

INFLUENCE OF A FRESHWATER RUNOFF ON TEMPORAL VARIATIONS OF AN INTERTIDAL MEIOFAUNA ASSEMBLAGE

R. RIERA^{*1}, J. NUÑEZ², M. DEL CARMEN BRITO²

¹ Centro de Investigaciones Medioambientales del Atlántico (CIMA SL), C/Arzobispo Elías Yanes, 44, 38206 La Laguna, Tenerife, Canary Islands, Spain

² Benthos Lab, Department of Animal Biology, Faculty of Biology, University of La Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain

* Corresponding author: rodrigo@cimacanarias.com

FRESHWATER RUNOFF
INTERTIDAL
MEIOFAUNA
TENERIFE
CANARY ISLANDS

ABSTRACT. – An intertidal meiofaunal assemblage in Los Cristianos Bay, Tenerife, Canary Islands, Spain was sampled monthly at one location from May 2000 through April 2001, at mean low tide. Nematodes dominated meiofauna assemblage, ranging from 73 % in November to 98 % in February and March. Turbellarians and harpacticoid copepods were the second and the third most abundant groups, respectively. During November 2000 at times of heavy rainfall, freshwater runoff from a ravine (temporary river) affected the intertidal location. Meiofaunal densities drastically decreased, particularly nematodes, during November and December 2000 and January 2001. Nematodes recovered to pre-disturbance densities in February 2001, while copepods recovered the second fortnight of November 2000, indicating the high mobility of this meiobenthic group. The most abundant species were the nematodes *Odontophora* aff. *wieseri*, *Theristus* sp. and *Daptonema hirsutum* that made up 88 % of the overall meiofauna density, showing significant differences in their abundances throughout the study period (May 2000-April 2001). *Odontophora* aff. *wieseri* showed its lowest densities during run-off period (November) and recovered gradually from December to March. *Theristus* sp. almost disappeared in the run-off period (November) and obtained highest abundances in summer months (June-August). *Daptonema hirsutum* was absent in November and in summer months (May-August). Significant differences were found in univariate parameters (abundance, species richness and Shannon's diversity). Multivariate analysis distinguished the freshwater runoff period (November) from the remaining months of the year, as well as throughout the study period.

INTRODUCTION

Temporal variation of faunal and plant assemblages are rather frequent in nature. In benthic communities, a variety of abiotic and biotic variables have to be taken into account for seasonal variations of benthic animal populations, but temperature and food availability are the factors that most influence temporal changes in abundance (Ólafsson & Elmgren 1997). Temporal meiofauna variations have been formerly reported for different coastal regions (Hicks & Coull 1983, Coull & Dudley 1985, Rudnick *et al.* 1985, Schizas & Shirley 1996, Nozais *et al.* 2005, among others). However, no consistent patterns were found among studies, with maximum abundances in winter (Coull 1988, Palacín 1990), spring and summer (Hicks & Coull 1983, Coull 1985, Rudnick *et al.* 1985, Gracia *et al.* 1996, Mazzola *et al.* 2000, Mirto *et al.* 2000, Albuquerque *et al.* 2007). Several studies have observed a lack of any seasonal pattern (Warwick & Buchanan 1971, Juario 1975, Boucher 1980, Riera *et al.* 2011). These inconsistencies could be due to the high variability of meiofauna assemblages, which is more accentuated in the intertidal. Shifts on intertidal benthic communities could be due to high-frequency events, e.g. tides, waves and currents or

to stochastic events that happen without any temporality, e.g. rough seas, heavy rains, spills, freshwater inputs, etc. One of the most important stochastic events that happen in subtropical regions are floods or runoff episodes from ravines (temporary rivers) (Gourbault *et al.* 1998). Runoff episodes are stochastic and their effects need to be studied in detail (Gourbault *et al.* 1998) and their occurrence may be more frequent in the next decades as a result of climate change (Milly *et al.* 2002, Palmer & Räisänen 2002).

Benthic assemblages have been traditionally used as indicators of natural, e.g. floods or runoffs, and man-induced environmental perturbations (Pearson & Rosenberg 1978). In the last decades, meiofaunal assemblages have acquired importance on monitoring environmental assessments, because this faunal fraction has several features favorable for use as bioindicators of environmental conditions (Schratzberger *et al.* 2000), even dealing with freshwater influence on meiofauna (Danovaro *et al.* 2000, Nozais *et al.* 2005). Meiofauna is defined as the mobile benthic invertebrates that pass through a 0.5 mm sieve but are retained on a 0.063 or 0.042 mm sieve (Higgins & Thiel 1988). Meiofauna is considered to be an important link in the benthic food web (Giere 2009) and as an important prey of invertebrate macrofaunal species and

during the early life history of several fish species (Gee 1989).

In general, sandy beach meiofaunal communities are characterized by having a high meiofaunal species diversity (Gheskiere *et al.* 2002). Diversity is usually higher on the mid- to upper shore and decreases downshore, the opposite trend from that of the macrofauna (McLachlan & Brown 2006). Nematode densities increased downshore across a dissipative beach, with highest diversity in the midshore, where there was an optimum balance between submergence, oxygen supply, and sediment stability (Gheskiere *et al.* 2004). In general, diversity of interstitial meiofauna should be highest on intermediate beaches of medium sands, where there is a balance between excess of organic input (very sheltered beaches) and water circulation (very reflective) (Rodríguez 2004).

The main aims of this study were: (i) to determine the existence or not of temporal variability of the intertidal meiofauna assemblage throughout the study period (May 2000-April 2001), (ii) to describe the effects of the freshwater runoff on the intertidal meiofaunal assemblage and (iii) to determine the recovery rate of meiofaunal taxonomic groups and species to the runoff episode.

MATERIAL AND METHODS

Study area: This study was conducted from May 2000 to April 2001 in Los Cristianos Bay, a locality on the south coast of Tenerife (Canary Islands, NE Atlantic Ocean, coordinates 28°02'58"N-16°42'54"W) (Fig. 1). There is no previous information on soft-bottom meiofaunal assemblages of this bay.

The study site is located in a sheltered bay, with a recreational harbour inside, and a mouth of a ravine (temporary river) ("Barranco de Aquilino") is situated on the surroundings of the station (ca. 50 m). The runoff disturbance persisted 7 days (10th-17th November 2000) on the beach throughout the study period. Unfortunately, no measures were taken of the disturbance level since cleaning works started immediately after the runoff episode.

The beach can be classified as reflective and sand flat, tide-dominated beach with wave average < 0.5 m in height (*sensu* Short 1999). Los Cristianos beach is characterized by the presence of fine sands and 2 m tide range. The beach is ca. 500 m long and ca. 150 m wide, uniform along-shore without rocky substrates, boulders or bar-horns. Salinity remains

constant along the year (36.4-36.8 PSU), with the exception of the runoff period (< 30 PSU) (Riera unpubl. data) (Table I).

Sediment samples were collected on a monthly basis (May 2000-April 2001), except for November 2000 when two collections were made (7 days and 21 days after the run-off episode), at one intertidal station. All samples were collected at the same tide level throughout the study period, mean low water level (MLW) during receding tides. Sediment cores (4.5 cm inner diameter) were pushed into the sediment to a depth of 30 cm. Five replicates were collected for faunistic analysis and one for analysis of abiotic factors (organic matter, total nitrogen and grain size), except for the second fortnight of November 2000 (immediately after the run-off episode) when the sample for abiotic factors was not collected.

Analysis of environmental factors: To assess grain size composition of the analyzed sediment, 100 g sediment from each month was oven dried at 105 °C, passed through a graded series (2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm and 0.063 mm) of sieves, and then weighed (Buchanan 1984). Organic matter content of the sediment was determined by oxidizing carbon with KMnO₄ (Walkley & Black 1934). Total nitrogen was determined by the Kjeldahl method (Bradstreet 1965). This method comprises three steps, digestion (with sulfuric acid), distillation (with sodium hydroxide) and titration (with hydrochloric acid).

