7	2	96,4	24,5	34	0,0	3,2	1505,6	72,1
jan01fm	223	1	1	48	29	11	2	92,3	25,3	33	150,9	1,6	547,6	31,4
jan01nm	211	1	9	54	29	6	1	92,3	24,6	33	150,9	1,5	317,1	21,4
feb01fm	238	-	19	43	32	6	0	114,8	27,5	32	141,6	3,4	1331,2	70,1
feb01nm	283	0	8	36	21	20	4	109,9	25,6	33	141,6	2,4	623,2	41,1
mar01fm	241	0	9	43	35	11	1	114,6	27,5	34	113,8	2,9	-	-
mar01nm	204	1	14	50	31	49	0	102,8	27,4	34	113,8	2,6	-	-
abr01fm	194	-	14	52	24	7	1	118,1	27,4	32	21,1	11,0	295,7	-
abr01nm	231	0	8	48	32	11	2	90,2	25,0	33	21,1	7,5	367,3	-
may01fm	214	-	15	43	25	15	3	97,2	25,4	34	2,2	-	3467,0	284,9
may01nm	301	-	4	34	41	18	3	90,6	23,1	34	2,2	4,8	1026,1	-
jun01fm	241	-	9	43	33	13	2	91,6	23,1	34	1,9	7,1	4686,4	365,4
jun01nm	237	1	10	43	34	11	1	99,3	21,4	34	1,9	2,1	120,4	22,7
jul01fm	191	0	15	54	23	7	1	88,3	22,4	34	10,5	4,0	128,8	20,7
jul01nm	201	1	13	51	25	9	2	93,7	23,3	34	10,5	4,2	1453,3	95,4

ANNEX 8. Environmental variables from San Pedro de Manglaralto at low water level (June 2000-July 2001); fm= full moon, nm= new moon; m.g.s (median grain size); SST (Sea Surface Temperature); SPM (Suspended Particular Matter); POM (Particular Organic Matter).

Sampling Date	Nematoda	Turbellaria	Copepoda	Polychaeta	Isopoda	Cladocera	Rotifera	Ostracoda	Tardigrada	Bivalvia	Copepoda	Nauplii	Insecta	Oligochaeta	Total
june00fm	1380,0	16,0	2321,7	30,7	4,0	0,0	19,7	0,0	11,0	0,0	0,7	123,0	0,0	0,0	3906,7
jul00nm1	375,7	12,0	56,0	0,0	5,0	0,0	43,7	0,7	0,7	0,0	0,0	0,3	0,0	0,0	494,0
jul00fm	1395,7	8,7	989,7	30,7	3,3	0,3	35,3	1,0	218,3	0,0	0,0	74,3	0,0	0,0	2757,3
jul00nm2	258,7	6,0	211,3	0,3	2,0	0,0	11,0	0,0	3,3	0,0	0,0	12,7	0,0	0,0	505,3
aug00fm	1048,3	27,0	499,0	47,7	0,0	0,0	2,3	0,0	345,3	0,0	0,0	142,7	0,3	0,0	2112,7
aug00nm	672,0	26,5	546,5	0,0	0,0	0,0	20,0	0,0	433,5	0,0	0,0	31,5	0,0	0,0	1730,0
sep00fm	557,7	14,3	368,7	0,0	0,0	0,0	6,0	3,3	34,3	0,0	0,0	16,3	0,0	0,0	1000,7
sep00nm	305,3	16,3	78,7	3,7	1,3	0,0	5,0	0,0	23,7	0,3	0,7	8,0	0,0	0,0	443,0
oct00fm	198,0	0,3	56,3	4,0	4,0	0,0	4,3	0,7	7,7	0,0	0,0	11,7	0,0	0,0	287,0
oct00nm	147,7	8,7	19,7	0,0	0,0	0,0	3,3	0,3	3,3	0,0	1,3	1,7	0,0	0,0	186,0
nov00fm	304,0	4,0	112,0	0,0	3,0	0,0	1,0	0,0	33,0	0,0	0,3	20,3	0,0	0,0	477,7
nov00nm	253,3	2,7	42,0	0,0	1,0	0,0	5,0	0,0	16,0	0,0	0,7	15,0	0,0	0,0	335,7
dec00fm	154,0	8,0	49,3	0,0	0,0	0,0	2,0	0,0	0,3	0,3	0,3	1,0	0,0	0,0	215,3
dec00nm	193,7	4,7	49,7	8,0	1,3	0,0	12,0	0,3	7,0	1,0	0,0	16,3	0,0	0,0	294,0
jan01fm	255,3	21,7	178,3	1,0	0,3	0,0	24,3	0,0	7,7	0,3	3,0	23,7	0,0	2,0	517,7
jan01nm	620,3	11,7	128,3	2,7	0,0	0,0	0,3	2,0	13,7	0,3	1,0	6,0	0,0	0,0	786,3
feb01fm	397,3	33,3	84,0	1,0	0,0	0,0	7,3	0,3	3,0	0,0	4,7	35,0	0,0	0,0	566,0
feb01nm	268,3	14,7	46,7	2,0	0,0	0,0	1,3	0,3	0,0	0,0	0,3	10,7	0,0	0,0	344,3
mar01fm	229,3	0,0	105,7	0,3	0,0	0,7	0,0	0,0	0,0	0,0	1,0	17,3	0,7	0,0	355,0
mar01nm	979,0	6,3	621,0	9,3	0,3	0,0	10,3	0,0	0,0	0,0	1,0	33,7	0,0	0,0	1661,0
abr01fm	244,0	8,0	44,7	2,3	0,0	0,0	0,0	0,0	0,3	0,0	3,3	6,3	0,0	0,0	309,0
abr01nm	339,7	17,0	86,0	0,3	0,0	0,0	0,7	0,3	0,7	0,0	1,7	40,0	0,0	0,0	486,3
may01fm	1260,0	28,0	192,7	4,7	0,0	0,0	0,0	0,0	3,3	0,3	0,0	43,7	0,0	0,0	1532,7
may01nm	1672,7	21,0	196,7	21,0	2,0	0,0	0,0	0,0	4,7	0,3	0,7	26,3	0,0	0,0	1945,3
jun01fm	668,0	20,7	171,3	0,7	0,0	0,0	0,0	0,0	0,7	0,0	2,0	29,7	0,3	0,0	893,3
jun01nm	756,7	22,0	172,3	5,0	0,3	0,0	0,0	0,0	0,0	0,0	1,7	13,7	0,0	0,0	971,7
jul01fm	1084,0	11,7	138,7	7,0	1,0	0,0	0,0	0,0	5,3	0,0	0,0	31,3	0,0	0,0	1279,0
jul01nm	407,0	5,0	127,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	22,7	0,0	0,0	562,7

