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Meiofauna and macrofauna community structure in relation to sediment composition at the Iberian margin compared to the Goban Spur (NE Atlantic)

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Abstract

Meiofauna and macrofauna communities and several sediment characteristics were compared between a slope situated far from the coast (Goban Spur) and two transects across the Iberian Margin with steep slopes and close to the shore. The northern Galician transect (off La Coruña) was situated in an area subjected to wind-induced upwelling events. The western Galician transect was also subjected to upwelling, was additionally influenced by outflows of water rich in organic matter from the Rías Bajas. This transect also included the Galicia Bank. Macrofauna density decreased exponentially from the shelf edge (154 m) to the abyssal plain (4951 m) and different communities occurred on the shelf, the upper- and lower slope and on the abyssal plain. Apart from two extremely low-density stations on the Iberian Margin, there were no significant differences in the meiofauna between the Goban Spur and the Iberian Margin. Along the La Coruña-transect a station where meiofaunal densities were low occurred at a depth of 1522 m, where the sediment was characterised by having a high median-grain size, ripple structures, a low C_{org} and total N content. There were relatively high numbers of macrofaunal filter-feeders but low numbers of crustaceans, indicating a high current velocity regime. On top of the Galicia Bank (~770 m) the sediment consisted mainly of shells of pelagic foraminifers, and had low contents of C_{org} and N. The macrofauna was dominated by filter-feeding and carnivorous taxa. At both these stations meiofauna densities were low. Meiofauna densities and community structure differed between the Goban Spur and the Iberian Margin. Meiofauna densities on the Galician shelf were more than double those on the Goban Spur shelf. The two deep stations on the La Coruña transect and the deepest station on the Galicia Bank transect all contained meiofaunal densities that were higher than found at similar depths off the Goban Spur. The meiofaunal densities were inversely correlated with $\%CaCO_3$ content and, excluding the shelf stations, were positively correlated with both $\%C_{org}$ and total N at the Iberian Margin. Neither upwelling nor the enriched outflows from the rias affected the macrofauna, but meiofaunal densities were greatly enhanced. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Meiofauna; macrofauna; benthic community structure; Iberian margin; sediment characteristics

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Contents

1. Introduction

Coastal seas are an important source of dissolved and particulate matter to the neighbouring open ocean, because of their enhanced productivity and the strong influence of continental inputs. Conversely, cross-slope transfer of nutrient-rich deep oceanic water and local upwelling conditions along the continental margin and at the shelf edge may help to sustain the high productivity of shelf seas (Van Weering, McCave, & Hall, 1998). In the framework of the Ocean Margin EXchange (OMEX I and II) programme of the EU (Van Weering & McCave, 2002), holistic studies were undertaken of the physical, chemical and biological processes at ocean margins — the shelf break and the continental slope — that determine the transport of material from the shelf to the deep sea. The slope is an environment of complex hydrography and topography. Primary production in the surface waters is often higher than further offshore so the sedimentation rates of fresh organic material are high, and are influenced by complex advective and near-bottom transport by along-slope currents and in nepheloid layers (Huthnance, 1995; McCave, 1984). It is therefore difficult to generalise and to evaluate the role of the continental-oceanic interface in the global carbon budget. So the question central to OMEX has been to establish the fate of such exported organic material in relationship to the global carbon cycle.

The biota inhabiting the sediments are completely dependent on the fresh organic matter that reaches the sea-floor, and have to adapt to both the quality and quantity of organic matter reaching the sea floor that varies both spatially along and across the slope, and seasonally. Their adaptations reflect therefore conditions averaged over very different time scales. Studies of the structure of benthic communities present integrated information on the complex patterns of organic matter sedimentation and subsequent transformation in the slope sediments. Activity of benthic organisms may completely change the nature of benthic-pelagic interactions and the geochemistry of the upper sediment layers. Above some critical current velocity, benthic animals provide the main mechanism whereby material from the water column is transferred to the sediment, either directly by their feeding activity or indirectly by their changing bottom topography and near-bed current regimes (Thomsen & Flach, 1997).

In the present study we compare the benthic fauna and the sedimentary environment between two contrasting areas. The slope off the Goban Spur that bounds a broad shelf area and the Porcupine Abyssal

Plain is relatively gentle and is situated well away from the coastal sources of terrestrial inputs. Whereas along the steep Iberian Margin the slope is steep and intersected by a series of canyons, which connect the narrow shelf with the deep environments of the North Atlantic Abyssal Plain. The region is also subject to seasonal coastal upwelling. We have sampled along a single transect at the Goban Spur (Flach & Heip, 1996b) and two transects across the Galician shelf, a northern transect off La Coruña and a western transect from the Galicia Bank perpendicular to the coast. Summertime upwelling occurs more frequently along the northern transect, than along the western transect but the latter transect receives additional organic enrichment via the outflows of enriched water from the Rias Bajas (López-Jamar, Cal, González, Hanson, Rey, Santiago et al., 1992; Tenore, Alonso-Noval, Alvarez-Ossorio, Atkinson, Cabanas, Cal et al., 1995).

2. Material and methods

Samples for meiofauna, macrofauna and sediment analyses were taken along two transects along the Iberian Margin in June/July 1997 by RV *Pelagia* (Lavaleye, Duineveld, Berghuis, Kok, & Witbaard, 2002). The first transect extended offshore from the coast off La Coruña out over the abyssal plain, covering water depths ranging from 175 to 4909 m (stations C0 to C59). The second transect extended from the Galicia Bank perpendicular to the coast along 42°40′N (stations G100 to G0). In June 1998 five stations were sampled at depths ranging from 770 to 4950 m of which two (G100 at ~770 m and C59 at ~4910 m) were at positions close to those previously sampled in 1997 (Fig. 1). Station C125 proved to be very difficult to sample with the box corer, so we lack good macrofaunal samples from this station. So although we present data from this station it is less reliable than from the other stations. Fig. 2 shows the depth profiles along the two transects and the position of the sampling points. Detailed information on the Goban Spur transect (stations A to E) are given in Flach & Heip, 1996b). Exact sampling dates, positions, water depths and number and size of box core-samples from all three transects are listed in Table 1. Besides the stations mentioned for macrofauna, multicorer samples (meiofauna and sediment composition) were also available for station C14 (43°46.8′N, 8°54.0′W) on the La Coruña transect at a water depth of 734 m.

At these stations macrofaunal samples were collected using the cylindrical box-corer of the Netherlands Institute of Sea Research (NIOZ). Logistical restraints resulted in different numbers of boxes of different sizes being collected at different stations. Box-cores with diameters of 30 cm (mainly at the shallow stations) and 50 cm were used (Table 1). So the data are presented as mean densities and biomass per m^2. The box-core-samples were sliced in sediment layers of 0–1, 1–3, 3–5, 5–10 and 10–15 cm before they were sieved through a 0.5 mm-sieve. The sieved samples were then stored in 4% seawater formaldehyde, stained and sorted under a stereomicroscope. Macrofauna were sorted to major taxonomic groups (phyla, order, class), polychaetes of all transects were sorted to family-level and all taxa of the Goban Spur samples to species-level. Details of the taxonomical analysis of the macrofauna are given in Flach and De Bruin (1999). Meiofaunal taxa (Nematoda, Harpacticoida etc.) have been excluded from total macrofauna data. Biomass was estimated by wet weight after the animals of each major taxon (e.g. Isopoda and Amphipoda) were dried for a few seconds on absorbent paper. Large specimens were treated individually. Because of the small size of most bivalve individuals, no attempt was made to puncture their shells and drain them of water. Weighing was done to 0.1 mg accuracy. Biomass values were then converted into organic carbon (C_{org}) per major taxon using the conversion factors given by Rowe (1983). For the final analysis of biomass large individuals, i.e. those weighing >1 mg wet weight, were eliminated from the comparisons. A list of those species is given in the section on results.

Meiofauna were sampled either using a multicorer or by taking subsamples from a box-core sample. Meiofauna was analysed to genus level (nematodes) and higher taxonomic level (other meiofauna groups) by Vanaverbeke (Goban Spur) and Muthumbi (Galician Margin). Two small cores of 10 cm^2 per station were sliced into layers of 0–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50 and 50–100 mm and again stored

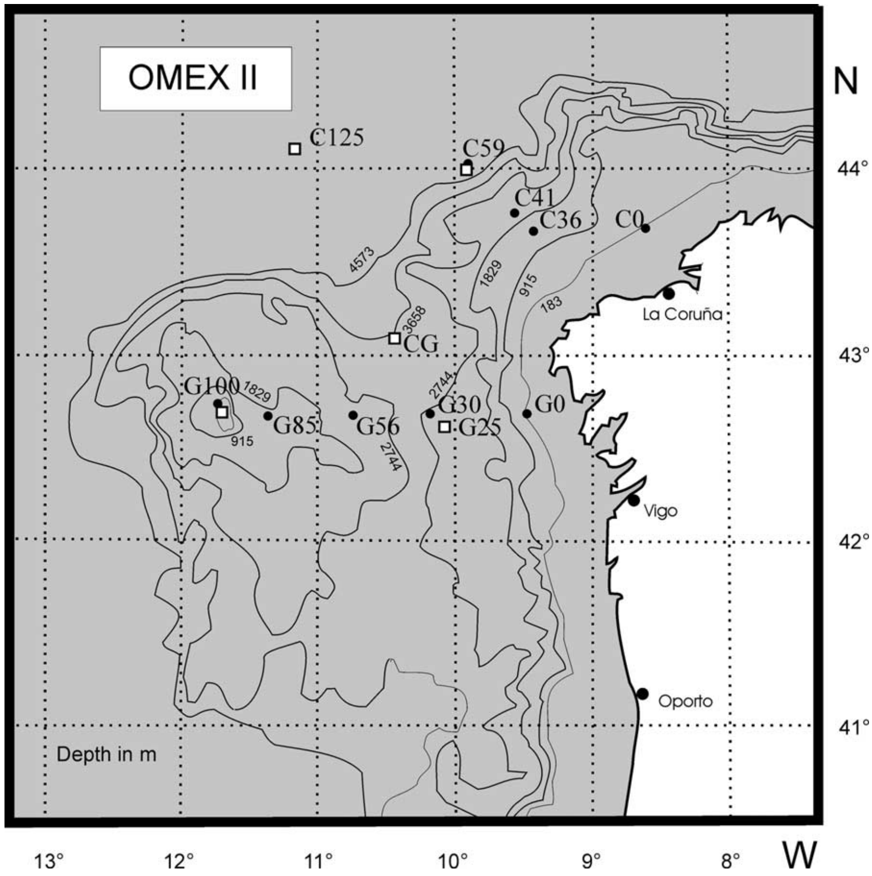


Fig. 1. Position of the stations sampled at the Iberian Margin off NW Spain. Solid circles stations sampled in June/July 1997, open squares stations sampled in May/June 1998.

in 4% formaldehyde. The meiofaunal organisms were extracted from the sediment by centrifugation with Ludox (Heip, Vincx, & Vranken, 1985). Foraminifera were excluded and macrofauna was excluded by means of a 1-mm sieve. All animals retained on a 32 μm sieve were counted, and a subsample of nematodes were picked out at random from each site and mounted in glycerine slides. Nematode length (excluding filiform tails, if present) and maximal width were measured using a Quantimet 500+ image analyser. Nematode wet weight biomass was calculated from volume calculated with Andrassy's formula (Andrassy, 1956) assuming a density of 1.13. Nematode wet weight was converted to organic carbon using the conversion factor (12.4%) given by Jensen (1984). Meiofauna biomass is thus restricted to nematode biomass, but since nematodes were the most abundant meiofaunal taxon (~90%, Vanaverbeke, Soetaert, Heip, & Vanreusel, 1997) they give a good estimate of meiofaunal biomass.

