

TEMPORAL VARIABILITY OF A SUBTROPICAL INTERTIDAL MEIOFAUNAL ASSEMBLAGE: CONTRASTING EFFECTS AT THE SPECIES AND ASSEMBLAGE-LEVEL

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MEIOFAUNA
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ABSTRACT. – Meiofaunal assemblages were sampled monthly at an intertidal beach (Los Abrigos del Porís, Tenerife, Canary Islands) during one year (May 2000-April 2001). We aimed (1) to determine whether patterns in the assemblage structure, total meiofaunal abundance, and the abundance of the most common species, followed a temporal pattern, and (2) to assess if three environmental variables (grain size, organic content and total nitrogen) affected the meiofaunal assemblage structure throughout this annual cycle. The five most abundant taxa (the copepod *Ectinosomatidae* sp.1, the polychaete *Microphthalmus pseudoaberrans*, the turbellarian *Catenulida* sp.3 and the nematodes *Enoplolaimus propinquus* and *Theristus* sp.) showed significant differences in abundance throughout the study period. However, the total abundance and assemblage structure of meiofauna did not change throughout the study period. The contribution of measured environmental variables to explain variation in meiofaunal assemblage structure was considerably low. Consequently, the study of meiofaunal patterns through time can reach contrasting results when patterns are evaluated at the species or assemblage-level: individual species can counterbalance their abundances to mask patterns at the assemblage-level.

INTRODUCTION

Meiofauna (small invertebrates that can pass through a 0.5-1 mm mesh but retained by a 30-45 µm mesh) constitute an important component in the functioning of benthic ecosystems, especially where the main energy fluxes come from detrital ways (Heymans & Baird 1995). Indeed, the major ecological role of this benthic group is decomposition of detritus, and so recycling of nutrients, as well as the establishment of a link between organic matter and higher trophic levels, mainly macrofauna (Coull 1999). Meiofaunal assemblages are highly variable throughout space and time, with patterns of richness and abundance largely scale-dependent (Higgins & Thiel 1988). Several factors have been proposed to explain these fluctuations, including physical disturbances (Hourston *et al.* 2005, Nozais *et al.* 2005, Riera *et al.* submitted) and changes in the magnitude of a suite of environmental variables, such as temperature, dissolved oxygen concentration (Dye & Furstenberg 1978), sediment grain size (Ndaro & Ólafsson 1999, Schratzberger *et al.* 2004) and salinity (Ingle & Parulekar 1986, Yamamuro 2000, Ólafsson *et al.* 2000).

Seasonal variations in the abundance, diversity and assemblage structure of meiofaunal assemblages have been previously reported for different coastal regions (Hicks & Coull 1983, Coull & Dudley 1985, Rudnick

et al. 1985, Schizas & Shirley 1996, Nozais *et al.* 2005), although several studies have observed that meiofaunal assemblages may lack any seasonal pattern (Warwick & Buchanan 1971, Juario 1975, Boucher 1980). In turn, temperature is one of the main environmental drivers controlling variations in meiofaunal assemblage structure living in the intertidal. This factor can affect meiofaunal abundances directly, e.g. *via* dehydration of meiofaunal specimens, and indirectly as well, e.g., controlling the growth of food items such as bacteria and diatoms (Harris 1972). In temperate regions, meiofaunal abundances reach maximum abundances during winter (Coull 1988, Palacín 1990), 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 the particular case of subtropical regions, several studies have documented 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 are usually higher (Albuquerque *et al.* 2007).

Across small spatial scales, meiofauna is horizontally and vertically variable. The grain size and the degree of sorting of the sand grains determine the available space for interstitial meiofauna (Coull & Bell 1979). For exam-

ple, high levels of organic matter are typically found where silt and clay dominate the granulometric fractions (Snelgrove & Butman 1994), with two direct effects: i) an increase in food resources for detritivorous fauna (Danovaro *et al.* 2000) and (ii) a decrease in the oxygen content in the pore water (Mazzola *et al.* 2000). Meiofaunal assemblages are subjected to these temporal (e.g. temperature) and spatial (e.g. organic content and grain size) changes; therefore, a high variation in the abundances of these assemblages might be expected.

