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Meiofauna distribution along a gradient of sandy beaches in northern Spain

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Abstract

Ten sandy beaches located in northern Spain were studied during the summer of 1999 to analyse the patterns in number of major taxa, abundance and biomass of meiofauna along a gradient of morphodynamic beach types and exposure rate. Sediment samples were collected with metallic cylinders (23 cm^2 cross-sectional area, 120 cm long) at 10 equally spaced shore levels along six replicated transects extended from the drift line down to the low tide level. Wave exposure rate and Dean's parameter were estimated at each sampled beach. The meiofauna was primarily represented by Nematoda and Harpacticoidea. Meiofaunal abundances ranged between 64×10^6 and 296×10^6 ind. m^{-1}, whereas biomass (ash free dry weight) per linear meter of beach ranged between 30 and 166 g m^{-1}. The results showed two significant trends: (1) the meiofaunal biomass increases exponentially with exposure rate from exposed to very exposed beaches; and (2) the number of major taxa increases exponentially with exposure rate and linearly with average grain size. These trends are opposite to the general patterns of the sandy beach macroinfauna, which is generally negatively affected by increases in wave exposure and grain size. This suggests that macro- and meiofauna are affected in different ways by the physical processes associated with wave action.

Keywords: meiofauna; sandy beach; wave energy; beach morphodynamic state; northern Spain

1. Introduction

High energy sandy beaches are the most dynamic of soft bottom habitats (McLachlan, de Ruyck, & Hacking, 1996) and have high presence in the open coasts of tropical and temperate regions (Davies, 1972) harbouring diverse and abundant macroinfauna and meiofauna (Brown & McLachlan, 1990). Several studies in these extreme environments have shown that the variation in macroinfaunal community is partly related to composite abiotic characteristics such as morphodynamic state and wave exposure (see e.g. Defeo, Jaramillo, & Lyonnet, 1992; Dexter, 1984; McLachlan, Fisher, Al-Habsi, Al-Shukairi, & Al-Habsi, 1998; McLachlan, Jaramillo, Donn, & Wessels, 1993; McLachlan, Wooldridge, & Dye, 1981; McLachlan et al., 1996). Studies on the influence of these composite factors on meiofaunal community are scarce. In relation to wave exposure, pioneer studies of McIntyre (1971) and McLachlan et al. (1981) suggested that meiofauna in sandy beaches is not so negatively affected by the increases in exposure and coarser sediments than the macroinfauna. Nevertheless, to our knowledge, this prediction remains unchecked.

In relation to morphodynamics, McLachlan and Turner (1994) predicted that optimum conditions for the development of diverse and abundant meiofauna are likely to occur in intermediate beaches (sensu Short & Wright, 1983). Their prediction is based on the fact that the intermediate morphodynamics represent an equilibrium state between organic inputs (which increases towards the dissipative beach state, according to Short & Wright, 1983) and aerobic interstitial conditions (which increases towards the reflective beach state, according to Short & Wright, 1983). Both factors are most favourable to the presence of meiofauna in intertidal habitats (e.g. Giere, 1993). The study of

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Rodríguez (2001) at a sandy beach which harbours different morphodynamics agreed with McLachlan and Turner's prediction. Thus, the highest abundance and number of major taxa were found at the intermediate position close to reflective area of the beach. The study of Rodríguez, López, and Jaramillo (2001) on Chilean sandy beaches found the highest abundance of meiofauna at the dissipative beach and the highest number of major taxa was observed at the reflective beach.

The main objective of this work was to follow the pioneer studies cited earlier on the possible influence of the morphodynamic state and/or the wave exposure rate on the sandy beach meiofauna. Thus, the between-beach variation in biomass, abundance and number of taxa of the intertidal meiofauna was analysed at 10 sandy beaches in northern Spain. This is an area dominated by rocky shores in which sandy beaches occur in a relatively wide range of morphodynamic and exposure conditions.