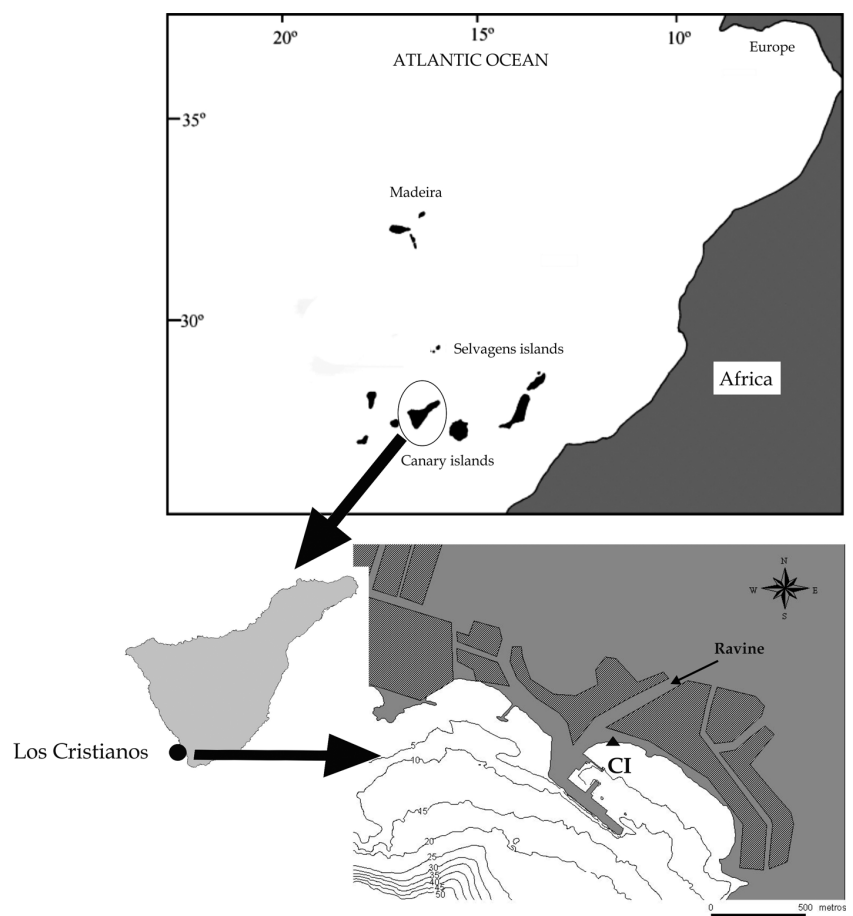


Fig. 1. – Location of Los Cristianos sampling station.

Table I. – Values of abiotic factors throughout the study period from the sampling station.

	May 2000	Jun. 2000	Jul. 2000	Aug. 2000	Sept. 2000	Oct. 2000	Nov. 2000	Dec. 2000	Jan. 2001	Feb. 2001	Mar. 2001	Apr. 2001
Salinity (PSU)	36.7	36.7	36.8	36.7	36.8	36.7	29.8	36.7	36.6	36.6	36.7	36.6
% Nitrogen	0.01	0.02	0.01	0.01	0.05	0.01	0.01	0.01	0.01	0.01	0.02	0.01
% Carbonates	23.59	18.29	18.63	25.13	20.68	19.49	17.78	15.90	16.24	19.49	21.03	18.97
% Organic matter	1.24	0.93	0.61	0.39	0.46	0.42	0.81	0.52	0.65	0.99	0.75	0.29
% Gravels	0.2	0.63	1.83	0.89	0.06	0.99	6.11	6.78	5.87	3.25	0.04	5.98
% Very coarse sands	1.25	1.56	2.42	0.29	0.36	0.77	3.22	4.42	9.24	1.46	0.17	2.05
% Coarse sands	3.62	6.95	2.85	0.37	0.9	1.35	4.51	4.66	5.21	1.75	0.42	2.76
% Medium sands	25.75	66.45	27.13	13.22	18.36	17.67	20.41	18.94	27.51	18.93	19.11	24.96
% Fine sands	62.74	23.76	62.83	81.32	74.17	72.35	58.92	55.69	47.66	68.7	76.82	57.94
% Very fine sands	5.94	0.55	2.73	3.69	5.91	6.45	6.21	8.91	4.12	5.5	3.28	6.12
% Silt/clay	0.49	0.1	0.21	0.22	0.23	0.41	0.63	0.6	0.39	0.41	0.16	0.2

Analysis of meiofauna: The whole sediment sample (4.5 cm inner diameter, 30 cm height) was preserved in 10 % seawater buffered formaldehyde solution and decanted through a 0.5 and a 0.063 mm mesh sieve. The fraction remaining on the 0.063 mm mesh sieve was separated into different taxonomic groups using a binocular microscope and preserved in 70 % ethanol. Meiofaunal specimens were mounted in glycerine jelly (Palacín 1990) and examined with a Leica DMLB microscope equipped with Nomarski interference contrast and identified to the lowest taxonomic level (species), whenever possible. All meiofaunal specimens were identified using the microscope and subsamples of 200 individuals were used for nematodes (Sommerfeld & Warwick 1996). Certain taxonomic groups (i.e. harpacticoid copepods, turbellarians) that need dissection or taxonomic characters of internal anatomy were determined by their body shape in putative species. Nematodes and polychaetes were identified to the lowest taxonomic level (e.g. species or genus) by means of current taxonomic works and monographs, as well as during predoctoral stays of the first author (R.R.) in the United Kingdom (Plymouth Marine Lab) and Belgium (Department of Marine Biology, University of Ghent).

Statistical analysis: Biological descriptors of the community (density, species richness, n° of taxonomic groups, Shannon's diversity and Pielou's evenness) were calculated. Differences of Shannon's diversity among months were tested with one-way ANOVA, after verifying normality using the Kolmogorov-Smirnov test and Levene's test for homogeneity of variances. When there was no normality and/or homogeneity of variances, the Kruskal-Wallis ANOVA (KW ANOVA) test was used.

To visualize affinities in meiofaunal assemblage structure through the study period, a MDS (non-metric multidimensional scaling) was carried out on square rooted-transformed abundance data via the Bray-Curtis similarity index. The ANOSIM routine (Clarke 1993) was used to explore the significance of differences between months throughout the study period (May 2000-April 2001).

The relationship between the entire set of environmental variables (sedimentary types, total nitrogen and organic mat-

ter) and meiofauna assemblage structure was investigated using a db-RDA (distance-based redundancy analysis, Legendre & Anderson 1999). Multivariate multiple regression, using the DISTLM routine via 4999 permutations of the data (Anderson 2001), tested then the significance of these relationships by fitting a linear model based on Bray-Curtis dissimilarities on squared-root transformed abundance data. All multivariate procedures were carried out by means of the PRIMER 6.0 package (Clarke & Warwick 2001).

RESULTS

Environmental factors

The sediment was dominated by fine sands (61.91 % average) during the study period, except June (66.45 % of medium sands). Medium sands were the second most important grain size fraction (24.87 % average) and silt/clay content was negligible (0.34 %).

The organic matter content had an average of 0.54 %, ranging from 0.006 % (November) to 1.01 % (September). Nitrogen content was characterized by low values, with an average of 0.015 %, ranging from 0.046 % (September) to 0.009 % (January and February) (Table I).