In this study, we investigated patterns in the assemblage structure and abundance of meiofauna inhabiting an intertidal beach at the Canary Islands through an annual cycle. We aimed (1) to determine whether patterns in the assemblage structure, total meiofaunal abundance, and the abundance of the most common species, followed a temporal trend, and (2) to identify if three environmental variables (grain size, organic content and total nitrogen) affected the meiofaunal assemblage structure throughout this annual cycle.

MATERIAL AND METHODS

Study area and sampling: This study was conducted from May 2000 to April 2001 at Los Abrigos del Porís Bay, a beach located at the southeast coast of Tenerife (Canary Islands, NE Atlantic Ocean, 28°08'34.26"N, 16°26'20.82"E) (Fig. 1). The study site is located in a sheltered bay (classified as bay beach, *sensu* Short 1999), dominated by the presence of medium and coarse sands. Tides can reach up to 2 m of amplitude in this area.

Sediment samples were collected monthly on the intertidal during low tide. Samples were taken from the low water mark (LW). Sediment cores (10 cm²) were pushed into the sediment to a depth of 30 cm. Each month, five replicates were collected

for faunistic determinations and one for the analysis of three environmental variables: organic matter, total nitrogen and the granulometric composition of the sediment.

Analysis of environmental variables: To assess the granulometric composition of the sediment, ca. 100 g of sediment from each sample was oven dried at 105° C, passed through a graded series of sieves (2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm and 0.063 mm), and then weighted (Buchanan 1984). The method of Walkley & Black (1934) was used to determine the organic matter content (% OM) of the sediment; this involved using dichromate oxidation under acidic conditions through the addition of sulphuric acid. In the process of oxidizing of a sample, the potassium dichromate (K₂Cr₂O₇) is reduced to Cr³⁺. The amount of Cr³⁺ was determined after the oxidization was complete, which is an indirect measure of the organic content in the sample. This method is suitable for determining low concentrations of organic carbon in the water and sediments (Sawyer *et al.* 2003). Total nitrogen (%) was determined following the Kjeldahl method (Bradstreet 1965). This method followed three steps: (i) digestion through sulphuric acid that decomposes the organic matter by oxidation to liberate ammonium sulphate; (ii) distillation with sodium hydroxide to convert the ammonium salt into ammonia, which is then determined via back titration through hydrochloric acid; and finally, (iii) the solution is dipped into a solution of boric acid, that reacts with the ammonia, and the remaining fraction of the boric acid is subsequently titrated with a sodium carbonate solution using a methyl orange pH indicator.

Analysis of meiofauna: Samples were preserved in a 10 % seawater formaldehyde solution and subsequently decanted through a 0.5 and a 0.063 mm mesh sieves. A standard procedure (Sommerfield & Warwick 1996) of faunal extraction from the sediment was made where supernatant with meiofaunal organisms were decanted. The fraction remaining on the 0.063 mm

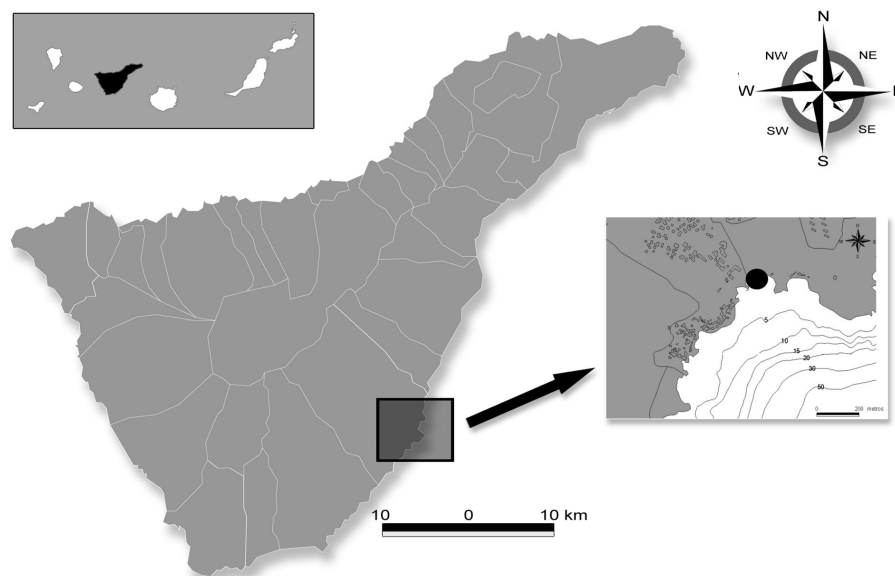


Fig. 1. – Map of the study area, showing the sampling site (•).