ANNEX 9. Average meiofauna densities (ind./10 cm^2) at San Pedro de Manglaralto beach at the high water level from June 2000 to July 2001 (n= 3); fm= full moon, nm= new moon.

Sampling Date	Nematoda	Gastrotricha	Turbellaria	Copepoda	Polychaeta	Isopoda	Rotifera	Ostracoda	Tardigrada	Bivalvia	Halacaroida	Nauplii	Insecta	Oligochaeta	Total
june00fm	1053,0	130,0	125,0	0,0	3,3	0,0	4,7	12,7	1,0	3,0	0,0	1,3	0,0	0,0	1334,0
jul00nm1	414,7	52,0	9,7	0,0	2,0	0,0	16,3	0,7	0,3	0,0	0,0	3,7	0,3	0,0	499,7
jul00fm	333,7	103,0	10,3	1,3	0,7	0,7	25,3	0,0	0,0	0,0	2,0	6,7	0,0	0,0	483,7
jul00nm2	638,7	85,0	15,7	1,0	2,0	0,0	8,0	0,0	0,3	0,0	0,7	2,0	0,3	0,0	753,7
aug00fm	1073,0	53,3	33,7	0,7	2,3	0,0	1,0	0,0	0,0	0,3	0,0	1,0	0,0	0,0	1165,3
aug00nm	358,3	245,3	3,0	4,0	0,3	0,7	14,7	1,3	0,0	0,0	0,0	4,3	0,0	0,0	632,0
sep00fm	660,0	88,7	17,3	0,0	0,7	0,0	1,7	1,7	0,0	0,7	2,0	2,7	0,0	0,0	775,3
sep00nm	298,0	73,7	29,3	3,0	0,0	0,0	1,3	0,3	1,0	0,0	2,0	9,0	0,3	0,3	418,3
oct00fm	419,0	32,0	30,3	12,3	1,0	0,7	0,7	0,7	0,0	1,7	1,0	18,0	0,0	0,0	517,3
oct00nm	358,7	109,7	67,7	2,7	0,3	0,0	2,0	0,3	6,3	0,7	0,3	26,3	0,0	0,0	575,0
nov00fm	344,3	43,7	26,3	2,0	0,3	0,0	1,0	0,0	0,0	0,0	0,0	8,0	0,0	0,0	425,7
nov00nm	1093,7	59,7	28,7	0,0	0,3	0,0	3,3	0,0	0,3	0,7	1,3	3,3	0,0	0,0	1191,3
dec00fm	837,0	70,3	29,3	2,3	1,3	0,0	0,7	1,7	0,0	1,7	1,0	11,7	0,0	0,0	957,0
dec00nm	981,0	43,0	47,0	5,3	0,7	0,0	0,7	5,0	0,0	1,0	0,7	3,7	0,0	0,0	1088,0
jan01fm	844,0	63,7	28,3	1,0	8,0	0,0	0,3	3,0	0,0	3,0	0,0	2,7	0,0	0,0	954,0
jan01nm	1651,7	202,0	50,3	16,7	10,7	0,3	0,3	0,0	0,0	0,7	1,0	6,3	0,0	0,0	1940,0
feb01fm	572,3	80,7	53,3	4,0	2,0	1,0	43,0	1,0	0,3	0,0	0,0	3,3	0,0	0,0	761,0
feb01nm	592,7	91,3	38,7	20,0	1,0	0,0	0,3	0,3	0,0	1,7	1,0	13,7	0,0	0,0	760,7
mar01fm	860,0	171,7	0,0	0,3	2,0	0,0	0,0	0,0	0,0	0,0	0,3	1,0	0,0	0,0	1035,3
mar01nm	933,0	184,3	20,7	19,0	7,3	0,3	1,0	0,0	0,0	0,0	3,3	3,0	0,0	0,0	1172,0
abr01fm	368,0	12,0	27,3	3,3	3,0	0,0	0,0	0,3	0,0	0,0	1,7	1,0	0,3	0,0	417,0
abr01nm	786,7	24,3	83,3	1,0	8,0	0,0	0,0	0,0	0,0	0,0	1,3	2,7	0,0	0,0	907,3
may01fm	357,7	19,3	79,0	4,3	1,3	0,0	1,0	0,0	0,3	0,7	0,0	0,0	0,0	0,0	463,7
may01nm	780,7	104,0	133,7	11,7	0,7	0,0	0,0	0,0	0,0	0,0	1,0	14,7	0,0	0,0	1046,3
jun01fm	1123,3	51,3	88,0	9,0	3,0	0,0	0,3	0,3	0,0	0,3	0,7	7,3	0,3	0,3	1284,3
jun01nm	843,0	54,0	79,3	0,7	0,3	0,0	0,0	0,0	0,0	0,7	1,0	9,3	0,3	0,0	988,7
jul01fm	900,0	22,7	46,0	0,3	1,0	0,0	0,3	0,0	0,0	0,3	0,0	2,7	0,0	0,0	973,3
jul01nm	1195,3	35,3	160,3	0,7	3,0	0,0	0,0	0,0	0,0	0,0	0,0	2,0	0,0	0,0	1396,7

ANNEX 10. Average meiofauna densities (ind./10 cm^2) at San Pedro de Manglaralto beach at the low water level from June 2000 to July 2001 (n= 3); fm= full moon, nm= new moon.

Nematode species:			Jun-00		Jul		Aug		Sep		Oct		Nov		Dec		Jan-01		Feb		Mar		Apr		May		Jun		Jul	