Multicorer samples were taken for sediment analysis. The upper 20 mm of these samples were sliced into 5 mm layers and from 20–150 mm in 10 mm layers for sediment analysis. Particle sizes of the sediments were estimated using a Malvern laser particle sizer 3600 EC. $CaCO_3$ was determined by gas volumetry (Scheibler method). Porosity was calculated from the percentage of moisture in the sediment. For C/N analysis samples were immediately frozen at -25°C on board. The total nitrogen and the organic carbon content of the sediments were analysed with a Carlo Erba type NA-1500 elemental analyser accord-

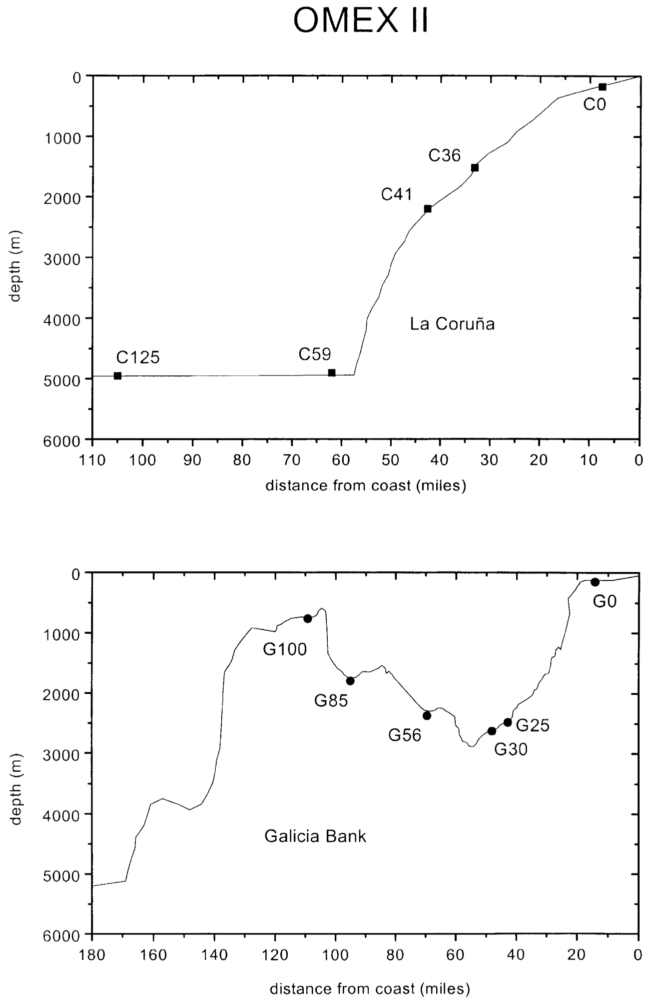


Fig. 2. Depth profile of the two transects sampled and the position of the sampled stations for the La Coruña-transect (upper) and Galicia Bank-transect (lower).

ing to the protocols of Nieuwenhuize, Maas and Middelburg (1994). Carbon was partitioned into its inorganic and organic fractions by acidification with 25% HCl in situ within silver sample cups.

All data on macrofauna and meiofauna taxonomic composition, density and biomass as well as all sediment analyses are available upon request from the authors and at the British Oceanographic Data Centre BODC within the OMEX Data Base.

The Bray-Curtis Cluster Analysis (single link) of the © BioDiversity Program of the Scottish Association for Marine Science (SAMS) and the Natural History Museum of London was used to estimate similarities in community structure between the stations for meiofauna and macrofauna separately. Differences between meiofauna and macrofauna densities and biomass between the stations were tested with a *t*-test (Statistica Program). Correlations between meiofauna and macrofauna densities, biomass and mean individual weight and various physical factors were tested using Pearson Product-Moment Correlation (Statistica Program).

Table 1
Station listing for macrofaunal samples along the Goban Spur and the Iberian Margin transects

Station	Sampling date	Depth (m)	Latitude °N	Longitude °W	Numbers of cores	Size of boxcore
A	23/05/94	208	49° 29.0’	11° 08.4’	3	30cm
	18/08/95	231	49° 28.5’	11° 12.4’	3	30cm
I	19/10/93	670	49° 24.7’	11° 31.9’	1	50cm
	23/05/94	670	49° 24.9’	11° 31.4’	2	30cm
	19/08/95	693	49° 24.7’	11° 31.9’	2	50cm
B	20/10/93	1034	49° 22.0’	11° 48.1’	1	50cm
	24/05/94	1034	49° 22.4’	11° 45.1’	2	50cm
	20/08/95	1021	49° 22.0’	11° 48.0’	3	50cm
II	23/10/93	1425	49° 11.2’	12° 49.2’	1	50cm
	26/05/94	1425	49° 11.3’	12° 49.7’	2	50cm
	21/08/95	1457	49° 11.2’	12° 49.2	3	50cm
F	25/10/93	2182	49° 09.1’	13° 05.4’	2	50cm
	28/05/94	2254	49° 09.5’	13° 05.3’	2	50cm
	22/08/95	2256	49° 09.1’	13° 05.4’	3	50cm
III	30/05/94	3673	49° 05.2’	13° 25.9’	2+1	50+30cm
	23/08/95	3648	49° 04.0’	13° 25.8’	3	50cm
E	01/06/94	4460	49° 02.3’	13° 42.2’	2+1	50+30cm
	24/08/95	4470	49° 02.3’	13° 42.2’	3	50cm
C0	28/06/97	175	43° 40.9’	08° 37.2’	4	30cm
C36	01/07/97	1522	43° 40.9’	09° 26.8’	2	50cm
C41	02/07/97	2200	43° 45.4’	09° 32.8’	2	50cm
C59	04/07/97	4909	44° 00.6’	09° 54.1’	2	50cm
G0	12/07/97	153	42° 39.8’	09° 28.2’	4	30cm
G30	11/07/97	2625	42° 40.0’	10° 10.0’	3	30cm
G56	09/07/97	2373	42° 39.9’	10° 44.0’	2	50cm
G85	08/07/97	1794	42° 40.1’	11° 22.1’	1	50cm
G100	07/07/97	764	42° 44.9’	11° 44.2’	4	30cm
C125	30/05/98	4951	44° 10.0’	11° 09.9’	1	50cm
C59	01/06/98	4915	44° 00.0’	09° 54.0’	2	50cm
CG	04/06/98	3800	43° 11.5’	10° 37.0’	2	50cm
G100	06/06/98	772	42° 44.8’	11° 44.7’	2	50cm
G25	07/06/98	2270	42° 38.2’	10° 02.5’	2	50cm

3. Results

3.1. Density and biomass

Meiofauna densities (Fig. 3a) decreased slightly with depth across the Goban Spur from 696 ± 339 (n.10 cm^{-2} ± SE) at the shelf station A to 528 ± 98 at the abyssal station E, but no significant correlation was found between density and depth (Table 2a, p = 0.089). Also along the Iberian Margin transect no correlation with depth was found, whereas along the Galicia Bank-transect there was a significant negative correlation (Table 2c, p = 0.017) with increasing distance from the shore. Meiofauna density was significantly ($p < 0.05$) higher at both the Iberian Margin shelf stations (C0 1802 ± 202: G0 1707 ± 5 per 10 cm^2) than at the shelf station at the Goban Spur. With the exception of station C36 (1522 m) all the La

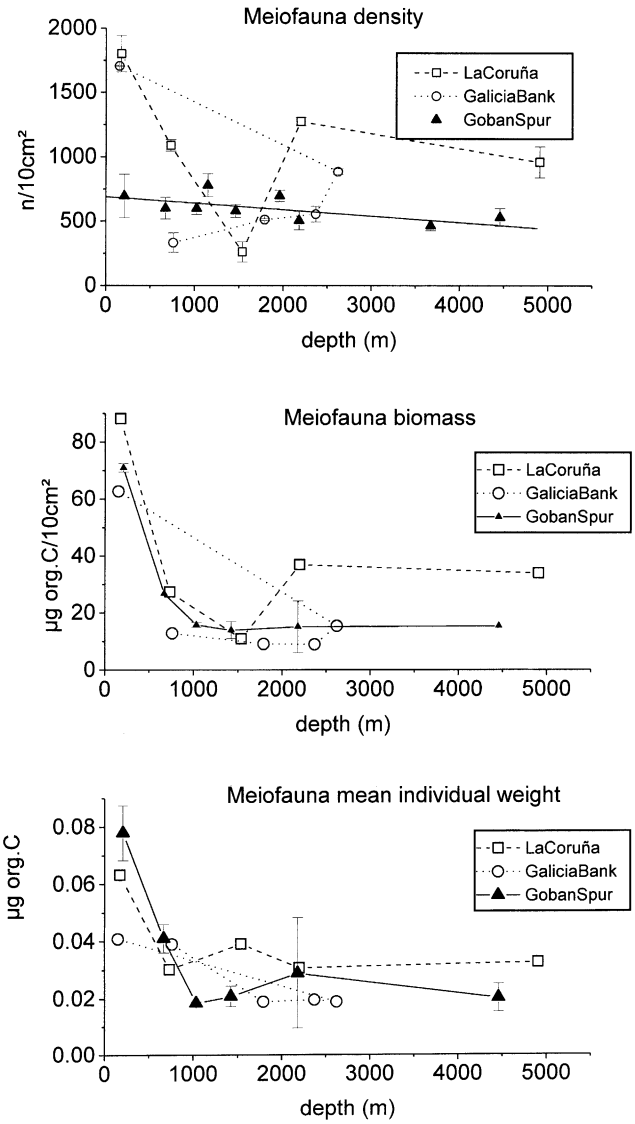


Fig. 3. Mean meiofauna density (n 10 cm^{-2}), biomass (μg C_{org} 10 cm^{-2}) and individual weight (μg C_{org}) ± SE at the two Iberian Margin transects, La Coruña and Galicia Bank, sampled in 1997 compared to the Goban Spur-transect (mean of 2 years). Goban Spur data provided by RU Gent.

Coruña transect stations had significantly ($p < 0.05$) higher meiofauna densities than were found along the Goban Spur transect at similar depths. But at station C36, meiofauna density was significantly ($p < 0.05$) lower than at all Goban Spur stations. On the Galicia Bank (G100, 764 m) meiofauna density was also relatively low considering its shallow depth, and significantly ($p = 0.036$) lower than at the Goban Spur station B (1034 m).

Meiofauna biomass (Fig. 3b) was high on the shelf at all three transects and decreased strongly with increasing water depth. This trend in meiofaunal biomass was mainly the result of a reduction in the mean size of the nematodes (Fig. 3c), which was large on the shelf at the Goban Spur and near La Coruña, but

Table 2
Pearson Product-Moment Correlation between meiofauna abundance (MeioN), biomass (MeioB), and mean individual weight (MeioW), macrofauna abundance (MacroN), biomass (MacroB) and mean individual weight (MacroW) and the abiotic factors water depth (m), distance from shore (km) (La Coruña transect only), median grain-size (grain), porosity (Por), %$CaCO_3$ (Carb), %orgC and %total N in the upper 1 cm of the sediment. Analyses have been done for the different transects separately, all Iberian Margin stations together and all stations together.