Table I. – Environmental variables (total nitrogen, organic matter and sedimentary types) measured throughout the study.

	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Nov-00	Dec-00	Jan-01	Feb-01	Mar-01	Apr-01
Nitrogen (%)	0.01	0.02	0.01	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.01	0.02
Organic matter (%)	1.33	1.30	1.03	1.11	0.32	0.76	0.88	1.07	1.33	1.62	0.96	0.85
Gravels (%)	0.14	0.91	3.46	2.76	1.16	7.57	1.68	5.86	0.46	12.44	2.13	0.38
Very coarse sands (%)	0.59	2.53	6.54	2.87	2.89	3.52	2.18	9.03	4.20	6.58	2.08	1.41
Coarse sands (%)	6.79	15.58	27.11	19.85	17.03	18.44	22.76	16.42	28.85	18.33	10.02	13.51
Medium sands (%)	80.86	64.53	50.87	58.84	61.85	52.98	59.21	53.42	62.16	48.69	61.09	74.54
Fine sands (%)	11.43	16.12	11.48	14.93	16.40	16.57	10.52	14.97	4.32	10.92	24.08	10.03
Very fine sands (%)	0.16	0.28	0.46	0.70	0.59	0.86	3.20	0.31	0.01	2.99	0.54	0.13
Silt/clay (%)	0.03	0.04	0.08	0.06	0.08	0.05	0.46	0.00	0.00	0.04	0.06	0.00

mesh sieve was separated into different taxonomical groups under a binocular microscope and preserved in 70 % ethanol. Meiofaunal specimens were then mounted on glycerine jelly and examined using a LEICA DMLB microscope equipped with Nomarski interference contrast. All meiofaunal specimens were identified and a subsample of 200 individuals taken for nematodes, following Somerfield & Warwick (1996). Some taxonomic groups (i.e. harpacticoid copepods, turbellarians) required a dissection, and/or careful inspection of taxonomic characters of internal anatomy. The remaining taxonomic groups were determined to the lowest taxonomic level using current scientific literature (see Annex I). Meiofaunal abundances were expressed as numbers of individuals per area (10 cm²).

Statistical analysis: Biological descriptors of the assemblage (total abundance and species richness) were calculated for each sample. Differences in abundance and species richness patterns among months (fixed factor) were tested through a one-way ANOVA, after verifying normality using the Kolmogorov-Smirnov & Levene's test for homogeneity of variances, respectively. When the requirements of normality and/or homogeneity of variances were not fulfilled, the Kruskal-Wallis ANOVA (KW ANOVA) test was used instead.

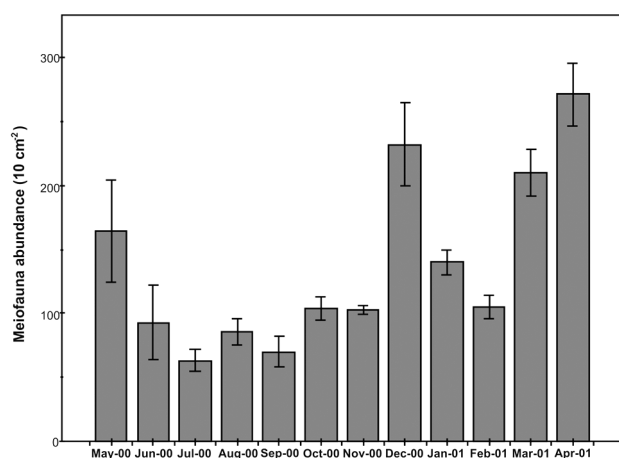


Fig. 2. – Overall meiofaunal abundances (10 cm²) throughout the study period. Bars show mean + SE.

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.

