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Macrofaunal abundance analyses in the Ría de Foz (Lugo, Northwest Spain).

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Abstract : The abundance and dominance of the major taxonomic groups (polychaetes, molluscs, crustaceans and other groups) of the macrobenthic (> 1 mm) fauna of the intertidal soft-bottom in Ría de Foz (Galicia, NW Spain) was investigated. The estuary can be divided into five distinct habitats characterized by the nature of their sediments, tidal level, degree of exposure and presence or absence of seagrass meadows. The macrofauna increases in abundance towards the inner estuary. In sandy sediments, the macrofaunal abundance depends largely on the rate of exposure and the tidal level. In the exposed sandy beaches of the mouth of the estuary, the mean density was 192 individuals m^{-2}, with the polychaetes and crustaceans dominating. In the sublittoral zone of the more sheltered sandy sites there was an increase in the mean macrofaunal density (855 individuals m^{-2}), with a notable enhancement of the quantitative importance of the molluscs. In the midlittoral zone of the sheltered sandy areas the mean density was 458 individuals m^{-2}, with crustaceans the dominant group. In the muddy sand flats, the mean macrofaunal density was 3 499 individuals in these sites the polychaetes reached their highest abundance. The meadows of *Zostera noltii* of the inner ría support an abundant population of the mud-snail *Peringia ulvae,* with a mean macrofaunal density of 20 526 individuals m^{-2}.

Résumé : L'abondance et la dominance des quatre principaux stocks (polychètes, mollusques, crustacés, autres groupes) du macrobenthos (> 1 mm) ont été étudiées dans les substrats meubles intertidaux de la ría de Foz (Galice, NW Espagne). Dans cet estuaire, on distingue cinq habitats, caractérisés par la nature des sédiments, le niveau dans l'intertidal, le degré d'exposition et la présence ou absence d'herbiers de *Zostera.* La macrofaune augmente en abondance vers l'amont de l'estuaire. Dans les sédiments sableux, cette abondance dépend en grande partie de l'exposition dans l'intertidal. Dans les plages sableuses exposées, au débouché de l'estuaire, la densité moyenne est de 192 individus.m^{-2} avec dominance des polychètes et des crustacés. Dans la partie sublittorale des zones sableuses les plus abritées, on constate une augmentation de la densité moyenne de la macrofaune (855 individus.m^{-2}), avec un accroissement notable de l'importance quantitative des mollusques, tandis que, dans la partie médiolittorale, cette densité est de 458 individus.m^{-2}, avec dominance des crustacés. Dans les zones sablo-vaseuses, où les polychètes atteignent leur plus forte abondance, la densité moyenne de la macrofaune est de 3 499 individus.m^{-2}. Les herbiers à *Zostera noltii* de la partie interne de la ría présentent une abondante population du gastéropode *Peringia ulvae* avec une densité moyenne de la macrofaune de 20 526 individus.m^{-2}.

INTRODUCTION

Amongst the factors considered to be of significance in the distribution and abundance of intertidal soft bottom macrofauna, sediment characteristics (Wolff, 1973 ; Eleftheriou & Nicholson, 1975 ; Grange, 1977 ; López-Cotelo *et al.*, 1982 ; Penas & González, 1983), exposure to wave action (Eleftheriou & Nicholson, 1975 ; Eleftheriou & McIntyre, 1976 ; Dexter, 1983 ; 1988), tidal level (Dahl, 1952 ; Salvat, 1964 ; Wolff, 1973 ; López-Cotelo *et al.*, 1982, Bally, 1983 ; Penas & González, 1983 ; Raffaelli & Boyle, 1986) and, when present, seagrass beds (Castel *et al.*, 1989) have been recognized as of major importance. In this study we examine the abundance and dominance of four macrofaunal taxonomic

groups (polychaetes, molluscs, crustaceans and other groups) in five different habitats, from exposed sandy beaches to sheltered mud flat seagrass meadows, along the Ría de Foz (Galicia, NW Spain). Previous studies on macrofaunal species (Junoy, 1987 ; Junoy & Viéitez, 1988, 1990a, b ; Gibson & Junoy, 1991), community structure (Junoy & Viéitez, 1990c) and cartography of superficial sediments (Junoy & Vieitez, 1989) have been presented in other papers.