2. Material and methods

2.1. The study area

Ten sandy beaches on the northern coast of Spain (southern shore of Bay of Biscay), at Oyambre, Liencres, Langre, Berria, Laredo, Salvaje, Bakio, Laga, Zarautz and Hendaya (Fig. 1), were sampled during spring tides of September 1999. The beaches were selected to represent a relatively wide variation in morphodynamic states and wave exposure but excluding very sheltered beaches (sensu McLachlan, 1980a). Tides in this region are semidiurnal with maximum ranges close to 4 m.

2.2. Sampling design

Sampling was carried out at the central area of the 10 sampled beaches (covering a long-shore distance of 40–50 m) during low tide. Sediment samples were collected with metallic cylinders (23 cm^2 cross-sectional area, 120 cm long) at 10 equally spaced shore levels along six replicated transects (separated haphazardly between 5 and 10 m) and extending from the drift line to the lowest limit of the swash zone (indicated by bore collapse). At Hendaya, the uppermost shore level was located at the limit where the promenade covered the upper intertidal (Fig. 2), i.e. a truly intertidal transect was not sampled at this beach. Previous studies of vertical distribution of meiofauna in exposed beaches (e.g. McLachlan, 1980b) showed that the highest meiofaunal abundances are usually found in wet sands above the water table level; thus, for quantitative studies, it is necessary to reach that level. Since water table depth increases upwards along the beach, the sampling depth increased from lower to upper beach levels (i.e. from 40 to 110 cm). For each shore level, the six replicated samples were mixed and homogenised before collecting subsamples of 100 and 66 cm^3 with plastic corers for meiofaunal and grain size analyses, respectively.

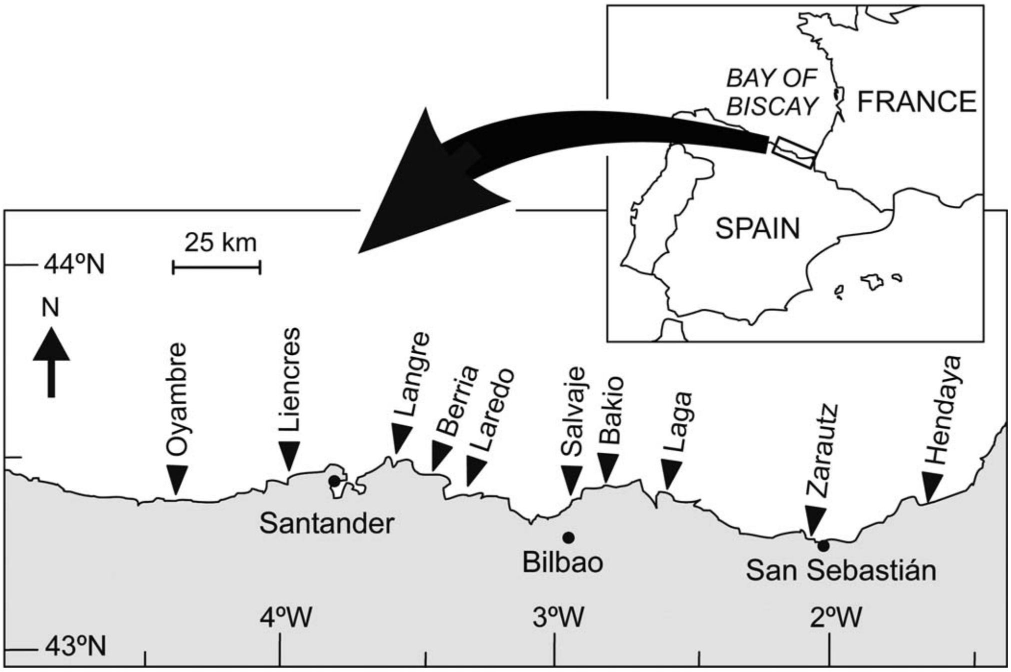

Fig. 1. Location of the sampled beaches at northern Spain.