The relationship between the entire set of environmental variables and the meiofaunal assemblage structure was investigated using a distance-based redundancy analysis (db-RDA, 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 variables

The sampling site was dominated by medium sands (0.25-0.5 mm) throughout the entire study period, ranging from a minimum of 48.69 % (February 2001) to a maximum of 80.86 % (May 2000). Coarse sands were also well represented, ranging from 6.79 % (May 2000) to 28.85 % (January 2001). The remaining sediment types were scarce. The mean percentage of organic matter content was 1.05 % throughout the study period, with a maximum content of 1.62 % (February 2001) and a minimum content of 0.32 % (September 2000). The mean percentage of nitrogen was 0.015 % throughout the study period, ranging from 0.010 % and 0.022 % (Table I).

Meiofaunal assemblages: univariate responses

A total of 11 taxonomic groups were collected (copepods, nematodes, turbellarians, polychaetes, oligochaetes, nemertean, acari, priapulids, ostracods, tanaids and amphipods). Various groups dominated the assemblage

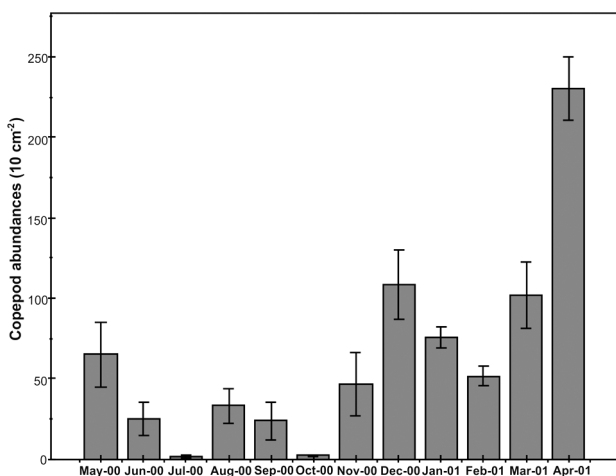
Table II. – Contribution of each faunal group to overall meiofaunal abundance during the study. The percentage of dominance is represented in bold.

	May-00	Jun-00	July-00	Aug-00	Sep-00	Oct-00	Nov-00	Dec-00	Jan-01	Feb-01	Mar-01	Apr-01	Mean
Copepoda (%)	39.66	26.88	2.03	42.89	33.62	2.02	41.35	46.00	56.18	46.99	47.09	76.44	38.55
Nematoda (%)	42.34	61.29	22.38	20.16	46.61	40.37	19.43	15.99	25.19	14.39	18.50	10.22	28.16
Turbellaria (%)	11.80	6.24	6.98	28.17	12.71	24.40	15.15	26.36	15.35	29.14	26.73	11.08	17.90
Polychaeta (%)	5.23	2.58	66.57	7.24	3.67	32.66	22.99	11.65	3.13	9.11	7.49	2.12	14.58
Oligochaeta (%)	0.24	1.94	2.03	1.29	0.85	0	0.18	0	0	0.18	0.19	0.13	0.59
Nemertea (%)	0	0.86	0	0.26	0	0	0	0	0	0	0	0	0.09
Acari (%)	0.12	0	0	0	0	0	0	0	0.15	0.18	0	0	0.04
Tanaidacea (%)	0.36	0	0	0	0	0	0	0	0	0	0	0	0.03
Priapulida (%)	0	0.22	0	0	0	0	0	0	0	0	0	0	0.02
Ostracoda (%)	0.12	0	0	0	0	0	0	0	0	0	0	0	0.01
Amphipoda (%)	0.12	0	0	0	0	0	0	0	0	0	0	0	0.01

Table III. – Results of univariate ANOVA testing for differences in overall meiofauna abundance, as well as the abundances of copepods, nematodes, polychaetes and turbellarians throughout the study period (May 2000-April 2001).