Meiofauna

A total of 20,665 specimens were collected during the study period; nematodes were the most abundant group with 19,958 individuals (94 % of the overall density). The second and third most abundant taxonomic groups were turbellarians and copepods, with 300 and 233 specimens, respectively. The remaining taxonomic groups (polychaetes, oligochaetes, nemertines, priapulids, isopods, gammarids, tanaids, kinorhynchs and sipunculids) were scarce during the study period. The number of taxonomic groups remained low, with maximum values in May and

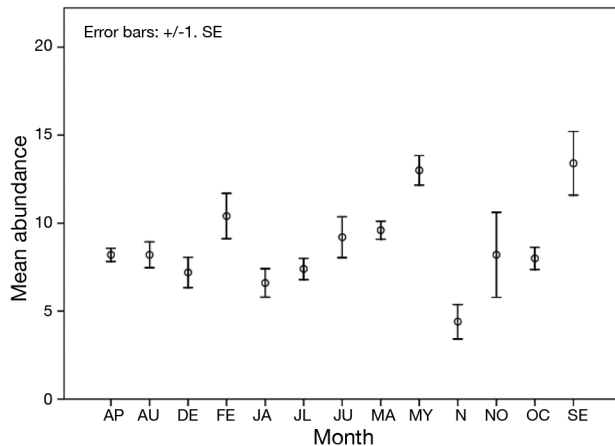


Fig. 2. – Average number of taxonomic groups \pm standard errors. N, 1st fortnight of November, NO, 2nd fortnight of November.

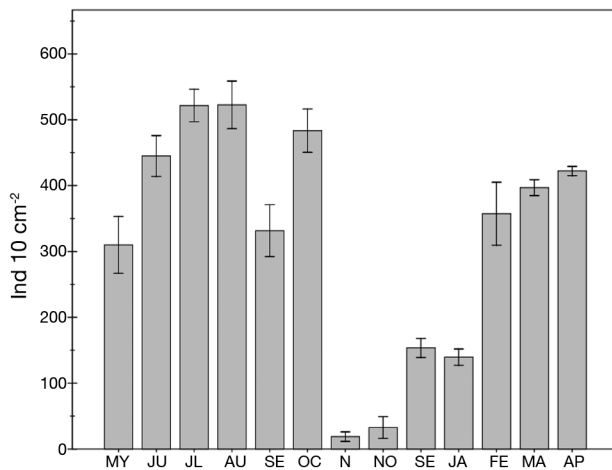


Fig. 3. – Average meiofaunal densities \pm standard errors. N, 1st fortnight of November, NO, 2nd fortnight of November.

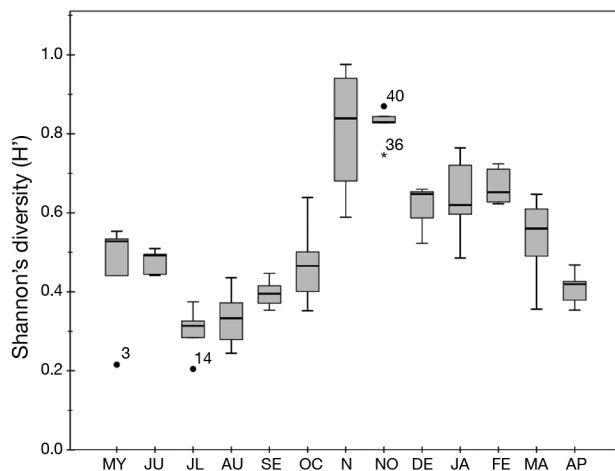


Fig. 4. – Average Shannon's diversity (H') \pm standard errors. N, 1st fortnight of November, NO, 2nd fortnight of November.

September and minimum values during November (N and NO) (Fig. 2).

Meiofaunal density ranged from 12 ± 7.6 to 328 ± 167.5 ind.10 cm⁻², in the first fortnight of November and

July, respectively (Fig. 3). Meiofaunal densities were more or less stable during the study year, with an abrupt decrease during November (N and NO), recovering to pre-disturbance densities in February 2001, three months after the runoff. Meiofaunal density showed significant differences over the study year (Kruskal-Wallis ANOVA, $H = 54.851$, $p = 0.0002$) (Fig. 3). Nematodes were always the predominant taxon, with an annual mean of 94 % (from 73.4 % the first fortnight of November to 98.3 % in March). The remaining taxonomic groups were represented by very low densities (< 2.5 % overall density).

In terms of species richness, 68 species were collected monthly (Table II). Nematodes were by far the most diverse group with 32 species, followed by turbellarians and polychaetes with 10 species. The number of species differed significantly during the study year (Kruskal-Wallis ANOVA, $H = 35.018$, $p = 0.0004$), being highest in May, June and October compared to the remaining months of the study period.

In terms of Shannon's diversity (H'), the sampled location was characterized by having values ranging from 0.6 to 1.7; significant differences were found among months (one-way ANOVA, $F = 3.843$, $p = 0.0003$). The maximum values were recorded in the second fortnight of November (1.58) and February (1.54). In contrast, minimum values occurred in July (0.6) and August (0.7) (Fig. 4).

The recovery of meiofauna assemblages from the runoff disturbance event was not complete throughout the study period. Meiofaunal species richness was lower after the runoff (7.8 ± 3.8 ind) compared to before-months (9.87 ± 5.4 ind). The same trend was observed in meiofaunal abundances (Before: 435.7 ± 20.55 ind; After: 217.31 ± 28.27 ind).

The most abundant species were the axonolaimid nematode *Odontophora* aff. *wieseri*, followed by the xyalids *Theristus* sp. and *Daptonema hirsutum* that made up 88% of the total meiofaunal density. *Odontophora* aff. *wieseri* was more abundant in August and October, with decreasing densities during November (N and NO) when the species was almost absent. *Odontophora* aff. *wieseri* densities recovered gradually from December to March, reaching pre-disturbance densities in April (Fig. 5). Significant differences were obtained during the study period (Kruskal-Wallis ANOVA, $H = 53.831$, $p = 0.003$). *Theristus* sp. presented a peak of density in July, being almost absent during November (N and NO) and April. Densities were intermediate in December, although they never reached the levels found during the summer months (June, July and August) (Fig. 6). *Theristus* sp. densities differed significantly during the study period (Kruskal-Wallis ANOVA, $H = 47.190$, $p = 0.0004$). *Daptonema hirsutum* was more abundant in March, but absent from May to August and the first fortnight of November (N and NO) (Fig. 7). Significant differences were found during the study period (Kruskal-Wallis ANOVA, $H = 48.453$, $p = 0.0002$).

Table II. – Mean abundances (\pm SE) of meiofaunal species throughout the study period at the sampling station.