	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	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	3 ±	3
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	122 ±	13
Camacolaimus sp.	2A	0,02	0 ±	0	0 ±	0	0 ±	0	1 ±	1	0 ±	0	1 ±	1	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	64 ±	18
Ceramonema sp. 2	1A	0,06	0 ±	0	0 ±	0	0 ±	0	4 ±	2	0 ±	0	1 ±	1	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0	0 ±	0	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	11 ±	5
*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	0 ±	0	0 ±	0	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	3 ±	3
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	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	109 ±	11
Enoplolaimus sp. 2	2B	3,06	56 ±	56	210 ±	27	7 ±	2	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	9 ±	9	1 ±	1	1 ±	1	0 ±	0	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	0 ±	0
Eumorpholaimus sp.	1B	0,35	0 ±	0	0 ±	0	0 ±	0	3 ±	3	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	3 ±	3	16 ±	3	6 ±	6	6 ±	0
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	14 ±	2
Halalaimus sp.	1A	0,09	0 ±	0	0 ±	0	5 ±	5	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	4 ±	1	0 ±	0
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	8 ±	8
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	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	6 ±	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	340 ±	7
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	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	0 ±	0	0 ±	0	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	6 ±	6
Molgolaimus sp.	1A	2,16	12 ±	12	0 ±	0	10 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	6 ±	6	55 ±	22	105 ±	25	11 ±	11
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	34 ±	7
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	14 ±	2
Omicronema sp. 1	1B	0,04	0 ±	0	0 ±	0	3 ±	3	1 ±	1	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	242 ±	13
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	0 ±	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	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	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	0 ±	0	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	0 ±	0	0 ±	0	0 ±	0	0 ±	0	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	0 ±	0
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	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	3 ±	3
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	17 ±	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	42 ±	21
Viscosia sp. 3	2B	0,03	0 ±	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	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	3 ±	3