Source of variation	df	Overall meiofaunal abundance			Copepod abundance			Nematode abundance			Polychaete abundance			Turbellarian abundance		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Months	11	23100	0.09	0.34	989.71	0.14	0.25	1417	0.45	0.10	1042.23	0.08	0.65	1689	0.09	0.52

in terms of abundance: copepods, nematodes, turbellarians and polychaetes accounted for a 99.21 % of total abundance. Copepods dominated the assemblage, in terms of abundance, in 7 months throughout the study period (August, November, December, January, February, March and April), from a minimum of 41.35 % of total meiofaunal abundance (November 2000) to a maximum of 76.44 % (April 2001). Nematodes were the most abundant group in May, June, September and October 2000, from a minimum of 40.37 % of total meiofaunal abundance (October 2000) to a maximum of 61.29 % (June 2000). Polychaetes dominated the meiofaunal assemblage in July 2000 (66.57 % of total abundance). The remaining

Fig.3. – Copepod abundances (10 cm⁻²) throughout the study period. Bars show mean + SE.

taxonomic groups were scarce, representing only 0.79 % of the overall meiofaunal abundance (Table II).

Total meiofaunal abundances fluctuated during the studied period. The highest value was recorded in April 2001 (273 ± 45 ind 10 cm⁻²) and the lowest in July 2000 (67 ± 28 ind 10 cm⁻²) (Fig. 2). However, differences in total meiofaunal abundances among months were not significant (1-way ANOVA, $F = 0.09$, $p = 0.34$, Table III).

Copepods

Copepods had the largest abundances in April 2001 (240 ± 38 ind 10 cm⁻²) and December 2000 (115 ± 21 ind 10 cm⁻²), while the lowest abundance was observed in July and October 2000, with less than 35 ind 10 cm⁻² (Fig. 3). Total copepod abundances fluctuated during the study period (Fig. 3), although differences were not significant among months (1-way ANOVA, $F = 0.14$, $p = 0.25$, Table III).

A total of 8 species of harpacticoid copepods were identified. The most abundant species was *Ectinosomatidae* sp.1 (3,606 individuals for the entire study). This copepod showed highly significant differences throughout the study period (1-way ANOVA, $F = 18.90$, $p < 0.0001$, Table IV). The least abundant species were *Tisbe* aff. *bulbisetosa* and *Asellopsis* sp. with only 3 individuals observed throughout the study.

Nematodes

Nematodes reached their maximum abundances in

Table IV. – Results of univariate ANOVA testing for differences in the abundances of Ectinosomatidae sp.1, *Microphthalmus pseudoaberrans*, Catenulida sp.3, *Enoplolaimus propinquus* and *Theristus* sp. throughout the study period (May 2000–April 2001). Significant differences are highlighted in bold.

Source of variation	Ectinosomatidae sp.1 abundance			<i>M. pseudoaberrans</i> abundance			Catenulida sp.3 abundance			<i>E. propinquus</i> abundance			<i>Theristus</i> sp. abundance		
	MS	F	p	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Months	20153	18.9	<<0.0001	1136	5.94	0.00005	1592	5.08	0.0003	242	2.43	0.017	99	3.31	0.002

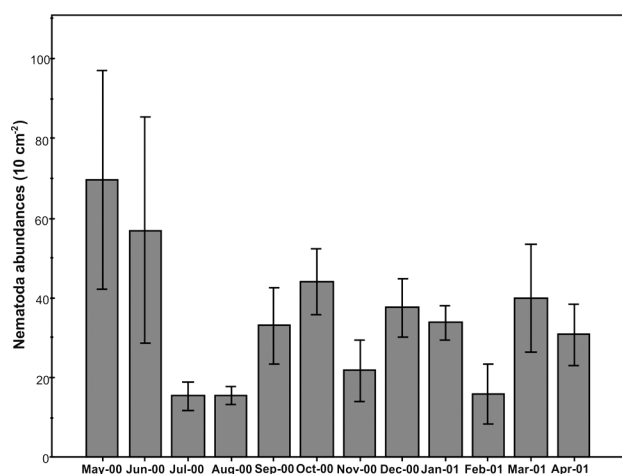


Fig. 4. – Nematode abundances (10 cm²) throughout the study period. Bars show mean ± SE.