Variables	km	OrgC	%N	grain	Carb	Por	MacroN	MacroB	MacroW	MeioN	MeioB	MeioW
a. Goban Spur, *n* = 6												
Depth		−0.46	−0.48	−0.65	0.79	0.86*	−0.88*	−0.66	0.64	−0.74	−0.54	−0.57
orgC			0.94**	−0.33	0.05	−0.27	0.05	0.14	−0.31	−0.01	−0.40	−0.43
%N				−0.33	0.11	−0.15	0.04	−0.02	−0.56	−0.65	−0.37	−0.36
grain					−0.95**	−0.78	0.92**	0.75	−0.20	0.90*	0.97**	0.97**
Carb						0.93**	−0.98**	−0.87*	0.21	−0.97**	−0.88*	−0.86*
Por							−0.92**	−0.94**	0.17	−0.90*	−0.70	−0.66
MacroN								0.80	−0.39	0.95**	0.84*	0.84*
MacroB									0.12	0.86*	0.73	0.65
MacroW										−0.16	−0.13	−0.26
MeioN											0.88*	0.81*
MeioB												0.98**
b. La Coruña, *n* = 4												
Depth	0.96*	0.38	0.50	−0.58	0.42	0.77	−0.70	−0.73	0.27	−0.33	−0.49	−0.74
km		0.44	0.61	−0.53	0.54	0.91	−0.84	−0.85	0.48	−0.45	−0.66	−0.90
orgC			0.96*	−0.91	−0.38	0.61	−0.14	−0.06	−0.13	0.44	0.09	−0.47
%N				−0.83	−0.10	0.80	−0.42	−0.33	0.15	0.17	−0.19	−0.70
grain					0.42	−0.53	0.07	0.04	0.34	−0.51	−0.22	0.37
Carb						0.49	−0.86	−0.89	0.91	−0.99**	−0.95*	−0.64
Por							−0.87	−0.83	0.62	−0.42	−0.71	−0.98*
MacroN								0.99**	−0.88	0.81	0.96*	0.94
MacroB									−0.85	0.84	0.95*	0.90
MacroW										−0.91	−0.97*	−0.74
MeioN											0.93	0.57
MeioB												0.82
c. Galicia Bank, *n* = 5												
Depth	0.19	0.56	0.91*	−0.85	0.42	0.92*	−0.82	−0.80	0.07	−0.47	−0.73	−0.96*
km		−0.59	−0.16	0.10	0.96**	0.44	−0.71	−0.66	0.07	−0.94*	−0.81	−0.29
orgC			0.83	−0.64	−0.44	0.39	−0.07	−0.05	0.43	0.39	0.09	−0.46
%N				−0.91*	0.05	0.75	−0.54	−0.48	0.25	−0.10	−0.42	−0.87
grain					−0.08	−0.60	0.49	0.49	−0.02	0.11	0.40	0.90*
Carb						0.64	−0.86	−0.84	−0.031	−0.99**	−0.93*	−0.47
Por							−0.87	−0.83	0.62	−0.42	−0.71	−0.98*
MacroN								0.95*	−0.10	0.89*	0.99**	0.82
MacroB									0.21	0.87	0.95*	0.78
MacroW										0.01	−0.06	−0.09
MeioN											0.95*	0.51
MeioB												0.75

(*continued on next page*)

smaller on the shelf near Vigo and at all the deeper stations. A significant (Table 2c, $p = 0.011$) negative correlation between nematode mean individual weight and depth was found along the Galicia Bank-transect and all stations taken together (Table 2e, $p = 0.039$). Unfortunately only one replicate was available for the Iberian Margin stations.

In a sieve-experiment using 1.0-, 0.5- and 0.3-mm sieves for fractionating the samples from the Iberian Margin 1997, resulted in only a very small fraction (<0.01% = 100 n/m^2) of meiofauna (Nematoda) being

Table 2 (*continued*)

Variables	km	OrgC	%N	grain	Carb	Por	MacroN	MacroB	MacroW	MeioN	MeioB	MeioW
d. Iberian Margin, n = 9												
Depth	0.28	0.48	0.65	−0.64	0.27	0.81*	−0.71*	−0.68*	−0.03	−0.29	−0.41	−0.53
km		−0.33	−0.01	−0.05	0.86*	0.36	−0.59	−0.35	0.37	−0.74*	−0.74*	−0.62
orgC			0.90*	−0.69*	−0.45	0.55	−0.11	−0.18	−0.08	0.48	0.24	−0.13
%N				−0.83*	−0.08	0.79*	−0.45	−0.44	0.02	0.11	−0.16	−0.49
grain					0.07	−0.56	0.26	0.34	0.07	−0.16	0.08	0.51
Carb						0.46	−0.73*	−0.62	0.27	−0.95**	−0.87**	−0.55
Por							−0.85**	−0.83**	0.12	−0.46	−0.59	−0.60
MacroN								0.78*	−0.28	0.80**	0.89**	0.75*
MacroB									0.24	0.60	0.56	0.35
MacroW										−0.35	−0.47	−0.50
MeioN											0.93**	0.57
MeioB												0.82**
e. All stations, n = 15												
Depth		0.27	0.38	−0.57*	0.42	0.82**	−0.77**	−0.65**	0.31	−0.23	−0.44	−0.54*
orgC			0.88**	−0.57*	−0.37	0.27	−0.10	−0.12	−0.11	0.47	0.14	−0.17
%N				−0.56*	−0.05	0.42	−0.39	−0.36	−0.10	0.23	−0.13	−0.36
grain					−0.10	−0.49	0.29	0.33	−0.01	0.00	0.27	0.54*
Carb						0.59*	−0.76**	−0.66**	0.22	−0.83**	−0.87**	−0.62*
Por							−0.85**	−0.88**	0.15	−0.28	−0.59*	−0.64*
MacroN								0.80**	−0.33	0.51	0.81**	0.76**
MacroB									0.16	0.37	0.58*	0.51
MacroW										−0.20	−0.30	−0.35
MeioN											0.80**	0.38
MeioB												0.83**

* significant $p < 0.05$, ** significant $p < 0.01$.

found in the 1-mm sieve subsample in three of the nine stations (C59, G0, G56), and none at the other six stations. So the upper size limit of 1 mm for meiofauna is realistic. In the 0.5 mm sieve subsamples, the densities of nematodes ranged from 1684 n/m^2 (G0) to 105 n/m^2 (C41) corresponding to 0.1 to 0.007% of total meiofauna densities. In the 0.3-mm sieve subsamples, densities ranged between 4052 and 737 n/m^2 with relative densities of 0.7 to 0.12%. No clear pattern for large meiofauna could be observed. Along the Goban Spur transect densities of large nematodes in the macrofaunal samples (0.5-mm sieve) ranged from 70 (at station E) to 488 n/m^2 (at station B), corresponding to 0.08 to 0.014% of total meiofauna densities respectively, but again no consistent trend was found (Flach & Heip, 1996b).

Macrofaunal (sensu stricto) density (Fig. 4a) decreased with increasing water depth. Significant negative correlations with depth were found along the Goban Spur transect (Table 2a, p = 0.021) and both the Iberian Margin transects (Table 2d, p = 0.031) as well as all stations taken together (Table 2e, p = 0.001). However, when the data for the La Coruña and Galicia Bank-transects were analysed separately the correlations ceased being significant. As for meiofauna, the macrofaunal density at the mid-slope station C36 of the La Coruña-transect was very low (407 ± 69 n/m^2) and significantly (p = 0.001) lower than at the Goban Spur station II at about the same depth. It was also significantly lower (p = 0.005) than the density at the nearby but deeper station C41 (2200 m). On the Galicia Bank macrofaunal densities were also relatively low; the density at station G100 was significantly (p = 0.0008) lower than at the Goban Spur station I at about the same depth.

However, if the few extremely large macrofaunal individuals were omitted from the analyses (Fig. 4b) marofaunal densities were no longer significantly correlated with depth along any of the three transects,

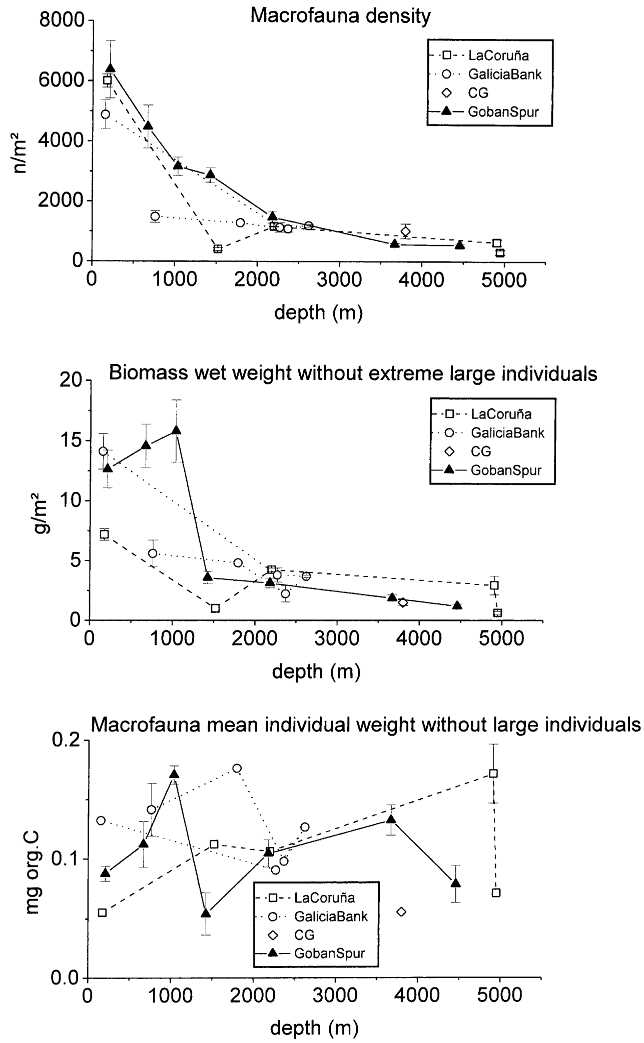


Fig. 4. Mean macrofauna density (n m^{-2}), biomass (g wet weight m^{-2}) and individual weight (mg C_{org}) ± SE at the two Iberian Margin transects, La Coruña and Galicia Bank and the station CG situated in between the two transects compared to the Goban Spur-transect (mean of 2 or 3 years, see Table 1).

although negative correlations re-emerged when the data for the two Iberian Margin transects were pooled (Table 2d, $p = 0.042$) and when all station data (Table 2e, $p = 0.007$) were pooled. Along the Goban Spur transect high biomass values were found on the upper slope, especially at ~1000 m as a result of the mean individual weight of the macrofauna being high (Fig. 4c). Along the La Coruña-transect biomass decreased only slightly with depth because there was an increase in mean individual weight (note: results of the deepest station C125 were unreliable). Biomass was significantly ($p < 0.05$) lower on the shelf near La Coruña than at the other two shelf stations because of the small mean size of the macrofauna, whereas it was large near Vigo. Biomass was significantly ($p < 0.05$) lower at station C36 than at the Goban Spur station II, the Galicia Bank station G56 and the deeper La Coruña transect station C41 simply because of the low density; the mean weight of the macrofauna at this station was slightly higher rather than lower. No correlation at all was found between the mean individual weight of the macrofauna and water depth.

At all ~2200 m stations macrofaunal densities, biomasses and mean individual weights were all very similar. Similarly at the deep (>3500 m) stations densities were similar but sizes differed, especially the large size of the macrofauna at station C59, just below the steep slope was notable. The largest differences were found between the shallow (<2000 m) stations.