Group	Species	May 2000	Jun. 2000	Jul. 2000	Aug. 2000	Sept. 2000	Oct. 2000	Nov. 2000	Nov. (I) 2000	Dec. 2000	Jan. 2001	Feb. 2001	Mar. 2001	Apr. 2001
Amphipoda	Lysianassidae	0.2 \pm 0.4	0	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0	0
Amphipoda	Bathyporeia sp.	0	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0	0	0
Copepoda	Canuella aff. perplexa	2.4 \pm 2.6	5.4 \pm 9.3	0.2 \pm 0.4	0.4 \pm 0.9	4.4 \pm 1.1	3.6 \pm 2.4	0	4.6 \pm 8.6	1 \pm 1.2	1 \pm 1	4.2 \pm 2.9	3.6 \pm 3.3	0.2 \pm 0.4
Copepoda	Halectinosoma sp.	0.2 \pm 0.4	0.4 \pm 0.5	0.2 \pm 0.4	0	0.6 \pm 0.9	0	0	0.6 \pm 0.9	0.4 \pm 0.5	0.2 \pm 0.4	0.4 \pm 0.5	0.8 \pm 1.3	0.2 \pm 0.4
Copepoda	Harpacticus aff. flexus	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0	0.2 \pm 0.4	1 \pm 0.7	0
Copepoda	Intermedopsyllus sp.	0	0	0	0	0	0	0	0.2 \pm 0.4	0	0	0	0.2 \pm 0.4	0
Copepoda	Tryphonema sp.	0.6 \pm 1.3	0	0	0	0.2 \pm 0.4	0	0	0.2 \pm 0.4	0	0	0	0	0
Isopoda	Eurydice pulchra	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0	0	0	0
Isopoda	Idotea sp.	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0
Isopoda	Sp. haeroma serratum	0.4 \pm 0.5	0.4 \pm 0.5	0.4 \pm 0.9	0	0	0	0	0	0	0	0	0	0.4 \pm 0.9
Kinorhyncha	Kinorhyncha	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0
Nematoda	Acanthopharynx sp.	0	0	0	1 \pm 2.2	0	0	0	0	0	0	0	0	0
Nematoda	Anticoma sp.	0	0	3.6 \pm 4.9	3.6 \pm 3.6	3.6 \pm 4.5	10.6 \pm 23.7	0	0	7.4 \pm 7.6	28.2 \pm 14	6.6 \pm 7.4	8.2 \pm 9.1	3.6 \pm 4.9
Nematoda	Areolaimus aff. elegans	0	0	1 \pm 2.2	1.2 \pm 2.7	0.8 \pm 1.8	0	0	0	2.4 \pm 4.5	0	1.4 \pm 3.1	0	1 \pm 2.2
Nematoda	Catanema sp.	0	0	0	0	1.6 \pm 2.3	0	0.4 \pm 0.9	0	2.8 \pm 4.4	1.2 \pm 2.7	24.4 \pm 25.4	15.8 \pm 19.5	0
Nematoda	Choriolaimus sp.	0	0	1 \pm 2.2	1.2 \pm 2.7	0	0	0	0	1.6 \pm 3.6	0	2.8 \pm 3.8	0	1 \pm 2.2
Nematoda	Deptonema aff. hirsutum	0	0	0	0	7.6 \pm 5.4	1 \pm 2.2	0	4 \pm 2.9	4.4 \pm 5	3.8 \pm 3.8	52.6 \pm 45.7	104.4 \pm 91.7	0
Nematoda	Enoploilaimus propinquus	0	0	1.8 \pm 4	0	0	0	0	0	0	0	0	0	1.8 \pm 4
Nematoda	Enoploides gryphus	0	0	0	0	0	0	0	0.4 \pm 0.5	0	0	0	0	0
Nematoda	Mesacanthion diplochma	1.6 \pm 3.6	0	0	0	0	0	0	0.6 \pm 0.9	0	0	0	0	0
Nematoda	Microlaimus aff. acinaces	7.4 \pm 9.0	8.2 \pm 5.4	2.8 \pm 6.3	0	1.2 \pm 1.6	0.8 \pm 1.8	0	0	0.8 \pm 1.8	0	0	0	2.8 \pm 6.3
Nematoda	Monoposthia aff. mirabilis	0	0	0	1.6 \pm 3.6	0	0	0	1.4 \pm 2.2	0	0	0	0	0
Nematoda	Monoposthia sp.	0	0	0	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0
Nematoda	Odontophora aff. longisetosa	10.8 \pm 10.5	7.6 \pm 10.8	1.4 \pm 3.1	0	0	0	0	0	0	0	0	0	1.4 \pm 3.1
Nematoda	Odontophora aff. wieseri	207.2 \pm 76.7	257.4 \pm 19.2	58.8 \pm 29.9	330.4 \pm 171	249.6 \pm 68.5	334.2 \pm 89.1	5.4 \pm 8.4	2.8 \pm 1.1	63.4 \pm 45.1	12.4 \pm 10.3	166 \pm 57.4	168.2 \pm 72	58.8 \pm 29.9
Nematoda	Oncholaimellus calvadosicus	18 \pm 8.2	18.8 \pm 9.7	2.6 \pm 5.8	12.2 \pm 11	37.2 \pm 15.8	23.6 \pm 13.4	0.4 \pm 0.9	7.6 \pm 9.2	3.4 \pm 5	9.4 \pm 11.3	8.6 \pm 6.2	11.2 \pm 10.7	2.6 \pm 5.8
Nematoda	Oncholaimus aff. skawensis	1 \pm 2.2	0	1 \pm 2.2	0	0	0	0	0	0	0	0	0	1 \pm 2.2
Nematoda	Oncholaimus campylocercoides	0.8 \pm 1.8	0	0	1.2 \pm 2.7	0.6 \pm 1.3	0	0	1.4 \pm 3.1	0	0	0	3.4 \pm 4.7	0
Nematoda	Paralinhomoeus sp.	0.4 \pm 0.9	0	0	1.2 \pm 2.7	2.4 \pm 2.5	0.8 \pm 1.8	1 \pm 1.1	0	0	0	4.2 \pm 6.3	1.8 \pm 4	0
Nematoda	Paralongicyatholaimus sp.	0	0	0	0	4.8 \pm 5.4	1.8 \pm 4	6.2 \pm 10.6	0	6.8 \pm 7.5	0	0	1.8 \pm 4	0
Nematoda	Pomponema aff. compactum	0	0	0	2 \pm 4.5	0	0	0	3 \pm 6.1	0	0	0	4.4 \pm 9.8	0
Nematoda	Pseudochromadora sp. 1	0	0	0	0	0.6 \pm 1.3	0	0	0	0	0	0	0	0
Nematoda	Pseudochromadora sp. 2	0	0	0	0	2.4 \pm 2.5	1.2 \pm 2.7	0	0.2 \pm 0.4	1.4 \pm 3.1	0	2.8 \pm 3.8	1.8 \pm 4	0
Nematoda	Ptycholaimellus sp.	0	0	0	0	0	0	0	0.4 \pm 0.9	0	0	0	0	0
Nematoda	Sabatieria aff. elongata	0	0	0	0	0	1.2 \pm 2.7	0.4 \pm 0.9	0.2 \pm 0.4	0	0	0	0	0
Nematoda	Setosabatieria aff. hilarula	0	0	0	0	0	0	0	0.8 \pm 1.3	0	0	0	0	0
Nematoda	Siphonolaimus aff. pellucidus	0	0	0	0	0	0	0	0.6 \pm 0.9	0	0	0	0	0
Nematoda	Siphonolaimus sp. 2	4 \pm 8.9	0	0	0	0	0	0	1.6 \pm 3	0	1.4 \pm 3.1	19 \pm 16.8	7.4 \pm 11.8	0
Nematoda	Theristus sp. 1	40 \pm 45.7	136.2 \pm 76.0	437.2 \pm 77.2	147.6 \pm 223.8	5.8 \pm 8.8	86.6 \pm 45.3	0	0	55.6 \pm 38.8	79.8 \pm 30.9	63 \pm 39.8	61.6 \pm 108	437.2 \pm 77.2
Nematoda	Viscosia glabra	0	0	1 \pm 2.2	0	0	0	0	0	0	0	0	0	1 \pm 2.2
Nemertea	Otopyphonemertes sp. 1	0	0	0	0.4 \pm 0.5	0	0	0	0	0	0	0	0	0
Nemertea	Otopyphonemertes sp. 2	3.2 \pm 2.4	4.2 \pm 7.4	3.2 \pm 2.5	2.4 \pm 1.8	2.6 \pm 1.5	1.4 \pm 1.3	0	0	0	0	0	0	3.2 \pm 2.5
Oligochaeta	Aktechilus sp.	0	0	0	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0
Oligochaeta	Grania sp.	0	0	0	0	0	0	0	0	0	0	0	0.2 \pm 0.4	0
Oligochaeta	Tubificidae	0	0	0	0	0	0.2 \pm 0.4	0	0	0	0	0	0	0
Polychaeta	Dispio uncinata	0	0.2 \pm 0.4	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Exogone brevientennata	0	0	0.2 \pm 0.4	0	0	0	0.2 \pm 0.4	0	0	0	0	0	0.2 \pm 0.4

Table II. Continued.