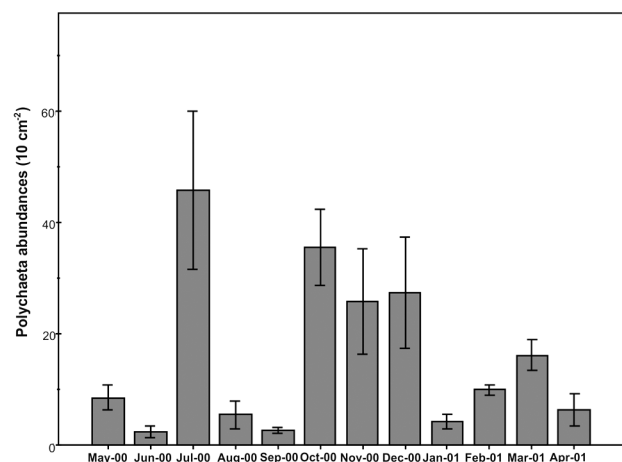


Fig. 5. – Polychaete abundances (10 cm²) throughout the study period. Bars show mean ± SE.

May 2000 (71 ± 45 ind 10 cm⁻²) and June 2000 (53 ± 34 ind 10 cm⁻²), while minimum abundances were observed in July 2000 (17 ± 8 ind 10 cm⁻²), August 2000 (18 ± 3 ind 10 cm⁻²) and February 2001 (18 ± 13 ind 10 cm⁻²) (Fig. 4). Nematode abundances varied during the study (Fig. 4); however, differences in total nematode abundance were not significant among months ($F = 0.45$, $p = 0.10$, Table III).

A total of 48 species of nematodes were found; the enoplid *Enoplolaimus propinquus* and the monhystrid *Theristus* sp. were the most abundant species, with 289

and 149 individuals, respectively, for the overall study. The former two species showed highly significant differences in abundance throughout the study period (1-way ANOVA, *E. propinquus*, $F = 2.43$, $p = 0.017$; *Theristus* sp. $F = 3.31$, $p = 0.002$, Table IV). The rest of nematodes were observed at low abundances (< 100 ind), being *Acanthopharynx* sp., *Bathylaimus australis*, *Pomponema* aff. *reducta*, *Rhabdocoma americana*, *Rhabdodemanina* sp. and *Viscosia glabra* the least abundant species (only one specimen observed).

Polychaetes

Polychaetes had maximum abundances in July 2000 (37 ± 18 ind 10 cm⁻²), followed by October, November and December 2000 (29 ± 15 ind 10 cm⁻²). The lowest abundances were observed in June 2000 (3 ind 10 cm⁻²) and January 2001 (5 ind 10 cm⁻²) (Fig. 5). No significant differences in total polychaete abundances were observed during the study period ($F = 0.08$, $p = 0.65$, Table III).

A total of 22 species of polychaetes were identified during the study; the most abundant species was the hesionid *Microphthalmus pseudoaberrans* (822 specimens). This species showed highly significant differences in abundance throughout the study period (1-way ANOVA, $F = 5.937$, $p < 0.0001$, Table IV). The remaining polychaete species showed low abundances in all cases (< 40 ind); 10 of them (*Tharyx marioni*, *Syllis proliferata*, *Syllides japonicus*, *Anoplosyllis edentula*, *Schoerella laubieri*, *Pionosyllis spinisetosa*, *Novafabricia* sp., *Hesionides arenaria*, *Exogone naidina* and *Dispio uncinata*) were exclusively represented by one individual.

Turbellarians

Turbellarians showed their largest abundances in December 2000 (50 ± 36 ind 10 cm⁻²) and March 2001 (47 ± 32 ind 10 cm⁻²), while the lowest abundance was detected in June and July 2000 (< 15 ind cm⁻²) (Fig. 6). Temporal fluctuations in total turbellarian abundances were not statistically significant during the study period ($H = 0.09$, $p = 0.52$, Table III).

A total of 12 species of turbellarians were determined. *Catenulida* sp.3 was the most abundant taxa (761 individuals). This species showed highly significant differences in abundance throughout the study period (1-way ANOVA, $F = 3.24$, $p < 0.0001$, Table IV). The remaining