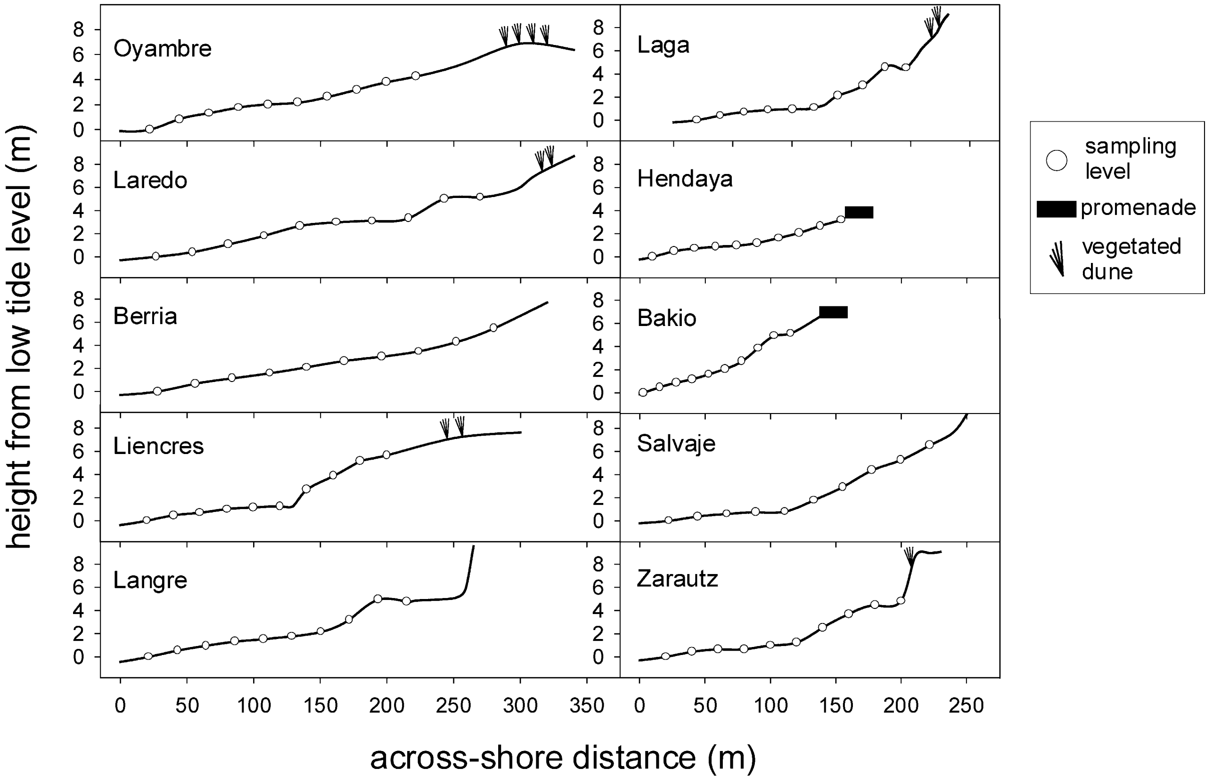

Fig. 2. Beach profiles of the sampled beaches.

2.3. Morphodynamic characteristics and wave exposure rate

Median grain size of 66 cm^3 sediment subsamples (see earlier) was analysed using a Coulter LS 200 laser diffraction particle size analyser, and the coarser fraction (>2 mm) by dry sieving (Folk, 1980). Wave height was estimated by measuring the height of breaking waves with graduated poles against the horizon. The wave period (measured with a stopwatch) was the time interval between breakers. From estimated mean wave height, wave period and sand fall velocity of particles (Gibbs, Matthews, & Link, 1971) from the swash zone, Dean's (Ω) dimensionless parameter was calculated: Ω = wave height (cm)/sand fall velocity (cm s^{-1}) wave period (s) (Short & Wright, 1983). The beach face slope (at the centre of the sampled area) was analysed with Emery's profiling technique (Emery, 1961). The 20-point rating system proposed by McLachlan (1980a) was used to estimate the wave exposure rate. McLachlan's rating system of exposure takes into account observations of wave action, median particle diameter, slope, depth of reduced layers and the presence of macrofaunal stable burrows.