The Ría de Foz (43° 34' N, 7°14' W) is an intertidal estuary approximately 3.8 km long and 0.9 km wide at its mouth. The study area (2.4 km^2) covers most of the ría (2.8 km^2), from the mouth to a railway bridge about 2.8 km upstream. The whole of the area is subjected to regular tidal fluctuation. Although receiving the outflow from the Masma River and two other streams, the Ría de Foz can best be considered an outer estuary, since it is subject to only a slight reduction in salinity ($\bar{x}$ = 31.5 ‰). Sedimentary characteristics graduate along the ría from sandy with low organic-matter content in the outer, northern region, to muddy with a high organic-matter content in the inner, southern region (Junoy & Viéitez, 1989).

MATERIALS AND METHODS

The sampling programme was primarily adjusted to provide adequate information on the distribution of macrozoobenthic species, and consisted of widespread sample points visited over the four seasons. From a total of 99 samples taken during June, September, and December 1984 and March 1985 we selected, for the purposes of this study, 88 samples at the following five habitats :

1°) *Beaches*. Represented by 22 samples located in the exposed sandy beaches of the mouth of the ría. The sedimentary type was medium sand (Median grain size, Md, $\bar{x}$ = 0.30 mm, sd = 0.06), with low silt-clay ($\bar{x}$ = 1.32 % ; sd = 0.40) and organic-matter ($\bar{x}$ = 1.60 % ; sd = 0.39) contents. The mean tidal level was 1.49 m (sd = 0.52).

2°) *Sublittoral sheltered sands*. Represented by 31 samples located in the sublittoral zone of sheltered sandbanks, in medium and fine sands (Md, $\bar{x}$ = 0.27 mm ; sd = 0.04) with low silt clay ($\bar{x}$ = 1.86 % ; sd = 0.84) and organic-matter ($\bar{x}$ = 1.69 % ; sd = 0.28) contents. The mean tidal level was 1.59 m (sd = 0.39).

3°) *Midlittoral sheltered sands*. With 18 samples located in the midlittoral zone of sheltered sandbanks. Sedimentary types were medium sands (9 samples), fine sands (6 samples) and fine muddy sands (3 samples) (Md, $\bar{x}$ = 0.26 mm ; sd = 0.04) with low silt-clay ($\bar{x}$ = 1.47 % ; sd = 1.07) and organic-matter contents ($\bar{x}$ = 1.57 % ; sd = 0.19). The mean tidal level was 2.3 m (sd = 0.19)

4°) *Muddy sand flats*. Represented by 9 samples located in the inner ría, in fine muddy sand flats (Md, $\bar{x}$ = 0.19 mm ; sd = 0.35) where the silt-clay fraction reaches a maximum of 39.40 % ($\bar{x}$ = 13.08 %, sd = 11.14). The median organic-matter content was 2.40 % (sd = 0.51). The mean tidal level was 1.8 m (sd = 0.23).