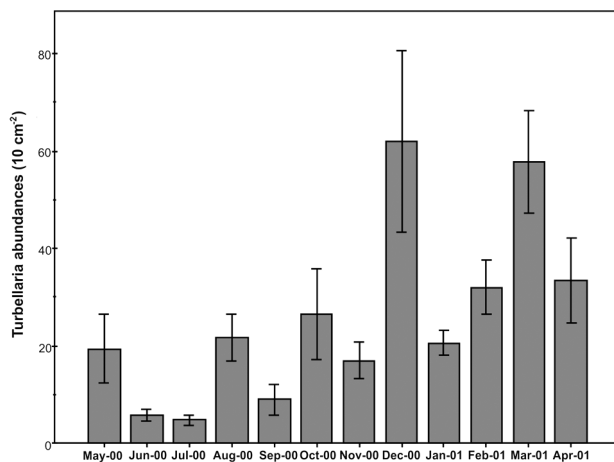


Fig. 6. – Turbellarian abundances (10 cm^{-2}) throughout the study period. Bars show mean + SE.

species were scarce (< 120 ind), and the least abundant taxa were *Haplopharyngida* sp.1 and *Macrostomida* sp.3 (only one individual).

Minor groups

Minor taxa were constituted by oligochaetes, acari, nemerteans, amphipods, ostracods and tanaids. A total of 10 species were identified; five of them were oligochaetes (*Grania* sp., *Enchytraeidae* sp.1, *Aktedrilus* sp., *Tubificidae* and *Heterodrilus* sp.), while one species contributed to each of the remaining taxonomic groups. The most abundant species was the oligochaete *Grania* sp. (16 ind for the overall study) followed by *Enchytraeidae* sp.1 (12 ind). The least abundant taxa were the nemertean *Otopyphonemertes* sp.2, the ostracod *Cypridina* aff. *mediterranea* and the amphipod *Bathyporeia guilliamsoniana* (only one individual).

Meiofaunal assemblage: multivariate responses

The meiofaunal assemblage structure showed no temporal pattern throughout the study period (Fig. 8, 1-way ANOSIM, $R = 0.088$; $p = 0.137$). The multivariate mul-

ti-ple regression showed that none of the measured environmental variables contribute significantly to explain patterns in meiofaunal assemblage structure (all p -values > 0.05 , Table V).

DISCUSSION

In this study, a lack of responses through time at the level of assemblage and major taxonomic groups may be indicative of a lack of temporal patterns for meiofauna. Results, however, can be misleading at the assemblage-level (Fleeger *et al.* 1989), since each individual species within each broad taxonomic group may react differently to environmental variability (Ólafsson 1991), i.e. by increasing or decreasing its abundance (Moens & Vincx 2000). Our study has demonstrated that the five most abundant species (the copepod *Ectinosomatidae* sp.1, the polychaete *Microphthalmus pseudoaberrans*, the turbellarian *Catenulida* sp.3 and the nematodes *Enoplolaimus propinquus* and *Theristus* sp.) showed significant differences in abundance throughout the study period, even though meiofaunal total abundance and assemblage structure did not change. This result demonstrates that temporal fluctuations of species constituting an assemblage can counterbalance to each other to mask temporal shifts at the assemblage-level.

On ultra-dissipative beaches, such as the study site, several factors such as food availability, particle size, temperature and salinity, have been proposed to explain variations in faunal composition and abundance at a range of spatial and temporal scales (Giere 1993). One of the main factors explaining the absence of seasonality on meiofaunal assemblages could be food patchiness in the intertidal, e.g. the local distribution of bacteria and diatoms, which is the most likely factor affecting small-scale distribution patterns of meiofaunal assemblages (Blome *et al.* 1999). The sediment temperature can also affect meiofaunal abundances (Albuquerque *et al.* 2007); e.g. causing events of nematode reproductive blooms (Heip *et al.* 1985, Moens & Vincx 2000). The sediment temperature can also affect meiofaunal assemblages by controlling the