2.4. Meiofaunal analyses

Subsamples for meiofaunal analyses were kept in 250 cm^3 plastic jars with 40 cm^3 of seawater previously filtered through APFF Millipore glass microfibre filters; 40–100 µg of menthol was added to each jar as an anaesthetic. After 24 h, the samples were stored in 4% formaldehyde with Rose Bengal and borax. To extract the meiofauna, water was added to each sample which was stirred and decanted in a plastic graduated cylinder (6.4 cm in diameter, 33 cm length). After decantation (and waiting less than 10 s), the supernatant was filtered through a 42 µm sieve (Pfannkuche & Thiel, 1988). These procedures (i.e. stirring, decanting and filtering) were repeated six times for each sample. Meiofaunal samples retained in the 42 µm sieve were separated through a set of sieves of different mesh sizes: 1000, 500, 200, 100 and 42 µm. The meiofauna was sorted to major taxa using an inverted microscope (100 ×) in a modified Bogorov zooplankton tray. Indirect estimations of biomass (ash free dry weights) were carried out using the individual weights previously measured in meiofaunal taxa by McLachlan (1977), Faubel (1982) and Widbom (1984). Abundance and biomass values per running meter of beach (i.e. estimations of total meiofauna in an intertidal across shore transect of 1 m wide) were obtained by linear interpolation between sampling stations, after obtaining values of biomass and abundances per m^2 at each sampling station.

2.5. Statistical analyses

Regression analyses to test for relationships between meiofaunal and abiotic variables were carried out with

Table 1
Physical characteristics of the studied beaches on the northern coast of Spain

Beach	W[a] (m)	Intertidal slope	Median grain size (µm)[b]	Grain size sorting[b,c]	Waves		Dean's parameter	Exposure rating[d]
					Period[e] (s)	Height of breaking[e] (m)		
Bakio	112	1/22	550 ± 41	1.5 ± 0.1	16.4 ± 4.4	1.4 ± 0.2	1.3	17
Berria	252	1/46	268 ± 22	1.7 ± 0.1	13.7 ± 7.4	1.2 ± 0.3	2.7	14
Hendaya	144	1/45	298 ± 30	1.8 ± 0.1	17.5 ± 6.7	0.4 ± 0.1	0.7	9
Laga	177	1/39	525 ± 52	2.1 ± 0.3	12.1 ± 2.1	0.8 ± 0.2	1.1	17
Langre	191	1/40	386 ± 51	1.6 ± 0.2	12.2 ± 4.8	0.9 ± 0.1	1.4	16
Laredo	243	1/47	247 ± 26	1.8 ± 0.1	15.7 ± 7.6	0.3 ± 0.1	0.6	11
Liencres	180	1/32	509 ± 44	1.7 ± 0.1	15.2 ± 8.5	2.1 ± 0.3	2.6	19
Oyambre	200	1/31	312 ± 51	1.8 ± 0.0	11.8 ± 3.7	1.3 ± 0.1	2.7	14
Salvaje	200	1/31	425 ± 75	1.7 ± 0.3	14.6 ± 4.8	2.8 ± 0.3	3.8	17
Zarautz	180	1/37	468 ± 41	1.6 ± 0.0	13.3 ± 5.1	3.2 ± 0.3	4.4	18

[a] Width of beach; it refers to the maximum distance between the uppermost and lowest sampled level during low tide.
[b] Mean ± SD of the measured values at each sampled level.
[c] Estimated as graphic standard deviation.
[d] Sensu McLachlan's (1980a) rating system.
[e] Mean ± SD of the measured values at low tide time ($n > 30$).

SPSS for Windows. The value of α (0.05) was modified with the progressive Bonferroni correction when the same dependent variable was analysed against various independent variables, according to Legendre and Legendre (1998).

3. Results

3.1. The beaches

Results of substrate analyses and characteristics of the beaches are presented in Table 1 and the beach profiles in Fig. 2. Intertidal slopes varied between 1/22 (Bakio) and 1/47 (Oyambre and Laredo). Median grain size ranged from 247 µm (Laredo) to 550 µm (Bakio). Sediment sorting varied between 1.5φ (Bakio: poorly sorted) and 2.1φ (Laga: very poorly sorted). The measurements of the wave environment indicate that mean wave periods during sampling dates varied between 11.8 s (Oyambre) and 17.5 s (Hendaya), with average wave height ranging from 0.3 m (Laredo) to 3.2 m (Zarautz).