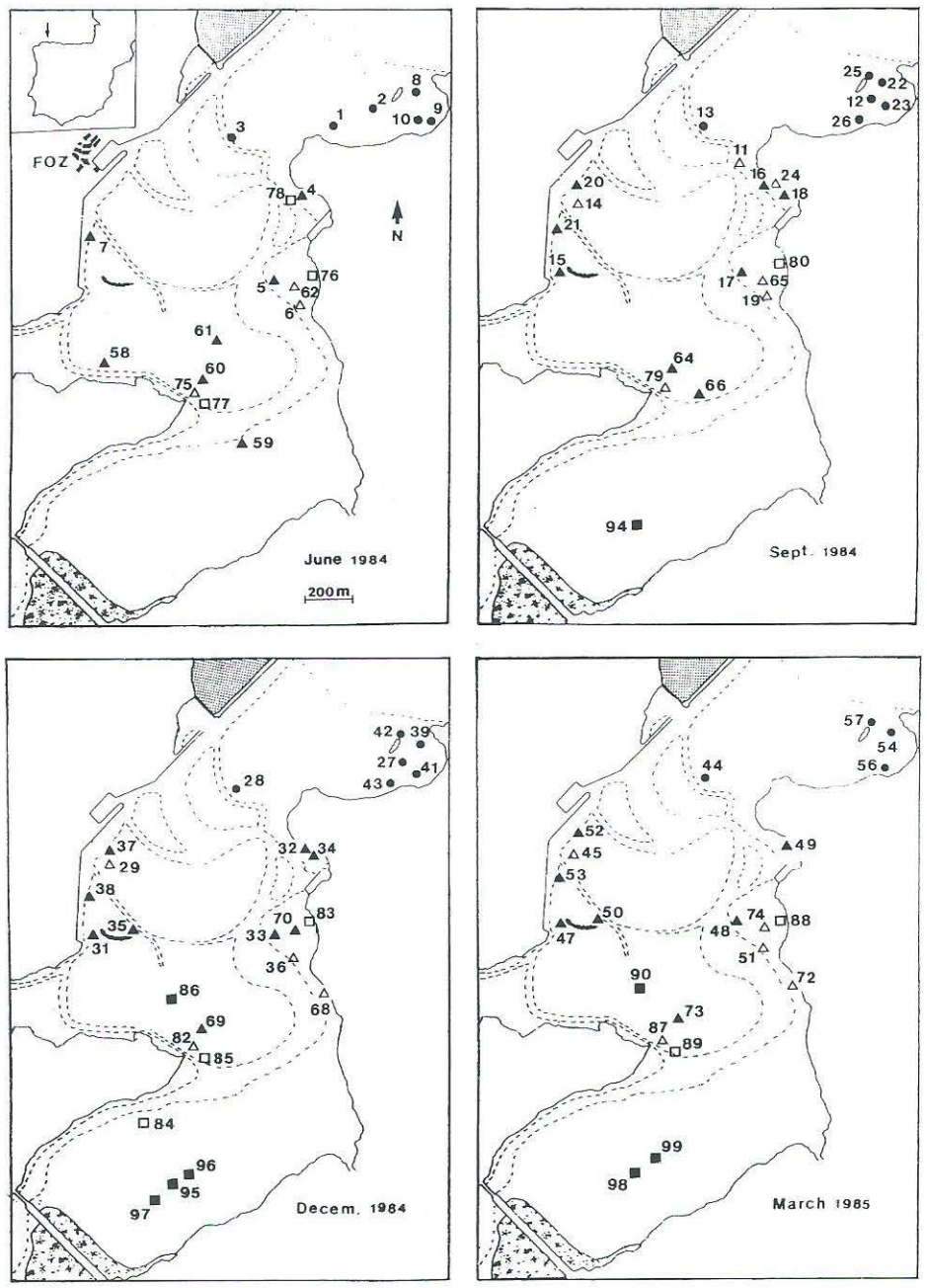

Fig. 1 : Location of 88 samples taken in the Ría de Foz, Northwest Spain ; inset shows coastline of Iberian Peninsula. Mouth of estuary is to the north, at the tip of the maps. Dots, samples on beaches ; black triangles, samples on sublittoral sheltered sands ; open triangles, samples on midlittoral sheltered sands ; open quadrats, samples on muddy sandy flats ; black quadrats, samples on seagrass meadows.

5°) *Seagrass meadows*. The inner ría was occupied by an extensive meadow of *Zostera noltii* Horneman, and some sparse patches of *Spartina* sp. A total of 8 samples were taken in these areas. Sedimentary types were fine muddy sands (2 samples) and mud (6 samples) (Md, $\bar{x}$ = 0.07 mm ; sd = 0.06). The silt-clay ($\bar{x}$ = 59.09 % ; sd = 27.14) and organic-matter ($\bar{x}$ = 6.55 % ; sd = 3.27) contents were always high. The mean tidal level was 2.42 m (sd = 0.27).

Fig. 1 shows the spatial and temporal distribution of the samples of each habitat. Details of the sampling procedures can be found in Junoy & Viéitez (1990c). From the data obtained from each sample of 1 600 cm^2 area by 30 cm depth, macrofaunal abundance, dominance of polychaetes, crustaceans, molluscs and other groups, and species density and frequency were calculated for each habitat. The Shannon-Wiener diversity index (H') and evenness (J') were calculated for each sample.