Group	Species	May 2000	Jun. 2000	Jul. 2000	Aug. 2000	Sept. 2000	Oct. 2000	Nov. 2000	Nov. (I) 2000	Dec. 2000	Jan. 2001	Feb. 2001	Mar. 2001	Apr. 2001
Polychaeta	<i>Haplosyllis spongicola</i>	0	0	0	0	0	0	0.2 ± 0.4	0	0	0	0	0	0
Polychaeta	<i>Matioceros</i> sp.	0	0	0	0	0	0.2 ± 0.4	0	0	0	0	0	0	0
Polychaeta	<i>Microphtalmus pseudoaberrans</i>	0	0	0	0.4 ± 0.9	0.2 ± 0.4	0	2.4 ± 3.9	0	0	0	0.6 ± 0.5	0	0
Polychaeta	<i>Platynereis dumerilii</i>	0.2 ± 0.4	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	<i>Pseudopolydora</i> sp.	0	0	0	0	0.4 ± 0.5	0	0	0	0	0	0	0	0
Polychaeta	<i>Rhynchospio glutaea</i>	1 ± 1.2	0	0	0	0.2 ± 0.4	0	0	0	0	0.2 ± 0.4	0.2 ± 0.4	0.6 ± 0.5	0.4 ± 0.5
Polychaeta	<i>Scolelepis squamata</i>	0.8 ± 0.4	1 ± 1.2	0.4 ± 0.5	0	0.2 ± 0.4	0	0	0.2 ± 0.4	0	0	0	0.4 ± 0.9	0
Polychaeta	<i>Spio filicomis</i>	2.2 ± 4.9	0.2 ± 0.4	0	0	0.2 ± 0.4	0	0	0	0	0	0	0	0
Polychaeta	<i>Streptosyllis bidentata</i>	0.6 ± 1.3	0	0	0	0	0	0	0	0	0	0	0	0
Priapulida	<i>Tubiluchus</i> sp.	0.2 ± 0.4	0.2 ± 0.4	0	0	0	0	0	0	0	0	0	0	0
Sipuncula	<i>Golfingia</i> sp.	0	0.2 ± 0.4	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea	<i>Apeurdes taipa</i>	0	0	0	0	0.2 ± 0.4	0	0	0	0	0	0	0	0
Turbellaria	<i>Catenulida</i> aff. <i>catenulidae</i>	0.4 ± 0.5	0	0	1.2 ± 2.7	0.2 ± 0.4	0.6 ± 1.3	0.2 ± 0.4	0	0	0	0.2 ± 0.4	0.4 ± 0.5	0
Turbellaria	<i>Catenulida</i> sp. 1 (L)	1.4 ± 1.5	2.8 ± 3.6	4.4 ± 3.3	13.8 ± 14.4	2.4 ± 1.5	14.8 ± 4.1	0.6 ± 0.5	0	2.2 ± 3.3	0.8 ± 1.3	0.2 ± 0.4	0	4.4 ± 3.3
Turbellaria	<i>Catenulida</i> sp. 2 (S)	0	0.2 ± 0.4	0	0.2 ± 0.4	0.4 ± 0.5	0.2 ± 0.4	0	0	0	0.6 ± 0.9	0	0	0
Turbellaria	<i>Catenulida</i> sp. 3 (M)	3.6 ± 3.2	1.4 ± 2.6	0.4 ± 0.9	0.2 ± 0.4	0.6 ± 1.3	0.6 ± 0.9	1.2 ± 1.3	0	0.2 ± 0.4	0.2 ± 0.4	0	0	0.4 ± 0.9
Turbellaria	<i>Haplopharyngida</i> sp. 1	0.4 ± 0.9	0	0	0	0	0	0	0	0	0	0	0	0
Turbellaria	<i>Macrostomida</i> sp. 1	0.4 ± 0.6	0	0	0	0	0	0	0	0	0	0	0	0
Turbellaria	<i>Macrostomida</i> sp. 3	0	0	0	0.2 ± 0.4	0	0	0	0	0.2 ± 0.4	0	0	0	0
Turbellaria	<i>Proseriata</i> sp. 1	0	0	0	0	0	0.4 ± 0.9	0.2 ± 0.4	0	0	0.4 ± 0.9	0	0	0
Turbellaria	<i>Proseriata</i> sp. 2	0.6 ± 0.9	0	0	0	0	0	0	0	0	0	0	0	0

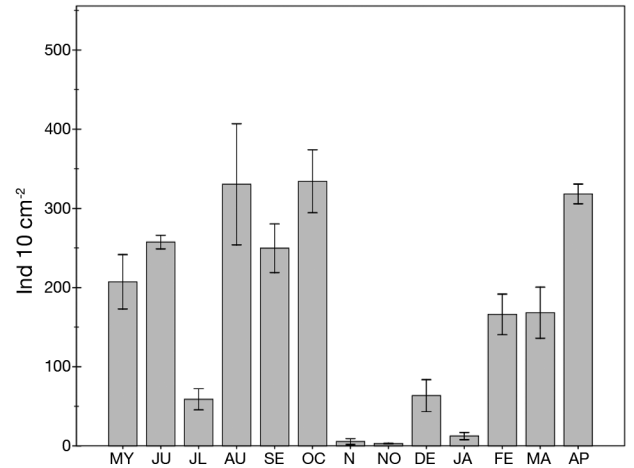


Fig. 5. – Average densities ± standard errors of *Odontophora* aff. *wieseri*.

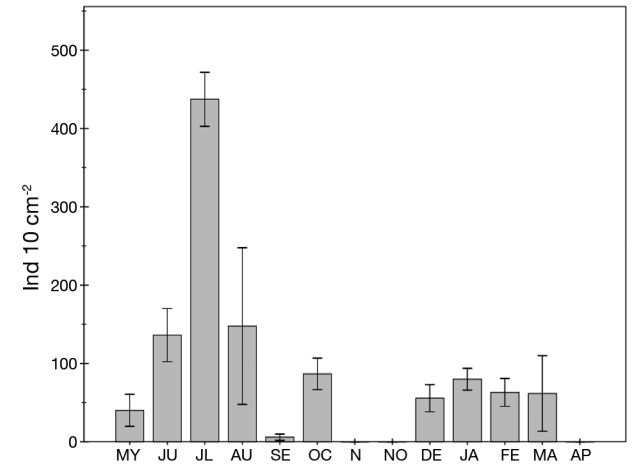


Fig 6. – Average densities ± standard errors of *Theristus* sp.

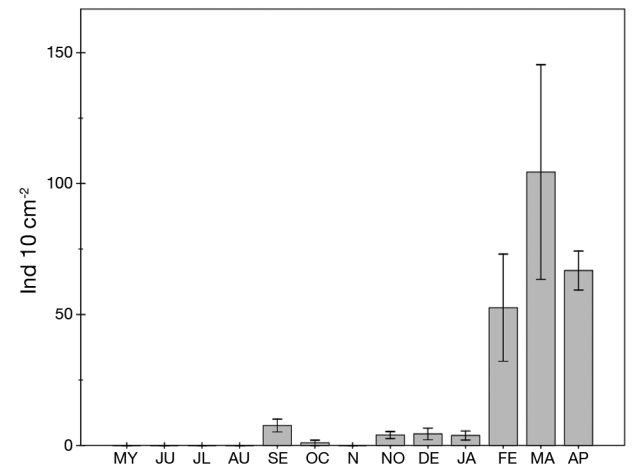


Fig. 7. – Average densities ± standard errors of *Daptonema hirsutum*.