The 20-point rating system proposed by McLachlan (1980a) defined the beach of Hendaya as sheltered (score = 9), the beaches of Laredo (11), Oyambre (13) and Berria (13) as exposed, whereas Langre (16), Salvaje (17), Laga (17), Bakio (17), Zaratutz (18) and Liencres (19) were very exposed.

The values of Dean's parameter, together with median grain sizes and beach profiles, indicated that the beach of Zarautz was dissipative; the beaches of Salvaje, Oyambre, Berria and Liencres were intermediate close to dissipative; whereas the rest of the beaches were intermediate close to reflective (sensu Short, 1999; Short & Wright, 1983).

3.2. The meiofauna

The abundance of meiofauna was primarily due to nematodes (44%) and harpacticoids (29%); crustacean nauplii (9%), foraminiferans (7%), turbellarians (4%) and gastrotrichs (2%) were also present but in lower abundances. Interstitial polychaetes, halacarids, ostracods, tardigrades, oligochaetes, bivalve larvae, insects, gnathostomulids, hydrozoans, mystacocarids, gastropods and cumaceans were also poorly represented.

Number of major taxa, abundances and biomass of meiofauna are shown in Table 2. Number of major taxa ranged between 8 and 14 per beach. Abundances per running meter ranged between 64×10^6 and 296×10^6 ind. m^{-1}, whereas biomass ranged between 30 and 166 g m^{-1}. Density averaged between 3×10^5 and 16×10^5 ind. m^{-2}, with average biomass ranging from 0.12 to 0.89 g m^{-2}.

Table 2
Characteristics of the intertidal meiofauna at the beaches studied in northern Spain

Beach	Number of major taxa	Abundance (10^6 ind. m^{-1})	Density (10^6 ind. m^{-2})[a]	Biomass	
				(g m^{-1})	(g m^{-2})[a]
Bakio	13	64	0.59 ± 0.29	30	0.28 ± 0.12
Berria	8	78	0.30 ± 0.08	31	0.12 ± 0.05
Hendaya	8	101	0.71 ± 0.27	41	0.30 ± 0.19
Laga	13	151	0.82 ± 0.34	72	0.39 ± 0.17
Langre	11	90	0.46 ± 0.12	54	0.27 ± 0.10
Laredo	10	210	0.82 ± 0.35	81	0.31 ± 0.25
Liencres	13	296	1.59 ± 0.74	166	0.89 ± 0.44
Oyambre	9	121	0.61 ± 0.43	41	0.21 ± 0.14
Salvaje	10	84	0.41 ± 0.27	40	0.20 ± 0.15
Zarautz	14	290	1.53 ± 0.95	111	0.59 ± 0.32

[a] Mean ± SD of the values at each sampled level.

3.3. Relationships between meiofauna and beach characteristics

The biplots of abundance, biomass and number of major taxa of the meiofauna vs. Dean's parameter, slope, grain size and exposure rating of the studied beaches are shown in Fig. 3. Abundance (per linear meter) and density (per square meter) of meiofauna were not correlated with any of the studied beach characteristics at $\alpha = 0.05$.

Meiofaunal biomass per square meter was exponentially correlated with the exposure rating (biomass $[\mathrm{g\,m^{-2}}] = 0.22 + 10^{-8}\exp(0.95 \times \text{exposure rate})$; $r^2 = 0.87$, $p < 0.01$, $\text{power}_{\alpha=0.05} = 0.99$). Biomass per linear meter was exponentially correlated with the exposure rating (biomass $[\mathrm{g\,m^{-1}}] = 43.8 + 7.0 \times 10^{-7}\exp(\text{exposure rate})$; $r^2 = 0.79$, $p < 0.01$, $\text{power}_{\alpha=0.05} = 0.96$). Number of major taxa of meiofauna was linearly correlated with average median grain size (number of major taxa $= 3.9 + 0.017 \times \text{grain size}$ [μm]; $r^2 = 0.75$, $p < 0.01$, $\text{power}_{\alpha=0.05} = 0.94$) and exponentially correlated with exposure rating (number of major taxa $= 7.3 + 0.13\exp(0.21 \times \text{exposure rate})$, $r^2 = 0.69$, $p < 0.05$, $\text{power}_{\alpha=0.05} = 0.87$; Fig. 3).