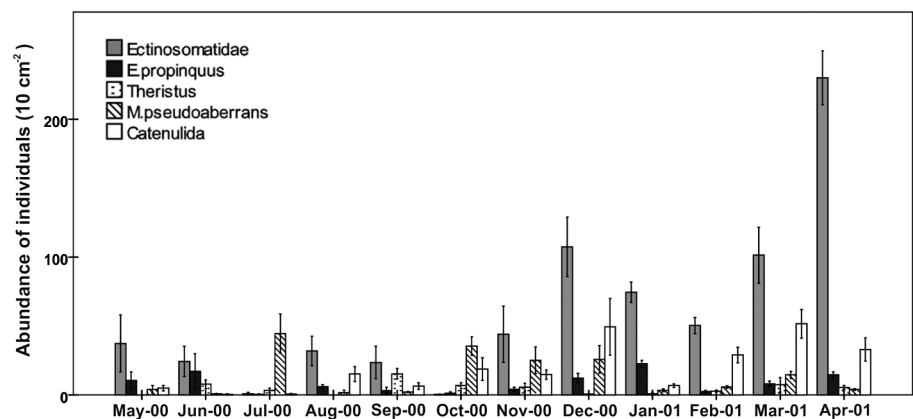


Fig. 7. – Abundances of the five most abundant meiofaunal species (10 cm^{-2}) throughout the study period. Bars show mean + SE.

Table V. – 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	prop
Total Nitrogen (%)	1114.7	0.544	0.819	0.051
Organic matter (%)	2062.7	10.562	0.387	0.095
Gravels (%)	1677.9	0.842	0.556	0.077
Very coarse sands (%)	1344	0.664	0.718	0.062
Coarse sands (%)	1767	0.891	0.5	0.082
Medium sands (%)	3170.6	17.211	0.109	0.147
Fine sands (%)	845.65	0.408	0.908	0.039
Very fine sands (%)	1333.7	0.658	0.739	0.062
Silt/clay (%)	1023.3	0.497	0.803	0.047

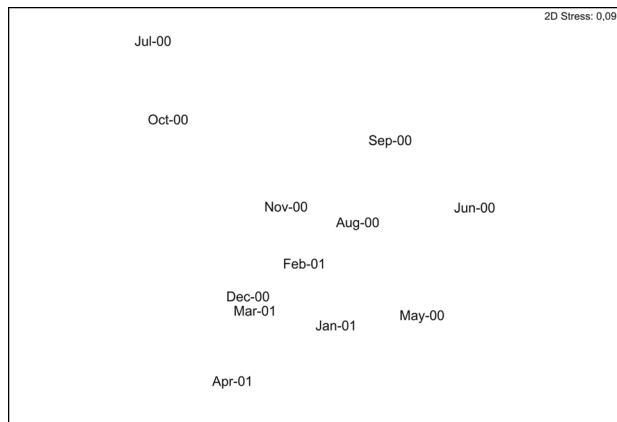


Fig. 8. – Two-dimensional multi-dimensional scaling ordination (nm-MDS) of the meiofaunal assemblage throughout the study period.

growth and availability of food, such as bacteria and diatoms (Harris 1972). In the Canary Islands, variation in sea water temperature during an annual cycle is considerably low, from a minimum of 17° C in winter (January) to a maximum of 23° C in summer (August) (Barton 2001). Moreover, canarian waters are typically oligotrophic (Barton *et al.* 1998), including low levels of phytoplankton primary production. As a result, peaks in phytoplankton biomass are hardly noticeable by meiobenthic assemblages in the study area, in contrast to other geographical areas (e.g. the Baltic), where meiofaunal assemblages response to pulses in the amount of phyto-detritus that reach the bottom after the spring phytoplankton bloom (Ólafsson & Elmgren 1997 and references therein).

The content of total nitrogen in the sediment was low throughout the study period, and so no significant influence over the meiofaunal assemblage structure was observed. The organic matter content of the sediment fluctuated during the study period; however, no significant effects were observed over the meiofaunal assem-

blage. Despite grain size is a crucial environmental factor explaining the distribution and abundance of meiofauna, no significant effects over the meiofaunal assemblage structure were observed. The most abundant sediment type (medium sands) allowed harpacticoid copepods to dominate over nematodes. Biological processes that were not measured during this study may have had an influence on the temporal fluctuations of meiofauna at the species-level. For example, predation and competition for food might be important on sandy beaches (Kotwicki *et al.* 2005). However, macrofaunal (predatory) abundances appeared to be characterized by rather low abun-

dances in the study site (Riera R unpubl data), dominated by spionid polychaetes (*Spio filicornis*) and amphipods (*Bathyporeia* sp.).

In summary, our results reinforce previous observations that highlight that responses of meiofauna across time can be overlooked when responses are investigated at the assemblage, rather than at the species level.

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