Meiofauna assemblage structure showed significant differences throughout the study period (Fig. 8, 1-way ANOSIM, R = 0.57, p = 0.001). Pairwise tests showed significant differences between all months, with the excep-

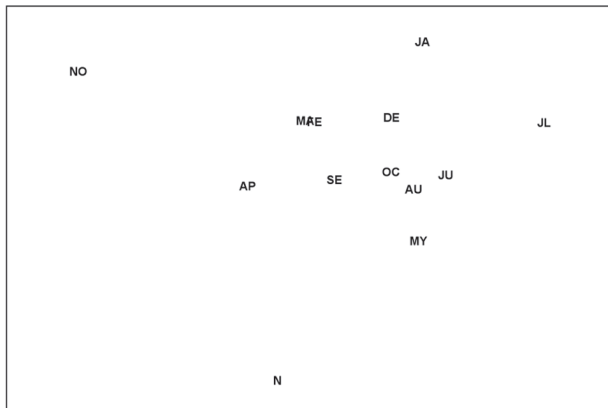


Fig. 8. – n-MDS plot of sampling months during the study period (May 2000–April 2001). N, 1st fortnight of November, NO, 2nd fortnight of November. Stress = 0.08.

Table III. - Multivariate multiple regression testing the effect of environmental variables over the meiofaunal assemblage structure SS(trace) = portion of sum of squares relative to the analysed predictor variable; pseudo-F = statistic; p = significance level; prop = proportion of variation explained.

Variable	SS (trace)	Pseudo-F	p	pro (%)
Gravels (%)	9154.7	2.876	0.889	0.032
Very coarse sands (%)	1181.7	1.863	0.431	0.056
Coarse sands (%)	1499.1	1.239	0.511	0.087
Medium sands (%)	967.5	0.634	0.418	0.098
Fine sands (%)	3226.1	0.318	0.066	0.201
Very fine sands (%)	2856.4	0.503	0.101	0.166
Silt/clay (%)	762.3	1.007	0.278	0.063
Total Nitrogen (%)	1452.3	2.118	0.821	0.038
Organic matter (%)	1003.8	0.567	0.145	0.102

tion of May–June ($R = 0.16$, $p = 0.095$), August–October ($R = 0.044$, $p = 0.246$), August–December ($R = 0.264$, $p = 0.079$), December–March ($R = 0.2$, $p = 0.151$) and February–March ($R = 0.164$, $p = 0.071$).

The multivariate multiple regression showed that none of the measured environmental variables did contribute significantly to explain patterns in meiofauna assemblage structure (all p -values > 0.05 , Table III). The most important sedimentary variables to explain meiofaunal assemblage structure were fine sands (20.1 %), very fine sands (16.6 %) and organic matter content (10.2 %).

DISCUSSION

Meiofauna assemblages inhabiting intertidal soft-bottoms of Los Cristianos bay varied throughout the year and were characterized by having low diversity and density values. These densities are lower than those reported by other authors (Coull 1985, Palacín 1990, Nozais *et al.* 2005) from intertidal sandy substrates. One of the main reasons for these low densities is the presence of

oligotrophic waters in the Canarian archipelago, which implies a low primary production (Barton *et al.* 1998). The canarian region, as a whole, presents low water-column integrated values of phytoplankton biomass and productivity during most of the year (Aristegui 1990). Moreover, no significant increase of organic matter content was observed after the runoff. Riera *et al.* (2011) observed low contents of organic matter in intertidal sediments from one beach in the east coast of Tenerife. Covazzi *et al.* (2000) showed low meiofaunal abundances in intertidal sandy beaches of the Ligurian Sea (Mediterranean Sea) and considered the oligotrophy of the system, stressed by the absence of primary organic matter (chloropigments) as one of the main factors determining meiofauna abundances in sandy beaches.

Meiofauna seasonality

Temporal variations in the abundance, diversity and assemblage structure of meiofaunal assemblages have been previously reported for different coastal regions (Nozais *et al.* 2005, Ólafsson & Elmgren 1997, among others), although several studies observed that meiofaunal assemblages may lack any seasonal pattern (Riera *et al.* 2011 and references therein). In temperate regions, meiofaunal abundances reach maximum abundances during winter (Coull 1988, Palacín 1990, Vanaverbeke *et al.* 2004, Franco *et al.* 2008), though some inconsistencies have also been reported, e.g. larger abundances of nematodes in spring and summer (Gracia *et al.* 1996, Mazzola *et al.* 2000, Mirto *et al.* 2000). In subtropical regions, several studies observed an increase in meiofaunal abundances during spring and summer (Hicks & Coull 1983, Coull 1985, Rudnick *et al.* 1985). In tropical latitudes, meiofaunal assemblages have shown different temporal patterns, although the highest abundances are found during the wet season, when temperatures were usually higher (Albuquerque *et al.* 2007), or monsoon season (Chaterjii *et al.* 1995). Thus, seasonal variations showed that inconsistencies are the rule in meiofaunal studies.

In the present study, no consistent temporal trends were observed on meiofaunal abundances and assemblage structure throughout the study period, with a clear dominance of nematodes *Odontophora* aff. *wieseri*, *Theristus* sp. and *Daptonema hirsutum*. A possible explanation could be the stability of organic matter content throughout the study period that only fluctuated during the runoff episode (November 2000).

Runoff disturbance

Several descriptors of disturbance regimes have been identified (Pickett & White 1985), i) frequency and ii) intensity. A central problem in relating disturbance to community structure lies in determining how that structure is affected by different size of disturbance events,

where “size” is defined as the quantity or amount of area disrupted by a disturbance effect (Morrisey *et al.* 2003 and references therein). For example, meiofauna responded to the organic matter accumulation associated with the river Po (Adriatic Sea), a continuous runoff disturbance, that always had higher densities in river plume and frontal sediments than in open-sea sediments, characterized by low organic matter content (Danovaro *et al.* 2000).

To the contrary, a stochastic event (freshwater runoff from the nearby ravine, “Barranco de Aquilino”) occurred in November 2000 at Los Cristianos beach, and produced drastic changes in meiofauna community structure. Meiofauna abundances and species richness decreased in the runoff period (first and second fortnight of November), recovering to pre-disturbance densities three months later (February 2001) but not to former levels. The most abundant species (*Odontophora* aff. *wieseri*, *Theristus* sp. and *Daptonema hirsutum*) decreased abruptly or even disappeared in the runoff period, with different gradual recoveries that never recovered densities of pristine conditions, before runoff disturbance.

The most important consequence of the runoff disturbance was physical stress, since no variations on sedimentary variables (grain size, total nitrogen and organic matter content) were found after the episode. In accordance with our observations, Eldose *et al.* (2008) demonstrated experimentally a relationship between physical disturbance and meiofauna abundances, since removal of sediment had harmful effects for short term on meiofauna assemblages.

Recolonization process

Earlier studies on coastal disturbances indicated that recolonization of the affected area might occur in 12-24 hours, months and even years depending on the nature of disturbance (Thistle 1980, Pequegnat 1975). Meiofauna communities can require a long time to return to pre-disturbance levels (Veit-Köhler *et al.* 2008). However, other studies reported a quick recovery of the dominant meiofaunal species or recolonization to higher densities, when favorable conditions prevailed (Altaff *et al.* 2005).