Significant correlation at $\alpha = 0.05$ was not found among studied meiofaunal characteristics with Dean's parameter, intertidal slope or grain size sorting.

4. Discussion

4.1. Meiofaunal characteristics

The densities of meiofauna recorded in the studied beaches (3×10^5–$1.6 \times 10^6\,\mathrm{ind.\,m^{-2}}$) fall within the range elsewhere: 10^3–$10^7\,\mathrm{ind.\,m^{-2}}$ (based on reviews of Coull, 1988; McIntyre, 1969). The biomass values (0.12–0.89 $\mathrm{g\,m^{-2}}$) are in accordance with the values obtained by McLachlan (1983) for South African beaches, i.e. 0.02–4.4 $\mathrm{g\,m^{-2}}$. It was also found that nematodes and harpacticoid copepods were the most abundant taxa, this being common in marine sediments (see reviews by Coull, 1988; Coull & Bell, 1979). Therefore, this study shows that intertidal meiofauna of sandy beaches of northern Spain does not differ from previously studied meiofauna in terms of density, biomass and relative abundance of major taxa.

4.2. Relationships between meiofauna and beach characteristics

The results of this study show two general trends: (1) the meiofaunal biomass increases exponentially with exposure rate from exposed to very exposed beaches; and (2) the number of major taxa increases exponentially with exposure rate and linearly with average grain size. These trends agree with the predictions of McIntyre