ANNEX 11. Nematode densities (ind./10 cm^2) at the high water level in San Pedro de Manglaralto, from June 2000 to July 2001.

Nematode species:			Jun-00		Jul		Aug		Sep		Oct		Nov		Dec		Jan-01		Feb		Mar		Apr		May		Jun		Jul	
	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	Av	SE
Anoplostoma sp.	1B	0.18	0	± 0	3	± 3	0	± 0	2	± 2	0	± 0	0	± 0	0	± 0	5	± 1	0	± 0	0	± 0	0	± 0	0	± 0	8	± 2	0	± 0
Bathylaimus sp.	1B	0.62	0	± 0	0	± 0	9	± 5	2	± 2	0	± 0	0	± 0	0	± 0	34	± 34	0	± 0	4	± 4	5	± 5	1	± 1	0	± 0	4	± 4
Camacolaimus sp.	2A	0.05	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	2	± 2	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
* *Ceramonema* sp. 1	1A	18.91	211	± 20	60	± 7	64	± 26	67	± 20	115	± 29	90	± 5	90	± 6	18	± 18	165	± 81	175	± 8	134	± 42	62	± 4	148	± 96	440	± 71
Ceramonema sp. 2	1A	8.40	104	± 9	36	± 7	6	± 2	27	± 20	44	± 21	64	± 12	75	± 32	5	± 5	43	± 29	123	± 48	52	± 19	35	± 5	109	± 71	94	± 30
Cobbia sp.	2A	0.03	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Daptonema sp.	1B	0.14	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	2	± 2	0	± 0	8	± 4	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	0	± 0
Daptonema sp. 1	1B	13.21	65	± 4	5	± 1	11	± 1	92	± 22	16	± 10	7	± 5	140	± 57	490	± 197	55	± 22	203	± 129	11	± 4	53	± 18	121	± 1	15	± 10
Daptonema sp. 2	1B	0.64	2	± 2	7	± 1	3	± 3	4	± 0	1	± 1	3	± 3	9	± 3	18	± 11	0	± 0	0	± 0	4	± 2	3	± 3	2	± 2	6	± 6
Daptonema sp. 3	1B	0.37	20	± 20	3	± 3	0	± 0	14	± 14	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Dasynemoides sp.	1A	0.02	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	1	± 1	1	± 1	0	± 0	0	± 0
Dichromadora sp.	2A	0.03	0	± 0	0	± 0	2	± 2	0	± 0	0	± 0	1	± 1	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Ditlevsenella sp.	2B	0.11	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 0	6	± 2	1	± 1	0	± 0	0	± 0	0	± 0
Enoplolaimus sp.	2B	0.15	0	± 0	1	± 1	0	± 0	2	± 2	1	± 1	0	± 0	0	± 0	2	± 2	0	± 0	2	± 2	2	± 2	0	± 0	5	± 5	0	± 0
Eumorpholaimus sp.	1B	0.03	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 1	0	± 0	0	± 0	0	± 0
Eurystomina sp.	2B	0.07	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	2	± 2	3	± 3	0	± 0	2	± 2	0	± 0
* *Gonionchus ecuadoriensis*	2A	4.72	181	± 39	11	± 1	94	± 0	40	± 3	8	± 1	13	± 4	25	± 7	2	± 2	71	± 69	6	± 6	1	± 1	1	± 1	3	± 3	3	± 3
Halalaimus sp.	1A	0.49	3	± 3	0	± 0	2	± 2	2	± 2	2	± 0	5	± 3	10	± 1	2	± 2	1	± 1	2	± 2	6	± 1	4	± 2	6	± 6	2	± 2