3.2. Community structure

The Bray-Curtis cluster analysis of the major meiofauna taxa produced two major clusters, a Goban Spur cluster that included two of the deep Galicia Bank stations (G56 2373 m and G85 1794 m) and an Iberian Margin cluster (Fig. 5a). The meiofaunal composition at all Goban Spur stations was highly similar, except shelf station A, which was placed separately. The two Iberian shelf stations also formed a separate cluster, as did the Galicia Bank station G100 and the low density La Coruña transect station C36. This pattern was mainly the result of the nematodes, which largely dominated the meiofaunal communities (Fig. 6a). At the Goban Spur the nematodes provided 93 to 97% of meiofauna communities. Whereas at the Iberian Margin the average relative abundance of nematodes was lower, varying between 81 to 94%. The

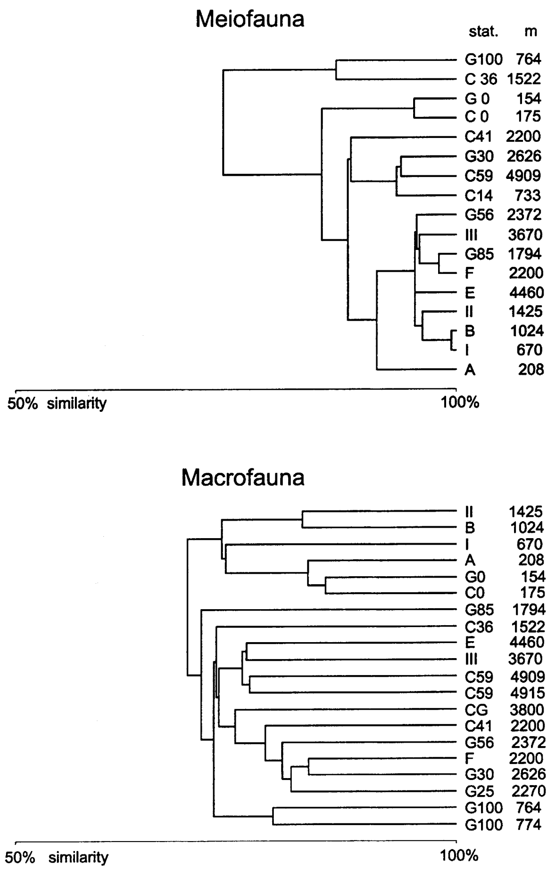


Fig. 5. Bray-Curtis Cluster Analysis (single link) of the meiofauna (upper graph) and macrofauna (lower graph) community structure of the major taxa (phyla, order, class) at the two Iberian Margin transects, La Coruña (C0-C59) and Galicia Bank (G0-G100) and the station CG situated in between the two transects compared to the Goban Spur-transect (A-E, mean of 2 or 3 years, see Table 1). Water depths (m) given in the last column.

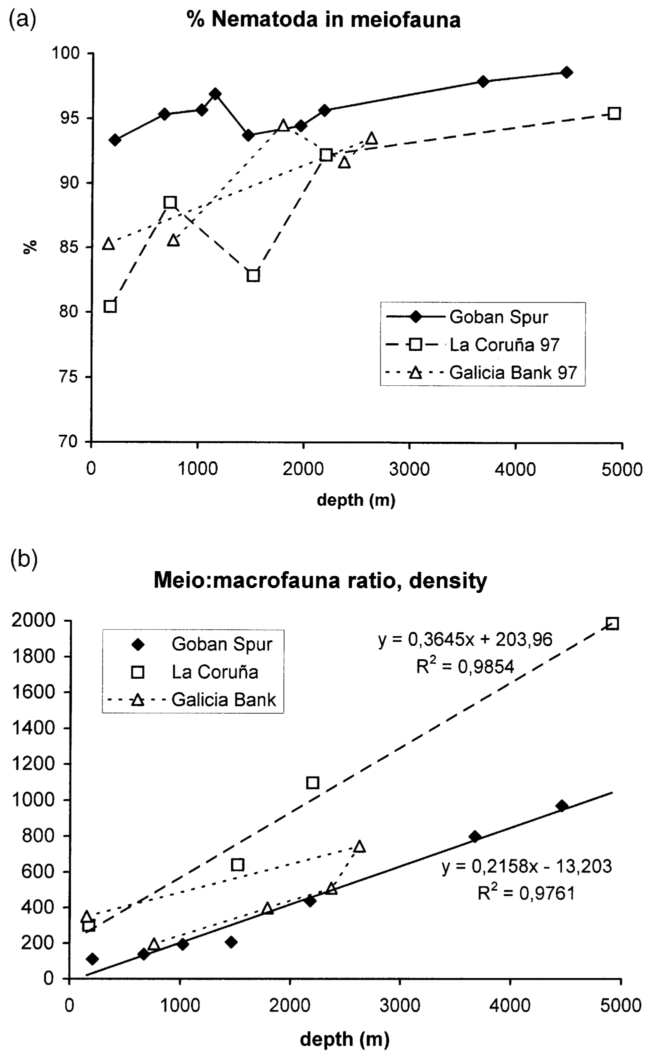


Fig. 6. The relative abundance (%) of the Nematoda within the meiofauna (a) and the meio:macrofauna ratio (density n m^{-2}) (b), at the two Iberian Margin transects, La Coruña and Galicia Bank, sampled in 1997 compared to the Goban Spur-transect (mean of 2 years). Meiofauna data of the Goban Spur provided by RU Gent.

lowest percentages of nematodes were on the shelf, on the Galicia Bank and at C36. On the shelf relative abundances of Turbellaria were high (C0 14%, G0 7.5%), and Copepoda were relatively abundant on the Galicia Bank (7%) and at C36 (9%). The overall pattern was for the percentage of nematodes to increase with increasing water depth. At the same time the ratio between the biomasses of meiofauna and macrofauna also increased with depth (Fig. 6b), so the benthic communities become progressive more dominated by nematodes with increasing water depth. The meio:macrofauna ratio was much higher along the La Coruña-transect than along the Goban Spur-transect. The shelf station of the Galicia Bank-transect was similar to that of the La Coruña shelf station, whereas the stations further offshore showed high similarity with the Goban Spur-transect.

The Bray-Curtis Cluster Analysis of the major macrofauna taxa revealed a depth related zonation (Fig.

5b). The three shelf stations were clustered together, although the two Iberian Margin stations were more similar than they were with the Goban Spur station. All ~ 2000 m stations clustered together indicating the existence of a characteristic lower slope community. The four deep stations formed another cluster, indicating the existence of an abyssal community. The saddle station CG (3800 m) was intermediate between the lower slope and abyssal clusters, although showing somewhat more similarity to the lower slope communities. The upper slope stations did not cluster together, but showed evidence of geographical separation. The Goban Spur stations formed a cluster that was more closely related to the shelf stations, whereas the Galicia Bank stations (G100, G85) and the La Coruña transect station C36 were placed apart but had higher similarity to the deeper stations. The three shelf stations were dominated by polychaetes (73–79%), whereas polychaetes were of minor importance at both the Galicia Bank station G85 (37%) and the deep Goban Spur station III (41%). There was an overall trend for the relative importance of the polychaetes to decrease and of the crustaceans to increase with depth (Fig. 7b), although densities could fluctuate greatly between the stations (Fig. 7a). At the low-density station C36 and on the relatively low-density station G100 the percentages of crustaceans were very low (Fig. 7a.b), 3.7 and 3.2% respectively. The few crustaceans that were found here were mainly tanaids and amphipods (Fig. 8a). The numbers of amphipods on average decreased with increasing water depth, whereas the numbers of tanaids were high at all shallow and the deep Iberian Margin stations. Very few isopods were at the shallow stations, but they became abundant at nearly all stations >1000 m, except at station G56 where high numbers of ostracods were found. Cumaceans were more abundant at the shallower stations, except at Goban Spur station A. At this shelf station crustacean densities were much lower than on the Iberian shelf, except for the number of decapods, which were generally only found at the shelf stations (Fig. 8a). Echinoderms, on the other hand, were much more abundant on the Goban Spur shelf than on the Iberian shelf (Fig. 8b). At all shallow (<1500 m) stations much higher numbers of ophiuroids were found on the Goban Spur. Only on top of the Galicia Bank (G100) were there relatively high numbers of ophiuroids along the Iberian Margin transects. At all deep (>1500 m) stations numbers of echinoderms, mainly holothurians and ophiuroids, were low, except at station G85 where remarkably high numbers of asteroids were found (Fig. 8b). Molluscs were abundant on the shelf near La Coruña and were also relatively abundant at the deep La Coruña transect station C59 (Fig. 8c). Considering molluscs, bivalves were the most abundant at nearly all stations. Gastropods were relatively abundant at the upper slope stations (B, II and C36 – 36, 57 and 23%, respectively). Scaphopods were relatively abundant at the deep (~3000m) stations (G30, II and CG – 22, 35 and 38% respectively), and aplacophorans were relatively abundant on the Galicia Bank (G100 ~20%). The miscellaneous group of small taxa showed a variable pattern (Fig. 8d). High numbers of nemertines were found at all three shelf stations and the high numbers of sipunculids at most of the deep stations and at the upper slope station I on the Goban Spur. High numbers of filter-feeding taxa were found on the summit of Galicia Bank (G100, ~80%), consisting mainly of sponges (Porifera). High numbers of filter feeders (mostly tunicates) were also found at the Goban Spur station II, and also at the other ~1500 m station C36 (mostly sponges and Bryozoa/Ectoprocta). Sponges and Bryozoa were also abundant at station G30, whereas Bryozoa were very abundant at the saddle station CG and relatively abundant at the deep La Coruña stations C59 and C125.

Overall the distribution pattern of the macrofaunal biomass distribution tended to be dominated by a few extremely large individuals that occurred at some of the stations (Fig. 7c), for example, on the Goban Spur two large echinoids were found at the station A, a single large sipunculid at station B and a large holothurian at station E. Along the Iberian Margin only one such extremely large individual was collected, a sipunculid at station G85. However, at the shelf station off Vigo some relatively large polychaetes (3 *Nephthys*, 1 *Magelone*, 1 *Onuphis*, 1 *Glycera*, 1 *Harmothoë*) were collected, and at the deep La Coruña station C59 a large bivalve (*Cuspidaria*) in 1998 and a large bivalve (*Pectinaria*) and echinoid (*Pourtalesia*) at station G30. If these large individuals were discounted, the biomass community structure was not so much dominated by polychaetes as by density (Fig. 7d), especially off the shelf. On the shelf crustaceans