During the runoff period (first fortnight of November) a drastic change in meiofaunal abundances and species richness was observed and meiofaunal populations had not completely recovered in April 2001 (6 months after the runoff). Nematodes reached pre-disturbance densities three months after the runoff episode, however, the effects of the freshwater runoff on the remaining taxonomic groups are difficult to discern, because of their fluctuating and low densities throughout the study period. Harpacticoid copepods recovered to pre-disturbance densities during the second fortnight of November, two weeks after the disturbance. Turbellarians reached pre-disturbance densities in December 2000, one month after the runoff period.

Meiofaunal assemblage structure differed from pre-disturbance months, even certain species were recorded only in the immediately after the runoff period (November 2000). Thus, the chromadorid nematode *Ptycholaimellus ponticus* was collected solely during the first fortnight of November and is considered a cosmopolitan species that reaches maximum densities in muddy sediments (Jensen & Nehring 1992). This species has been observed to be dominant in perturbed sediments with low competition with macrofauna (Van Colen *et al.* 2009). Schratzberger *et al.* (2002) showed a quick recolonisation of *P. ponticus* to defaunated sediments, possibly due to an enhancement of the quality and variety of food resources for exploitation by this species with the reproductive potential to take advantage of them (Schratzberger & Warwick 1998). In contrast, some species that characterized meiofaunal community structure throughout the study period were absent (*Theristus* sp. and *Daptonema hirsutum*) or had very low densities (*Odontophora* aff. *wieseri*) during the runoff period.

The species composition of undisturbed adjacent areas is a key factor in recolonisation events, since the pool of available colonists affects the recovery patterns in the disturbed areas (Cristoni *et al.* 2004). Nematodes were one of the most sensitive groups during the physical disturbance, possibly due to the non-immediate effects of the active lateral migration from undisturbed sediments (Schratzberger *et al.* 2004). However, fast nematode recovery has been observed in former studies (e.g. Atilla & Fleeger 2000) and is mainly attributed to strong currents, suspension in the water column (Commito & Tita 2002) or even some resident nematode species survive leading to reinvansion and rapid recolonization, as occurred in macrofaunal species (Platt & Connell 2003, Ritter *et al.* 2005).

In contrast, harpacticoid copepods were characterized by attaining their pre-disturbance abundances only two weeks after the runoff period. An alternative explanation is that they were dominated by epibenthic forms capable of leaving the sediment and actively swimming small distances (Armonies & Reise 2000). Moreover, sediment-dwelling copepods may have colonized the sediment after resuspension and settlement events (Thistle *et al.* 1995) and then increase by reproduction. Cristoni *et al.* (2004) suggested that the quick colonization of harpacticoid copepods could be due to a combination of modes of dispersal (active emergence and swimming ability) as well as weak water currents. These factors may have promoted fast movements from undisturbed areas to affected ones, even at deep seabeds (> 3000 m) (Gwyther *et al.* 2009).

In short, stochastic events such as freshwater runoffs could alter drastically meiofauna community structure, marked by decreases during the recovery period. In these cases, physical stress is a more important factor in structuring meiofauna assemblages compared to other effects such as nutrient loading, freshwater and low salinities. However, variations of meiofauna assemblages through-

out the sampling period could not mask the punctual effect of runoff in the study area. Differences among months were not largely explained by environmental factors (e.g. grain size, total nitrogen or organic matter content).

ACKNOWLEDGEMENTS. – We thank Dr P J Somerfield (Plymouth Marine Laboratory, UK) for statistical advice. Dr T Gheskiere and Dr M Vincx (Marine Biology Department, University of Ghent, Belgium) are also acknowledged for laboratory and bibliographic search facilities. We thank Dr R Huys and S Conroy-Dalton (Natural History Museum, London, England) for advice and identification of harpacticoid copepods. Dr. N. Schizas (University of Mayagüez, Puerto Rico) gave valuable comments on an earlier draft of the manuscript.

REFERENCES

- Albuquerque EF, Brandao-Pinto AP, d'Alcantara de Queiroz A, Gomes VV 2007. Spatial and temporal changes in interstitial meiofauna on a sandy ocean beach of South America. *Braz J Ocean* 55(2): 23-29.
- Altuff K, Sugumaran J, Naveed MS 2005. Impact of tsunami on meiofauna of Marina beach, Chennai, India. *Current Sci* 89(1): 34-38
- Anderson M. 2001. A new method for nonparametric multivariate analysis of variance. *Aust Ecol* 26: 32-46
- Arístegui J 1990. La distribución de la clorofila a en aguas de Canarias. *Bol Inst Esp Oceanogr* 6(2): 61-72
- Armonies W, Reise K 2000. Faunal diversity across a sandy shore. *Mar Ecol Prog Ser* 196: 49-57
- Atila N, Fleeger JW 2000. Meiofauna colonization of artificial substrates in an estuarine embayment. *PSZN I: Mar Ecol* 21: 69-83.
- Barton ED, Arístegui J, Tett P, Cantón M, García-Braun J, Hernández-León S, Nykjaer L, Almeida C, Almunia J, Ballesteros S, Basterretxea G, Escáñez J, García-Weill L, Hernández-Guerra A, López-Laatzén F, Molina R, Montero MF, Navarro-Pérez E, Rodríguez JM, Van Lenning K, Vélez H, Wild K 1998. The transition zone of the Canary Current upwelling region. *Prog Ocean* 41: 455-504.
- Boucher G 1980. Facteurs d'équilibre d'un peuplement de Nématodes des sables sublittoraux. *Mem Mus Nat Hist Nat Sér A Zool* 114: 1-81.
- Bradstreet RB 1965. The Kjeldahl method for organic nitrogen. Academic Press, 239 p.
- Buchanan JB 1984. Sediment analysis. In NA Holme and AD McIntyre eds, *Methods for the Study of Marine Benthos*, 2nd edit. Blackwell Scientific Publications, Oxford: 41-65.
- Chatterji A, Ansari ZA, Mishra JK, Parulekar AH 1995. Seasonality in meiofaunal distribution on a tropical beach at Barangari, northeast coast of India. *Ind J Mar Sci* 24: 49-55.
- Clarke KR 1993. Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18: 17-143.
- Clarke KR, Warwick RM 2001. Changes in marine communities: an approach to statistical analysis and interpretation, 2nd edit. Plymouth Marine Laboratory, Plymouth, UK.
- Commito JA, Tita G 2002. Differential dispersal rates in an intertidal meiofauna assemblage. *J Exp Mar Biol Ecol* 268: 237-256.
- Coull BC 1985. Long term variability of estuarine meiobenthos: an 11 year study. *Mar Ecol Prog Ser* 24: 205-218.
- Coull BC 1988. Ecology of the marine meiofauna. In Higgins RP & Thiel H eds, *Introduction to the Study of Meiofauna*. Washington, DC, Smithsonian Institution Press: 18-38.
- Coull B, Dudley BW 1985. Dynamics of meiobenthic copepod populations: a long term study (1973-1983). *Mar Ecol Prog Ser* 24: 219-229.
- Covazzi A, Pusceddu A, Della Croce N, Danovaro R 2000. Spatial and temporal changes in beach meiofaunal communities of the Ligurian Sea (NW Mediterranean). *Rev Biol Mar Ocean* 35(1): 57-64.
- Cristoni C, Colangelo MA, Ceccherelli VU 2004. Spatial scale and meiobenthic copepod recolonisation: testing the effect of disturbance in a seagrass habitat. *J Exp Mar Biol Ecol* 298: 49-70.
- Danovaro R, Gambi C, Manini E, Fabiano M 2000. Meiofauna response to a dynamic river plume front. *Mar Biol* 137: 359-370.
- Eldose PM, Ravikumar B, Antony PJ, Lyla PS, Ajmal-Khan S 2008. Impact of physical disturbance on the community structure of estuarine benthic meiofauna. *Asian J Sci Res* 1: 239-245.
- Franco MA, Soetaert K, Van Oevelen D, Van Gansbeke D, Costa MJ, Vincx M, Vanaverbeke J 2008. Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types. *Mar Ecol Prog Ser* 358: 51-62.
- Gee M 1989. An ecological and economic review of meiofauna as food for fish. *Zool J Linn Soc* 96: 243-261.
- 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). *Bull Inst R Sci Nat Belg* 72(S): 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, ultradissipative sandy beach (De Panne, Belgium). *J Sea Res* 52: 211-226.
- Giere O 2009. Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments, 2nd edit. Springer-Verlag, Berlin: 328 p.
- Gourbault N, Warwick RM, Helléquet MN 1998. Spatial and temporal variability in the composition and structure of meiobenthic assemblages (especially nematodes) in tropical beaches (Guadeloupe, FWI). *Cah Biol Mar* 39: 29-39.
- Gracia L, Bayó G & Palacín C 1996. Temporal fluctuations of sublittoral meiofauna in sandy Blanes Bay (northwest Mediterranean). *Publ Espec Inst Esp Ocean* 22: 55-60.
- Gwyther D, Batterhan GJ, Waworuntu J, Gultom TH, Prayogo W, Karnan S 2009. Recolonisation of mine tailing by meiofauna in mesocosm and microcosm experiments. *Mar Poll Bull* 58: 841-850.
- Hicks G, Coull BC 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr Mar Biol Ann Rev* 21: 67-175.
- Higgins RP, Thiel H 1988. *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington: 488 p.
- Jensen P, Nehring S 1992. Review of *Ptycholaimellus* Cobb (Nematoda, Chromadoridae), with descriptions of three species. *Zool Scr* 21(3): 239-245.
- Juaro J 1975. Nematode species composition and seasonal fluctuation of a sublittoral meiofauna community in the German Bight. *Veroff Ins Meeer Bremerh* 15(4): 283-337.
- Legendre P, Anderson MJ 1999. Distance-based redundancy analysis: testing multi-species responses in multi-factorial ecological experiments. *Ecol Monog* 69: 1-24.