Leptolaimus sp.	1A	0.05	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	0	± 0	0	± 0	0	± 0	2	± 2	0	± 0	0	± 0	0	± 0
Metachromadora cf. *gerlachi*	2B	11.43	112	± 44	36	± 7	220	± 48	16	± 8	26	± 0	50	± 1	72	± 13	32	± 7	44	± 36	20	± 7	3	± 3	28	± 0	277	± 24	174	± 32
Metadesmolaimus sp. 1	1B	4.79	141	± 63	29	± 4	55	± 4	82	± 8	12	± 1	18	± 7	23	± 4	11	± 11	18	± 13	23	± 1	4	± 2	4	± 3	22	± 16	23	± 3
Metadesmolaimus sp. 2	1B	0.68	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	14	± 1	15	± 1	15	± 4	13	± 6	9	± 4
Microlaimus sp.	2A	3.37	5	± 5	8	± 4	0	± 0	0	± 0	4	± 1	14	± 9	14	± 8	13	± 1	16	± 12	79	± 22	33	± 9	65	± 9	42	± 10	34	± 17
Neochromadora sp.	2A	0.65	2	± 2	7	± 2	0	± 0	4	± 0	1	± 1	1	± 1	17	± 5	0	± 0	0	± 0	24	± 24	1	± 1	1	± 1	5	± 5	0	± 0
Odontanticoma sp. 1	2A	1.64	43	± 18	8	± 1	40	± 5	2	± 2	10	± 4	12	± 1	12	± 9	3	± 3	15	± 13	8	± 8	4	± 0	0	± 0	0	± 0	2	± 2
Omicronema sp. 1	1B	2.28	35	± 6	6	± 2	46	± 4	25	± 15	9	± 5	1	± 1	18	± 9	12	± 1	16	± 5	19	± 7	11	± 2	4	± 0	21	± 8	0	± 0
Paracyatholaimus sp. 1	2A	3.83	70	± 11	7	± 2	49	± 6	24	± 4	26	± 2	12	± 1	31	± 6	10	± 3	28	± 21	29	± 10	13	± 2	4	± 1	23	± 9	44	± 8
Paracyatholaimus sp. 2	2A	0.63	18	± 9	2	± 2	3	± 3	2	± 2	3	± 2	3	± 1	5	± 5	0	± 0	10	± 4	4	± 4	2	± 2	2	± 2	0	± 0	6	± 6
Paramonohystera sp.	1B	3.70	23	± 4	21	± 1	8	± 8	59	± 12	13	± 3	13	± 2	92	± 31	56	± 19	10	± 0	2	± 2	2	± 2	2	± 0	60	± 21	0	± 0
Pareurystomina sp.	2B	0.10	0	± 0	0	± 0	0	± 0	0	± 0	1	± 1	2	± 2	2	± 2	0	± 0	0	± 0	2	± 2	1	± 1	0	± 0	0	± 0	2	± 2
Parodontophora sp. 1	1B	4.47	13	± 6	34	± 3	28	± 0	9	± 3	12	± 7	15	± 0	43	± 6	24	± 5	33	± 9	61	± 17	31	± 8	72	± 16	42	± 3	20	± 15
Pomponema sp.	2B	0.41	0	± 0	3	± 3	6	± 2	0	± 0	1	± 1	3	± 3	0	± 0	0	± 0	0	± 0	4	± 0	0	± 0	1	± 1	0	± 0	22	± 9
Pseudosteineria sp.	1B	0.03	3	± 3	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
* *Rhynchonema* cf. *hirsutum*	1B	11.95	105	± 37	74	± 9	49	± 49	245	± 27	77	± 32	37	± 9	141	± 51	163	± 18	108	± 38	10	± 10	10	± 1	4	± 0	137	± 17	2	± 2
Synonchiella sp.	2B	0.03	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Viscosia sp. 1	2B	1.74	12	± 12	8	± 6	9	± 1	10	± 6	6	± 2	3	± 3	11	± 11	34	± 9	7	± 3	15	± 7	8	± 4	1	± 1	29	± 10	16	± 6
Viscosia sp. 2	2B	0.05	0	± 0	2	± 2	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	3	± 3	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0

ANNEX 12. Nematode densities (ind./10 cm^2) at the low water level in San Pedro de Manglaralto, from June 2000 to July 2001.