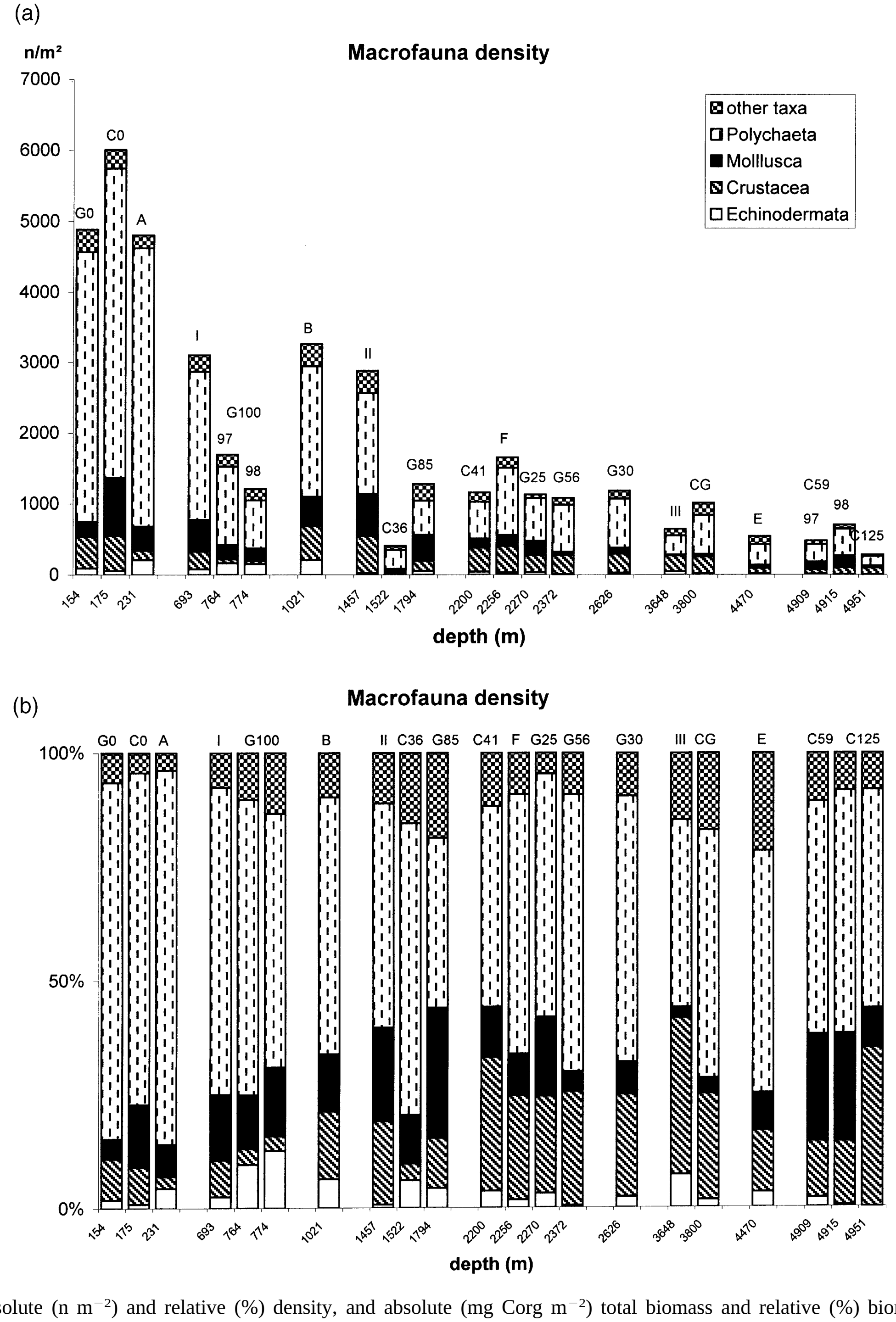
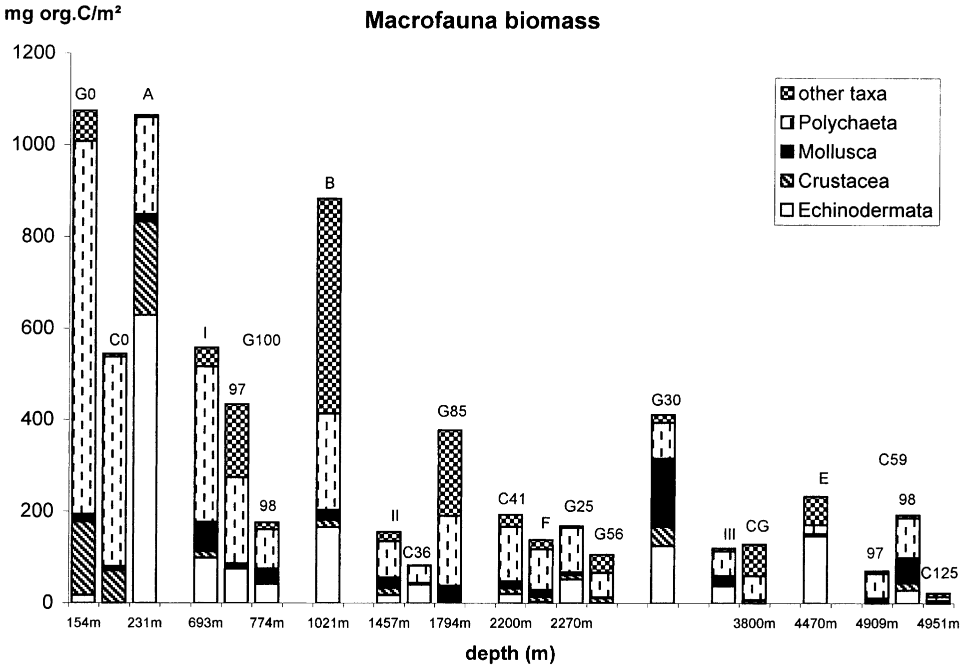


Fig. 7. Absolute (n m^{-2}) and relative (%) density, and absolute (mg Corg m^{-2}) total biomass and relative (%) biomass without large individuals of the major macrofauna taxa at the two Iberian Margin transects, La Coruña and Galicia Bank and the station CG situated in between the two transects compared to the Goban Spur-transect (mean of 2 or 3 years, see Table 1).

(c)



(d)

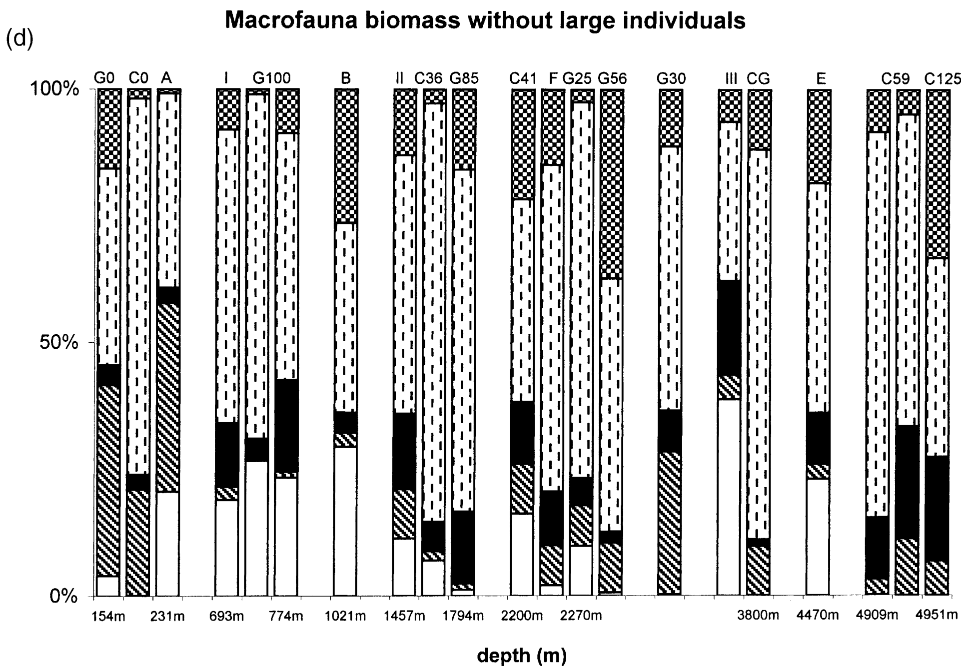


Fig. 7. *Continued*

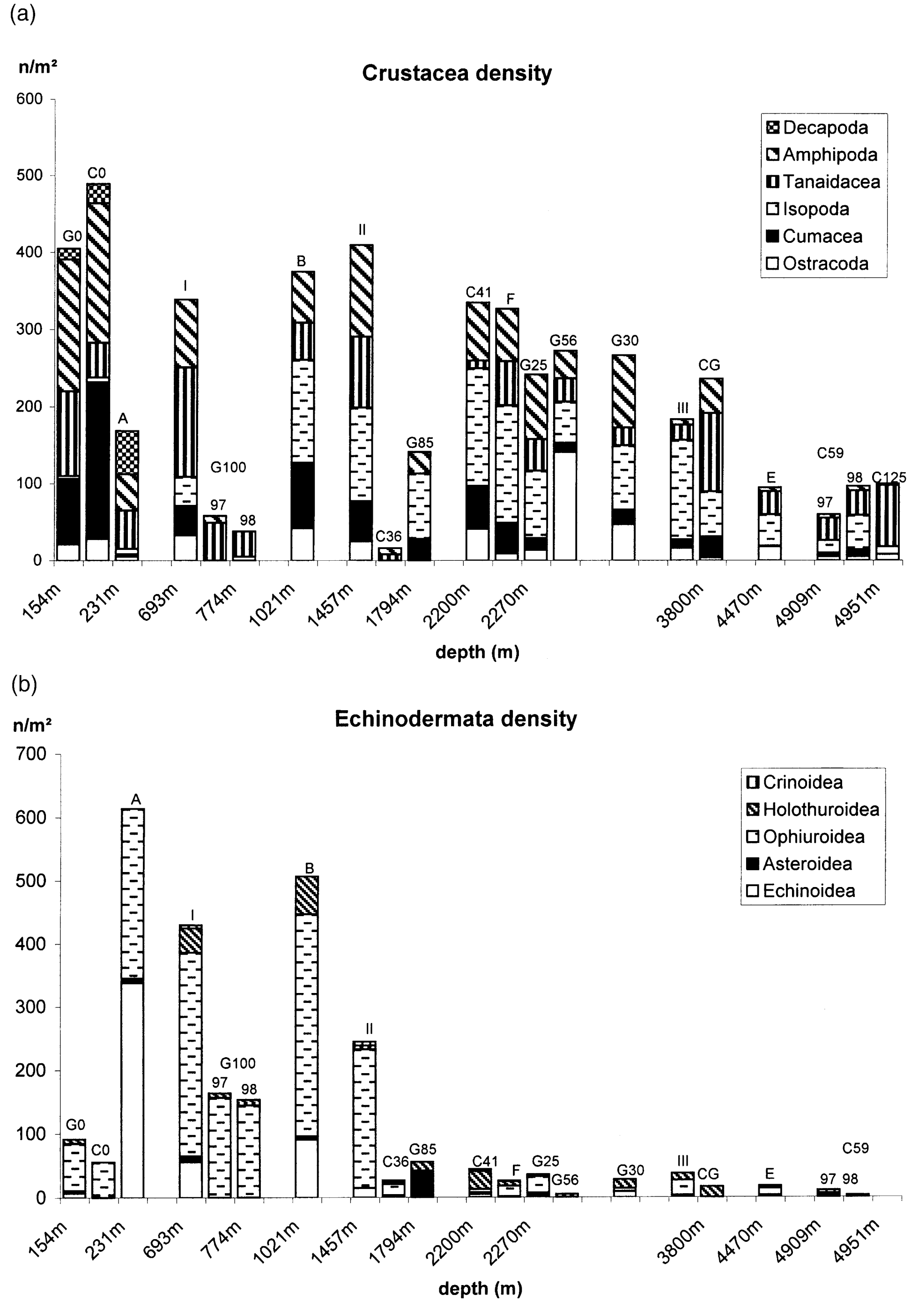
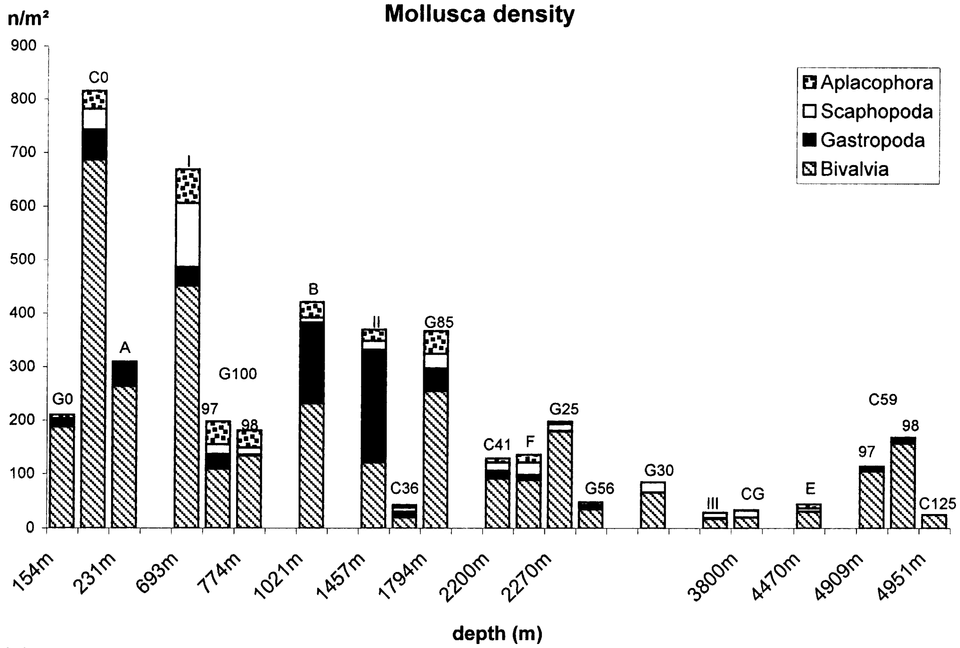