- 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. *J Mar Sci* 57: 1454-1461.
- McLachlan A, Brown A 2006. *The Ecology of Sandy Shores*. Elsevier, Sydney: 373 p.
- Milly PCD, Wetherald RT, Dunne KA, Delworth TL 2002. Increasing risk of great floods in a changing climate. *Nature* 415: 514-517.
- Mirto S, La Rosa T, Danovaro R, Mazzola A 2000. Microbial and meiofaunal response to intensive mussel-farm biodeposition in coastal sediments of the Western Mediterranean. *Mar Poll Bull* 40(3): 244-252.
- Morrisey DJ, Turner SJ, Mills GN, Williamson RB, Wise BE 2003. Factors affecting the distribution of benthic macrofauna in estuaries contaminated by urban runoff. *Mar Environ Res* 55: 113-136.
- Nozais C, Perissinotto R, Tita G 2005. Seasonal dynamics of meiofauna in a South Africa temporarily open/closed estuary (Mloti Estuary, Indian Ocean). *Estuar Coast Shelf Sci* 62: 325-338.
- Ólafsson E, Elmgren R 1997. Seasonal dynamics of sublittoral meiobenthos in relation to seasonality in a coastal marine ecosystem. *Estuar, Coast Shelf Sci* 45: 149-164.
- Palacín C 1990. Estudio ecológico de la meiofauna bentónica de la bahía de "Els Alfacs" (Delta del Ebro). Ecología y sistemática de las poblaciones de nematodos. PhD Thesis, Univ Barcelona, 406 p.
- Palmer TN, Räisänen J 2002. Quantifying the risk of extreme seasonal precipitation events in a changing climate. *Nature* 415: 512-514.
- Pearson TH, Rosenberg R 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Ocean Mar Biol Ann Rev* 16: 229-311.
- Pequegnat WE 1975. Meiobenthos ecosystems as indicators of the effects of dredging. In Cronin LE ed, *Estuarine Research*. Academic Press, New York: 573-584.
- Pickett STA, White PS 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York: 472 p.
- Platt WJ, Connell JU. 2003. Natural disturbances and directional replacement of species. *Ecol Monogr* 73(4): 507-522.
- Riera R, Núñez J, Brito MC, Tuya F 2011. Temporal variability of a subtropical intertidal meiofaunal assemblage: contrasting effects at the species and assemblage-level. *Vie Milieu* 61(3): 129-137.
- Ritter MC, Montagna PA, Applebaum S 2005. Short-term succession dynamics of macrobenthos in a salinity-stressed estuary. *J Exp Mar Biol Ecol* 323: 57-69.
- Rodríguez JG 2004. Intertidal water column meiofauna in relation to wave intensity on an exposed beach. *Sci Mar* 68: 181-187.
- Rudnick DT, Elmgren R, Frithsen JB 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. *Oecologia* 67: 157-168.
- Schizas N, Shirley TC 1996. Seasonal changes in structure of an Alaskan intertidal meiofauna assemblage. *Mar Ecol Prog Ser* 133: 115-124.
- Schratzberger M, Gee JM, Rees HL, Boyd SE, Wall CM 2000. The structure and taxonomic composition of sublittoral meiofauna assemblages as indicator of the status of marine environments. *J Mar Biol Ass UK* 80: 969-980.
- Schratzberger M, Wall CM, Reynolds WJ, Reed J, Waldox MJ 2002. Effects of paint-derived tributyltin on structure of estuarine nematode assemblages in experimental microcosms. *J Exp Mar Biol Ecol* 272: 217-235.
- Schratzberger M, Warwick RM 1998. Effects of physical disturbance on nematode communities in sand and mud: a microcosm experiment. *Mar Biol* 130: 643-650.
- Schratzberger M, Whomersley P, Warr K, Bolam SG, Rees HL 2004. Colonisation of various types of sediment by estuarine nematodes via lateral infaunal migration: a laboratory study. *Mar Biol* 145: 69-78.
- Short AD 1999. *Beach and Shoreface Morphodynamics*. Wiley, Chichester: 392 p.
- Somerfield P, Warwick R 1996. *Meiofauna in marine pollution programmes. A laboratory manual*. Ministry of Agriculture, Fisheries, and Food, Directorate of Fisheries Research, Lowestoft: 71 p.
- Thistle D 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance. *J Mar Res* 38: 381-395.
- Thistle D, Weatherly GL, Wonnacott A, Ertman SC 1995. Suspension by winter storms has an energetic cost for adult male benthic harpacticoid copepods at a shelf site. *Mar Ecol Prog Ser* 125: 77-86.
- Vanaverbeke J, Steyaert M, Soetaert K, Rousseau V, Van Gansbeke D, Parent JY, Vincx M 2004. Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the southern North Sea. *J Sea Res* 52(4): 281-292.
- Van Colen C, Montserrat F, Verbist K, Vincx M, Steyaert M, Vanaverbeke J, Herman PMJ, Degraer S, Ysebaert T 2009. Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties. *Mar Ecol Prog Ser* 281: 189-197.
- Veit-Köhler G, Laudien J, Knott J, Velez J, Sahade R 2008. Meiobenthic colonization of soft sediments in arctic glacial Kongsfjorden (Svalbard). *J Exp Mar Biol Ecol* 363: 58-65.
- Walkley A, Black LA 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic and titration method. *Soil Sci* 37: 29-38.
- Warwick R, Buchanan JB 1971. The meiofauna off the coast of Northumberland. II. Seasonal variability of the nematode population. *J Mar Biol Ass UK* 51(1): 129-146.

Received October 24, 2011

Accepted July 27, 2012

Associate Editor: J Orignac