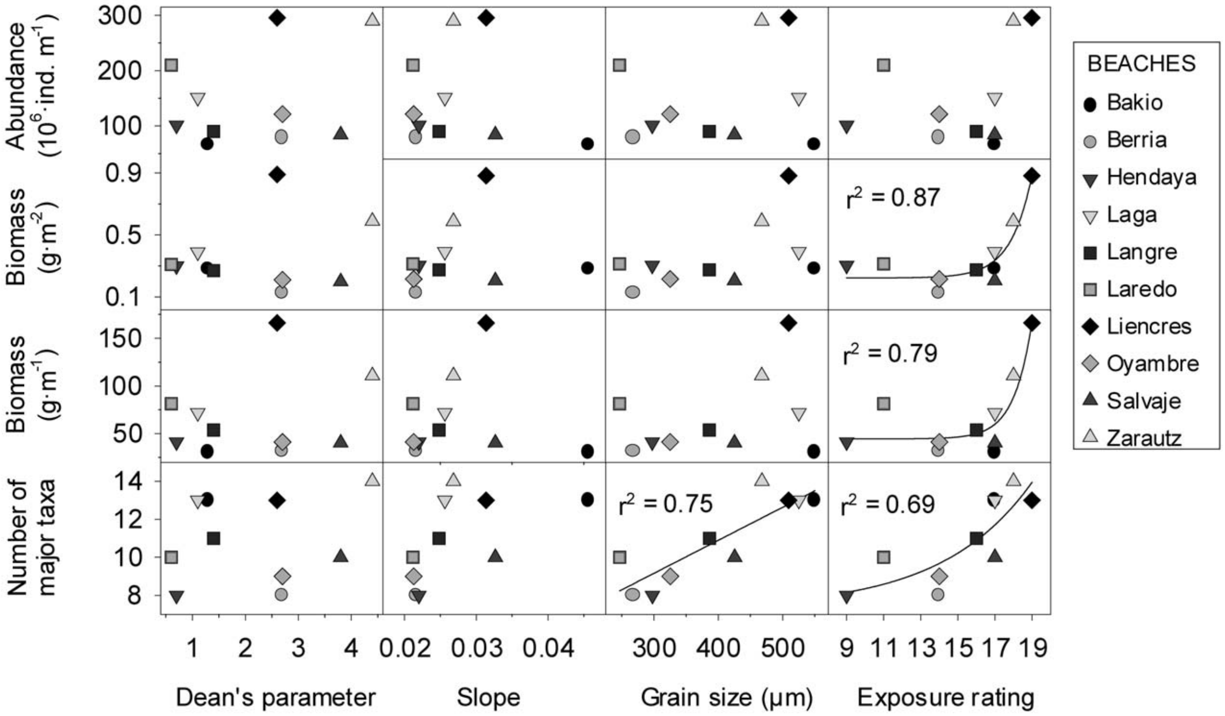

Fig. 3. Biplots of average values of abundance, biomass and number of major taxa vs. Dean's parameter (sensu Short & Wright, 1983), intertidal slope, median grain size and wave exposure rate (sensu McLachlan, 1980a). Lines indicate significant regressions at $\alpha = 0.05$.

(1971) and McLachlan et al. (1981) and are opposite to the general patterns of sandy beach macroinfauna which is negatively affected by increases in exposure and coarser sediments (McLachlan, 1996; McLachlan & Jaramillo, 1995; McLachlan et al., 1996). Nevertheless, these trends that are found should be treated with caution since this study only covered a range of particles up to 550 μm (Table 1) and cannot be extrapolated to coarser sands.

The opposite trends observed for macro and meiofauna might be related to the fact that the greater the grain size and the higher the exposure rate, the higher flushed and oxygenated interstitial space will be (McLachlan, 1989); the concentration of interstitial oxygen is one of the most relevant physical factors affecting the presence of meiofauna (Berninger & Epstein, 1995; Giere, 1993; Moodley, van der Zwaan, Herman, Kempers, & van Breugel, 1997). Therefore, while the meiofauna inhabiting sheltered and/or fine grain size beaches are confined to the oxygenated upper few centimetres, the meiofauna of exposed and/or coarse grain size beaches can reach deep into the sediment (e.g. McLachlan, 1983; Ólafsson, 1991), avoiding the surface effect of currents and wave action. On the contrary, macrofauna is not limited by oxygen concentration due to bioturbation of the sediment and the life habits of the species, mostly occupying the first centimetres or sediment surface. Consequently, macrofauna can be negatively affected by eroding and drifting effects of waves and currents in exposed sandy beaches, while sheltered beaches can be more favourable in that sense (McLachlan & Jaramillo, 1995; McLachlan et al., 1996).

The variability of abundance and density vs. slope or grain size showed a slightly Gaussian response. Thus the biomass and abundance values peaked at the 1/32–1/37 range of slope and at the 468–509 μm range of grain size (Zaratutz and Liencres, Fig. 3). The fact that biomass is better explained by the exposure rating (Fig. 3) than by 'single' variables such as slope or grain size, suggests that the use of 'composite' variables may help to study the ecology of sandy beach meiofauna as has been the case with macroinfauna (e.g. McLachlan et al., 1993, 1996).

On the other hand, no trend was found between the morphodynamic state of the beaches and meiofauna (Fig. 3, Dean's parameter). Nevertheless, it cannot be concluded that morphodynamics does not influence meiofaunal biomass or number of major taxa due to the fact that a whole spectrum of morphodynamic states was not sampled (truly reflective beaches were not studied and only one dissipative beach was sampled). More studies (covering a complete spectrum of morphodynamic states) are needed to check McLachlan and Turner's (1994) prediction in relation to morphodynamics.

In conclusion, this study has shown that the abundance, biomass and richness of intertidal meiofauna inhabiting exposed beaches of the southern Bay of Biscay are related to the average grain size and exposure. Thus, the number of major taxa was positively correlated with grain size and exposure rating, whereas biomass was positively correlated with exposure rating. More similar studies are needed to know if this trend still holds along a complete spectrum of exposure along the exposed coast of northern Spain or elsewhere. In this way, it will be possible to establish general patterns of sandy beach meiofaunal variability such as that have been relatively well identified in macrofaunal communities.

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