Fig. 8. Absolute (n m^{-2}) density of the minor macrofauna taxa at the two Iberian Margin transects, La Coruña (C0-C125) and Galicia Bank (G0-G100) and the station CG situated in between the two transects compared to the Goban Spur-transect (mean of 2 or 3 years, see Table 1). …zoa is the combined density of Hydrozoa, Anthozoa, Scyphozoa and Bryozoa (= Ectoprocta)

(c)



(d)

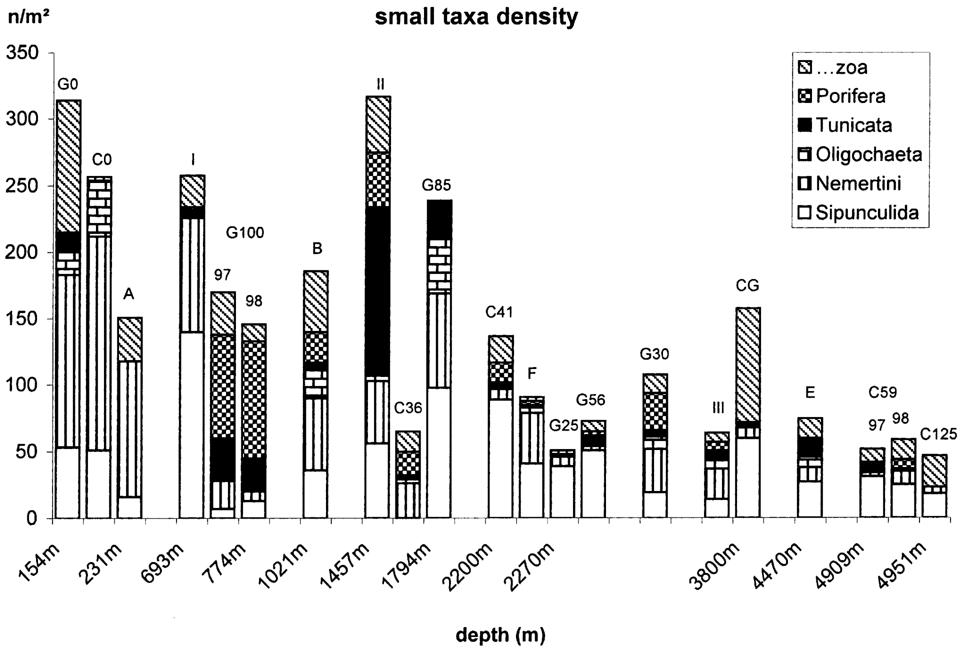


Fig. 8. *Continued*

(*Callianassa*) made important contributions to biomass, as did ostracods at station G30. At most shallow stations (~200–1500m) and at the deep Goban Spur stations, echinoderms were important contributors to the biomass.

3.3. Vertical distribution

The vertical distribution of the meiofauna within the sediment showed an increase in relative density in the upper 5mm from the shelf to the lower slope at the Goban Spur (Fig. 9a). On the shelf and at the two

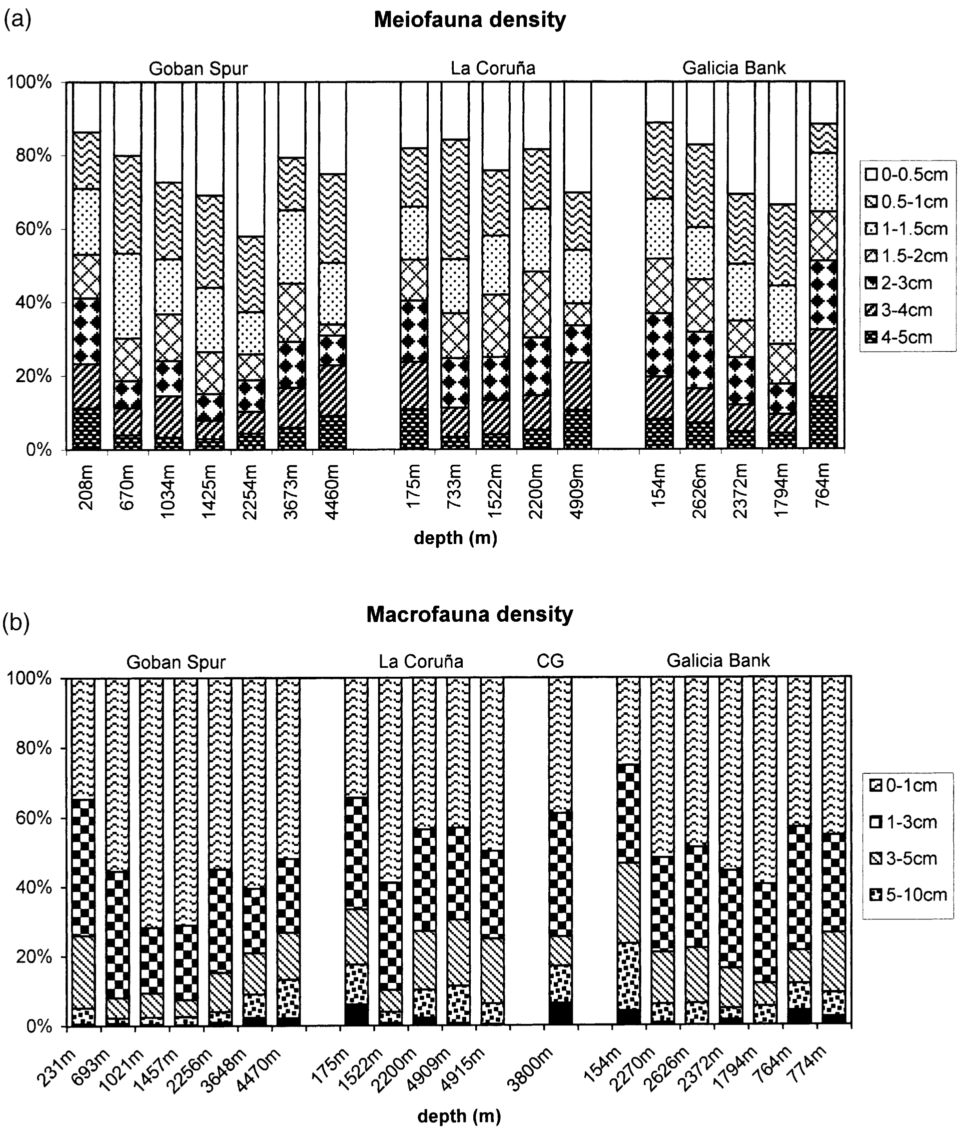


Fig. 9. The relative (%) distribution of the meiofauna (0–5 cm) and macrofauna (0–15 cm) density within the sediment at the two Iberian Margin transects, La Coruña and Galicia Bank, compared to the Goban Spur-transect (mean of 2 years). Meiofauna data of the Goban Spur provided by RU Gent.

deepest stations relatively more meiofauna was found in the deeper sediment layers. A similar pattern occurred along the Galicia Bank-transect, with increasing distance from the shore. On top of the Galicia Bank only ~20% of the meiofauna was found in the upper 1 cm of the sediment. No consistent pattern emerged along the La Coruña-transect. At all three shelf stations a similar pattern was found, with the meiofauna being more or less evenly distributed within the sediment to a depth of 5 cm (Fig. 9a).

Along the Goban Spur transect, the macrofauna was concentrated more in the upper 1cm of the sediment than at the Iberian Margin (Fig. 9b). At upper slope stations B and II (1021m and 1457m) >70% of the macrofauna was found in the upper 1 cm. On the Iberian Margin the highest percentage in the upper 1 cm was also found at similar depths (C36 1522 m and G85 1794 m), but remained <60%. On the shelf, the lowest percentage in the upper 1 cm was found at the shallowest station G0 (25%). On the Iberian shelf relatively more macrofauna was found below 5 cm in the sediment (C0 23%, G0 17%) than at the Goban Spur (5%). Also on the summit of the Galicia Bank relatively more macrofauna was found in deeper sediment layers, whereas at the deep La Coruña transect station C56 relatively less macrofauna was found below 5 cm compared to the other deep Iberian Margin station CG and the deepest Goban Spur station E.

3.4. Sediment characteristics

The sediment characteristics of the upper 1 cm are illustrated in Fig. 10. Median grain-size decreased with increasing water depth at the Goban Spur. High median grain-size values were found at the La Coruña station C36 and on top of the Galicia Bank. All deep (>1700 m) stations had a similar median grain-size (~10 μm). The percentage of calcium carbonate (%$CaCO_3$) increased with increasing water depth at the Goban Spur and increased significantly (Table 2c, $p = 0.01$) with increasing distance from the shore along the Galicia Bank-transect. Along the La Coruña transect a relatively high %$CaCO_3$ was found at station C36, although there was not much higher than at the Goban Spur station II at a similar depth. Most Iberian Margin stations contained lower % $CaCO_3$ than the Goban Spur stations, especially the deep stations (Fig. 10). Porosity increased significantly with water depth at all transects (Table 2, $p < 0.05$).

The percentages of organic carbon and total nitrogen were significantly different at the Goban Spur between May 1994 and August 1995 (Flach & Heip, 1996b). The %C_{org} and N were higher at the shelf and the upper slope in May 1994; N was especially higher at the lower slope in August 1995 (Fig. 10). Comparison between the Goban Spur and the Iberian Margin showed that on the shelf and the upper slope %C_{org} and N fall within the range of the Goban Spur values, but that the deeper Iberian Margin stations had much higher percentages. Comparing the percentages at the Iberian Margin between early July 1997 and early June 1998 showed high percentages in 1997 and higher C/N ratios in 1998. On the Galicia Bank relatively low %C_{org} and N were found, and C/N ratios were lower (~6, Fig. 10).

No correlations were found between %C_{org} and N with depth along the Goban Spur and La Coruña-transects, and only %N was significantly correlated with depth along the Galicia Bank-transect but this coincided with a significant negative correlation with grain-size (Table 2). At the Iberian Margin and at all stations taken together there were significant negative correlations between %C_{org} and N and grain-size, but not at the Goban Spur (Table 2). No correlations between %C_{org} and N and meiofauna and macrofauna were found anywhere (Table 2). However, if the shelf stations were excluded, significant positive ($p < 0.01$) correlations between meiofauna density and %C_{org} and N were found at the Iberian Margin. Meiofauna density and biomass did not show a correlation with depth, but a significant negative correlation with %$CaCO_3$ at all transects (Table 2).

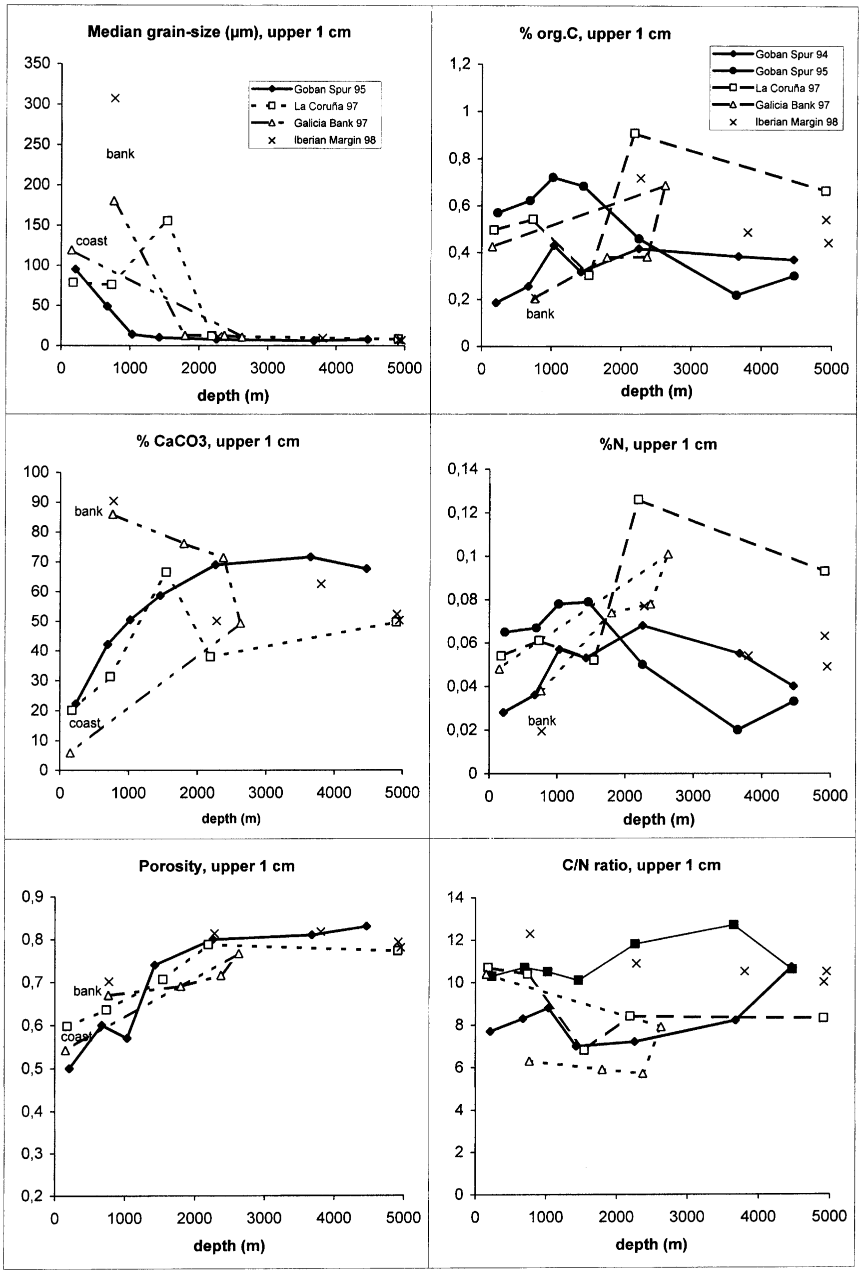


Fig. 10. Median grain-size (μm), %$CaCO_3$, porosity, %C_{org} and total N and C/N ratio (mol) in the upper 1 cm of the sediment at the two Iberian Margin transects, La Coruña and Galicia Bank sampled in June/July 1997 and the Iberian Margin stations sampled in May/June 1998 compared to the Goban Spur-transect sampled in May/June 1994 and August 1995.

4. Discussion

4.1. Comparison with other studies

Macrofaunal densities decreased with increasing water depth and, except for two special stations, densities on the Iberian Margin were not significantly different from those on Goban Spur. The Goban Spur densities fitted well on the line given by Jumars and Gallagher (1992) for the NW Atlantic, except that the deepest station had somewhat higher densities (Flach & Heip, 1996a). Comparing our results from all three transects with results from other studies in the NE Atlantic, they reveal a similar overall pattern, but with some regional differences, some of the canyon stations showing extreme densities (Fig. 11). Unfortunately, sieves of different mesh-sizes were used in the different studies (1 mm in the Skagerrak, 0.5 mm in our studies, 0.42 mm Hebridean, 0.3 mm Setubal, 0.25 mm during EUMELI) making comparisons difficult. The use of standardized methodology in deep-sea benthic faunal studies remains an important but as yet unresolved problem.

4.2. Two extreme stations

At stations with high current velocities more (small) filter-feeding taxa were found, whereas at stations where sedimentation rates were high, more (large) subsurface deposit-feeders were found (Flach, Lavaleye, Stigter & Thomsen, 1998). At the Iberian Margin exceptionally low faunal densities occurred at two stations. On the La Coruña transect, station C36, which was situated on a very steep part of the slope at 1522 m, the sediment surface had ripples parallel to the coastline and terraces, indicating there were relatively high velocity currents oriented perpendicular to the coast (Duineveld & Lavaleye, 1997). The megafauna consisted of ~80% filter-feeding taxa, which were mainly small colonial sea anemones (Duineveld & Lavaleye, 1997; Lavaleye, Duineveld, & Berghuis, 1999; Lavaleye, Duineveld, Berghuis, Kok, & Witbaard, 2002). Relatively high numbers of filter feeders were also found in the macrofauna, which mainly consisted

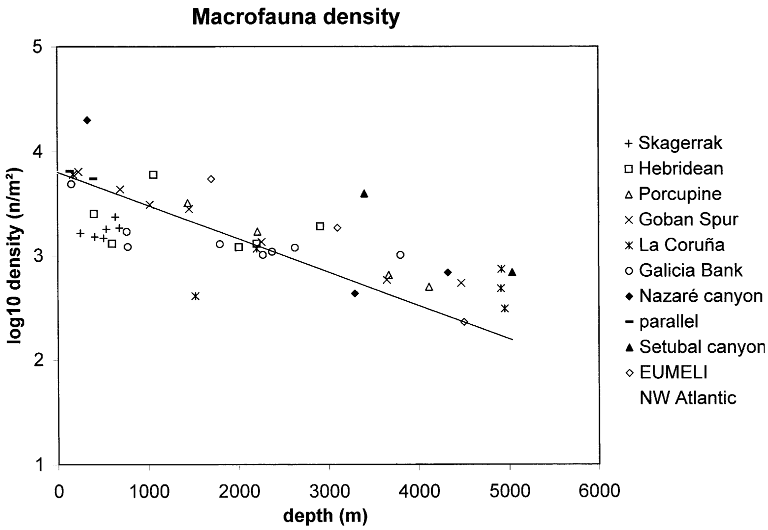


Fig. 11. Macrofauna densities (log 10 n m^{-2}) at different sites in the NE Atlantic compared to the regression line for the NW Atlantic of Jumars and Gallagher (1982). Data from the Skagerrak from Rosenberg, Hellman and Lundberg (1996) 1mm-sieve, Hebridean Slope (0.42 mm sieve) and Setubal Canyon (0.3 mm sieve) from Gage (pers. com.), EUMELI from Galéron, Sibuet, Mahaut and Dinet (2000) 0.25 mm sieve, other sites own data Flach 0.5 mm sieve.

of sponges and Bryozoa, with extremely low number of crustaceans. This station was situated at a similar depth to the Goban Spur station II, which was also characterised by high flow velocities and high numbers of filter-feeding taxa both in mega- and macrofauna and in the Foraminifera (Flach et al., 1998). The fauna was mainly concentrated in the upper 1 cm of the sediment (Flach & Heip, 1996a) and it was concluded that the fauna was actively capturing particles and burying them in the sediment that otherwise would have been advected through this high-energy region (Flach et al., 1998; Thomsen & Flach, 1997). At the Iberian Margin benthic Foraminifera (*Marsipella* sp.) dominated the mid-slope community and laboratory flume experiments showed POC biodeposition by these foraminifers to be 0.22–0.67 mgC.m^{-2}d^{-1}, roughly equivalent to 1–4% of the carbon deposition needed to sustain the mid-slope benthic community (Thomsen, 1999; Thomsen, Van Weering, & Gust, 2002). However, total macro- and meiofauna densities were very low at this station, indicating that overall food supply was low and/or conditions were unstable. The high median grain-size without extreme %$CaCO_3$ supports this idea.

The other low-density station G100 on the summit of the Galicia Bank was also characterised by surficial sediments with had high median grain-size and extremely high %$CaCO_3$. The sediment at this station was real foraminiferan ooze. The colonial coral *Lophelia* was the most prominent megabenthos species at this station (Duineveld & Lavaleye, 1997). Within the skeletal structure of this large coral were found large carnivorous polychaetes, mainly Nereidae and Polynoidae. The macrofauna also consisted of high numbers of filter feeders, mainly sponges and ophiuroids. Aplacophorans were also relatively abundant, as were small carnivorous syllid polychaetes. Thus the fauna mainly consisted of filter feeders and carnivores. Meiofaunal densities were very low at this station as was the %C_{org} and total nitrogen. Thus feeding conditions for deposit-feeders seemed to be poor and the food supply seemed to depend on pelagic sedimentation, whereas at similar depths (600–1000 m) on the Goban Spur pulses of labile matter from the shelf arrived to fuel a mainly surface deposit-feeding community (Flach & Heip, 1996a).

4.3. Shelf

Macrofaunal densities were slightly lower on the shelf off Vigo, and biomass was significantly lower on the shelf off La Coruña than at other stations. This seemed to be mainly because small polychaetes dominated the macrofauna near La Coruña whereas large ones dominated near Vigo. López-Jamar et al. (1992) also reported high numbers of mainly small, surface feeding and fast growing polychaetes on the northern shelf (La Coruña) but more subsurface deposit-feeding and large carnivorous polychaetes on the western shelf (Vigo). They related this pattern to differences in feeding conditions. The Galician shelf exhibits mesoscale spatial and temporal changes in biological productivity associated with upwelling (Tenore et al., 1995). Upwelling events are more common in summer than in winter and surface-reaching upwelling is more common and persistent on the northern coast. Offshore the Rías Bajas the coastal runoff, which is higher in winter than in summer, interacts with the upwelling. In early summer, upwelling penetrates to the surface less often because of the coastal runoff than later in summer. Growth and abundances of phytoplankton and bacterioplankton are greatest during upwelling conditions (Tenore et al., 1995). On the Galician shelf organic enrichment resulting from the increases in productivity resulting from upwelling reaches the seabed in pulses, and thus benthic fauna is dominated mainly by small surface detritus-feeding polychaetes, that are specialised to exploit opportunistically these irregular and unpredictable events (López-Jamar et al., 1992). In contrast, off the Rías Bajas the sediment is enriched by organic matter exported from the Rías as well as by the upwelling events. These more regular inputs of organic material enable a much higher proportion of subsurface deposit-feeders to thrive in the infaunal community, which are typical of a later successional stage. López-Jamar et al. (1992) concluded that both coastal upwelling and organic export from the Rías Bajas support high benthic production along the Galician shelf. Macrofaunal density and biomass on the shelf edge, however, were not significantly higher than at the Goban Spur. Meiofaunal densities, on the other hand, were more than double. Vanreusel, Vincx, Schramm and Van Gansbeke (1995) found a linear relationship between log-transformed meiofauna densities and log-transformed bacteria densities, and concluded that meiofaunal density increases with increasing food supply. On the Galician shelf benthic bacteria followed the fluctuating patterns of organic matter content seasonally and interannually. The highest numbers of bacteria occurred in the upwelling region off the northern shelf (López-Jamar et al., 1992). Meiofaunal density and especially biomass were higher near La Coruña.

4.4. Food supply

Excluding the shelf stations (where meiofauna is affected by a wide range of factors (Heip, Vincx, & Vranken, 1985)), meiofauna density was highly correlated with the $\%C_{org}$ and N within the sediment at the Iberian Margin. These values were higher at the lower part of the slope at the Iberian Margin than at the Goban Spur, especially on the northern transect. Enrichment as a result of upwelling thus seems to benefit the meiofauna of the lower slope of the Iberian Margin. During the cruise of July 1997 a high phytopigment concentration was found at station C59 below the steep slope, indicating a high input of fresh detritus (Lavaleye et al., 1999, Lavaleye et al., 2002). High $\%C_{org}$ and N were found in the upper 1 cm sediment layer in July 1997 and lower values in June 1998, thus suggesting either a seasonal or interannual variation in organic matter supply. Even at these great depths (4900 m) bacteria can respond quickly to an input of organic matter (Pfannkuche, 1993). As meiofauna is related to bacterial production this may explain the high meiofauna densities at the deep Iberian Margin stations. Both the percentage of nematodes within the meiofauna and the meio:macrofauna ratio increased with depth. This ratio was very high along the La Coruña transect so the benthic community was strongly dominated by nematodes numerically at the deep La Coruña stations, but not in terms of biomass. The macrofaunal biomass was still over double the meiofaunal biomass at this deep station C59. Macrofaunal densities were normal for this great depth, but on average the specimens were relatively large and mostly subsurface deposit-feeding polychaetes, indicative for a steady supply of refractory organic matter (Rice & Rhoads, 1989). Helder and Epping (1999) and Epping, van der Zee, Soetaert and Helder (2002) have reported an exponential decrease in organic carbon deposition flux with water depth and an increasing in the burial efficiency at the Iberian Margin, which was extremely high just near station C59. They concluded that both the amount of carbon arriving at the sea floor and its degradability, decrease with increasing water depth. Macrofauna also decreases exponentially in density and biomass with water depth and so may be linked directly to the deposition flux. The carbon deposition flux on the shelf near Vigo was nearly double that near La Coruña, exactly the same proportion was found for macrofauna biomass. A positive linear relationship ($y = 165.93x - 3.3663$, $R^2 = 0.9944$, $n = 6$) between the carbon deposition flux (mmol $Cm^{-2}d^{-1}$, data of Helder and Epping, 1999) and the total macrofaunal biomass ($mgCm^{-2}$) was found at the Iberian Margin. Cosson, Sibuet and Galeron (1997) reported a positive linear relation between macrofauna density and carbon flux. Sibuet, Lambert, Chesselet and Laubier (1989) concluded that, because about ~85% of the organic carbon that settles on the seabed is utilised before it gets buried, the organic carbon within the surface sediments represents mainly what was left unconsumed by the fauna and not what was available for consumption. They also concluded that the flux of orgC settling at the sediment-water interface controls the distribution of benthic biomass distribution in the deep Atlantic Ocean. Biomass values may therefore be considered as good proxies for the mean carbon flux, which is in agreement with the data from the Iberian Margin.

5. Conclusions

The characteristics of the macrofaunal and meiofaunal assemblages appear to be indicative of different environmental factors. Macrofauna density and biomass are related to the carbon deposition flux, whereas its community structure and vertical distribution are influenced by, and are indicative of, the current flow regime, food quality and the predictability of the food supply (pulses or steady). Meiofaunal assemblages are more linked to the local bacterial production and sediment characteristics (Vanreusel et al., 1995). The vertical distribution of nematodes in the sediment follows the depth profile of total nitrogen (Soetaert, Vanaverbeke, Heip & Herman, 1997) and can be related to both food and oxygen supply (Vanreusel et al., 1995). These factors, however, can also be related to the activity of larger fauna (Lambshead, Ferrero & Wolff, 1995; Soetaert, Vanaverbeke, Heip, Herman, Middelburg, Duineveld et al., 1997). Positive relationships between macrofaunal density and meiofauna density and biomass were found (Table 2) and the vertical profiles did show some similarities (Fig. 9). Thus if assessed together, meiofauna and macrofauna community characteristics may provide an integrated overview of the physical and biogeochemical conditions prevailing at the sampled sites.

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References

Andrassy, I. (1956). The determination of volume and weight of nematodes. *Acta Zoologica Academiae Scientiarium Hungricae*, *2*, 1–15.

Cosson, N., Sibuet, M., & Galeron, J. (1997). Community structure and spatial heterogeneity of deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. *Deep Sea- Research I*, *44*, 247–269.

Duineveld, G.C.A. & Lavaleye, M.S.S. (1997). Benthic Biology of the Iberian Upwelling Margin. *Cruise report R.V. Pelagia 108, OMEX II-leg 1.* Unpublished Report NIOZ.

Epping, E., van der Zee, C., Soetaert, K., & Helder, W. (2002). On the oxidation and burial of organic carbon in sediments of the Iberian Margin and Nazaré Canyon. *Progress in Oceanography*, *52*(2-4), 399–431.

Flach, E., & de Bruin, W. (1999). Diversity patterns in macrobenthos across a continental slope in the Northeast Atlantic. *Journal of Sea Research*, *42*, 303–323.

Flach, E., & Heip, C. (1996a). Vertical distribution of macrozoobenthos within the sediments on the continental slope of the Goban Spur area (NE Atlantic). *Marine Ecology Progress Series*, *141*, 55–66.

Flach, E., & Heip, C. (1996b). Seasonal variations in faunal distribution and activity across the continental slope of the Goban Spur area (NE Atlantic). *Journal of Sea Research*, *36*, 203–215.

Flach, E., Lavaleye, M., de Stigter, H., & Thomsen, L. (1998). Feeding types of the benthic community and particle transport across the continental slope of the Goban Spur. *Progress in Oceanography*, *42*, 209–231.

Galéron, J., Sibuet, M., Mahaut, M. -L., & Dinet, A. (2000). Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical Northeast Atlantic. *Marine Ecology Progress Series*, *197*, 121–137.

Heip, C., Vincx, M., & Vranken, G. (1985). The ecology of marine nematodes. *Oceanography and Marine Biology. Annual Review*, *23*, 399–489.

Helder, W. & Epping, E. (1999). Organic carbon mineralization in Iberian Margin sediments. *Report. Ocean Margin EXchange (OMEX II-II, 2nd Annual).*

Huthnance, J. M. (1995). Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. *Progress in Oceanography*, *35*, 353–431.

Jensen, P. (1984). Measuring carbon content in nematodes. *Helgoländer Meeresuntersuchungen*, *38*, 83–86.

Jumars, P. A., & Gallagher, E. D. (1982). Deep-sea community structure: Three plays on the benthic proscenium. In W. G. Ernst, & J. G. Morin (Eds.), *The Environment of the Deep Sea*. Prentice Hall, Inc.

Lambshead, P. J. D., Ferrero, T. J., & Wolff, G. A. (1995). Comparison of the vertical distribution of nematodes from two contrasting abyssal sites in the northeast Atlantic subject to different seasonal inputs of phytodetritus. *Internationale Revue der Gesamten Hydrobiologie*, *80*, 327–331.

Lavaleye, M.S.S., Duineveld, G.C.A. & Berghuis, E.M. (1999). Megabenthos, benthic respiration and phytopigments off NW Spain. *Report. Ocean Margin EXchange (OMEX II-II, 2nd Annual).*

Lavaleye, M. S. S., Duineveld, G. C. A., Berghuis, E. M., Kok, A., & Witbaard, R. (2002). A comparison between the megafauna communities on the N.W.Iberian margin and the Celtic continental margins - effects of coastal upwelling? *Progress in Oceanography*, *52*(2-4), 459–476.

López-Jamar, E., Cal, R. M., González, G., Hanson, R. B., Rey, J., Santiago, G., & Tenore, K. R. (1992). Upwelling and outwelling effects on the benthic regime of the continental shelf off Galicia, NW Spain. *Journal of Marine Research, 50,* 465–488.

McCave, I. N. (1984). Size spectra and aggregation of suspended particle in the deep ocean. *Deep-Sea Research*, *31*, 329–352.

Nieuwenhuize, J., Maas, Y. E. M., & Middelburg, J. J. (1994). Rapid analysis of organic carbon and nitrogen in particulate materials. *Marine Chemistry*, *45*, 217–224.

Pfannkuche, O. (1993). Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47°N, 20°W. *Deep-Sea Research II*, *40*, 135–149.

Rice, D. L., & Rhoads, D. C. (1989). Early diagenesis of organic matter and the nutritional value of sediment. In G. R. Lopez, G. L. Taghon, & J. S. Levinton (Eds.), *Ecology of Marine Deposit Feeding* (pp. 59–79). Springer-Verlag.

Rosenberg, R., Hellman, B., & Lundberg, A. (1996). Benthic macrofaunal community structure in the Norwegian Trench, deep Skagerrak. *Journal of Sea Research*, *35*, 181–188.

Rowe, G. T. (1983). Biomass and production of deep-sea macrobenthos. In H. T. Rowe (Ed.), *Deep-Sea Biology* (pp. 97–121). *The Sea*, 8. John Wiley & Sons.

Sibuet, M., Lambert, C. E., Chesselet, R., & Laubier, L. (1989). Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. *Journal of Marine Research*, *47*, 851–867.

Soetaert, K., Vanaverbeke, J., Heip, C., Herman, P. M. J., Middelburg, J. J., Duineveld, G., & Sandee, A. (1997). Nematode distribution in ocean margin sediments of the Goban Spur (north-east Atlantic) in relation to sediment geochemistry. *Deep-Sea Research, I*, *44*, 1671–1683.

Tenore, K. R., Alonso-Noval, M., Alvarez-Ossorio, M., Atkinson, L. P., Cabanas, J. M., Cal, R. M., Campos, H. J., Castillejo, F., Chesney, E. J., Gonzalez, N., Hanson, R. B., McClain, C. R., Miranda, A., Roman, M. R., Sanchez, J., Santiago, G., Valdes, L., Varela, M., & Yoder, J. (1995). Fisheries and oceanography off Galicia, NW Spain: Mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity. *Journal of Geophysical Research*, *100*, 943–966.

Thomsen, L. (1999). BBL Characteristics at the Iberian Sea transect. *Report. Ocean Margin EXchange (OMEX II-II, 2nd Annual).*

Thomsen, L., & Flach, E. (1997). Mesocosm observations of fluxes of particulate matter within the benthic boundary layer. *Journal of Sea Research*, *37*, 67–79.

Thomsen, L., Van Weering, Tj. C. E., & Gust, G. (2002). Benthic boundary layer characteristics at the Iberian continental margin. *Progress in Oceanography*, *52*(2-4), 315–329.

Vanaverbeke, J., Soetaert, K., Heip, C., & Vanreusel, A. (1997). The meiobenthos along the continental slope of the Goban Spur (NE Atlantic). *Journal of Sea Research*, *38*, 93–108.

Vanreusel, A., Vincx, M., Schramm, D., & Van Gansbeke, D. (1995). On the vertical distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic. *Internationale Revue der Gesamten Hydrobiologie*, *80*, 313–326.

Van Weering, Tj. C. E., McCave, I. N., & Hall, I. R. (1998). Ocean Margin Exchange (OMEX I) benthic processes study. *Progress in Oceanography*, *42*, 1–4.

Van Weering, Tj. C. E., & McCave, I. N. (2002). Introduction. *Progress in Oceanography*, *52*(2-4), 123–128.