Much doubt remained as to the correct identification of four species which displayed taxonomic characteristics between two other species, and these are referred to as *Spio martinensis-decoratus*, *Eteone longa-flava*, *Sphaeroma rugicauda-monodi* and *Bathyporeia sarsi-pilosa*. Two crustacean species with more than 30 cm depth burrows, *Callianasa* cf. *thyrrena* and *Upogebia pusilla*, were sub-sampled. Commercially important species, specially the bivalve molluscs *Cerastoderma edule* and *Venerupis decussata*, were subjected to human predation.

RESULTS

Figures 2 to 6 show the temporal distribution of the abundance and dominance of the polychaetes, molluscs, crustaceans and other groups in the beaches, sublittoral sheltered sands, midlittoral sheltered sands, muddy sand flats and seagrass meadows. Table I shows the median density and frequency on samples of species collected at each habitat.

In the beaches, the abundance of the macrofauna varied from 18.75 ind.m^{-2} (Sample 27) to 825 ind.m^{-2} (Sample 28), with polychaetes and crustaceans as the most abundant groups. Polychaete density ranged from 6.25 ind.m^{-2} (Sample 22) to 675 ind.m^{-2} (Sample 28), with *Scolaricia typica*, *Scolelepis mesnili* and *Nephtys cirrosa* as the most abundant species. No crustaceans were collected on four occasions (Samples 1, 2, 8 and 27), but they reached a maximum density of 312 ind.m^{-2} (Sample 42). The most abundant species were *Urothoe brevicornis*, *Sphaeroma rugicauda-monodi* and *Bathyporeia pelagica*. Polychaetes and crustaceans together always comprised more than 90 % of all macrofaunal individuals. Polychaete dominance was more than 80 % in six samples (100 % in samples 2, 8 and 27) whereas crustaceans exceeded the 80 % of dominance in two samples.

In the sublittoral sheltered sands, with sediment characteristics similar to those of beaches, there was a notable increment in the macrofaunal abundance promoted by the more sheltered condition. This varied from 137 ind.m^{-2} (Sample 32) to 6 206 ind.m^{-2} (Sample 61). Molluscs, polychaetes and crustaceans were the most abundant groups.

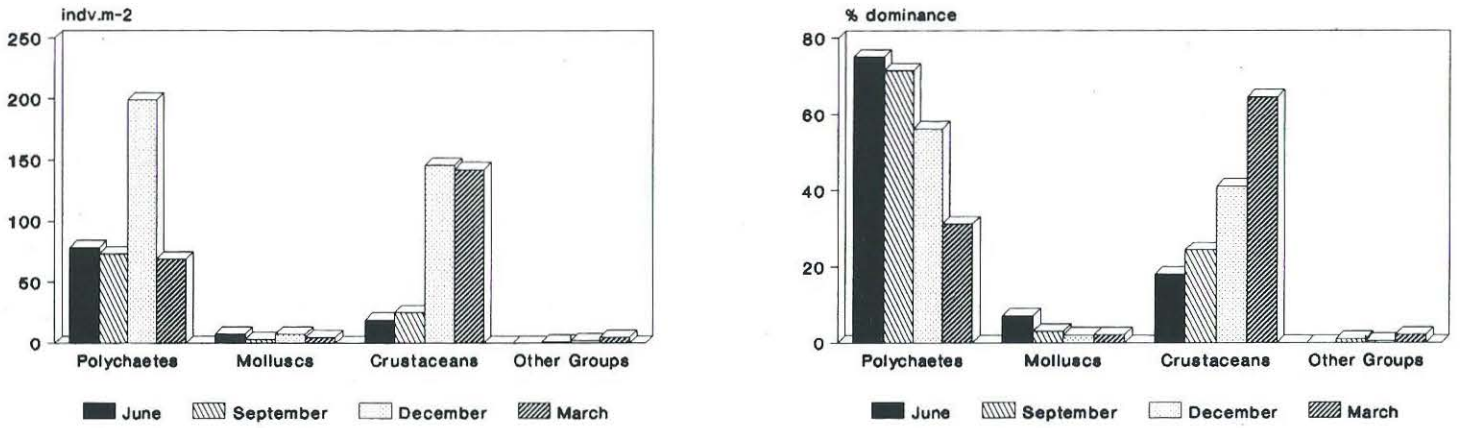

Fig. 2 : Abundance and dominance of polychaetes, crustaceans, molluscs and other groups in beaches of Ría de Foz during the sampling periods.

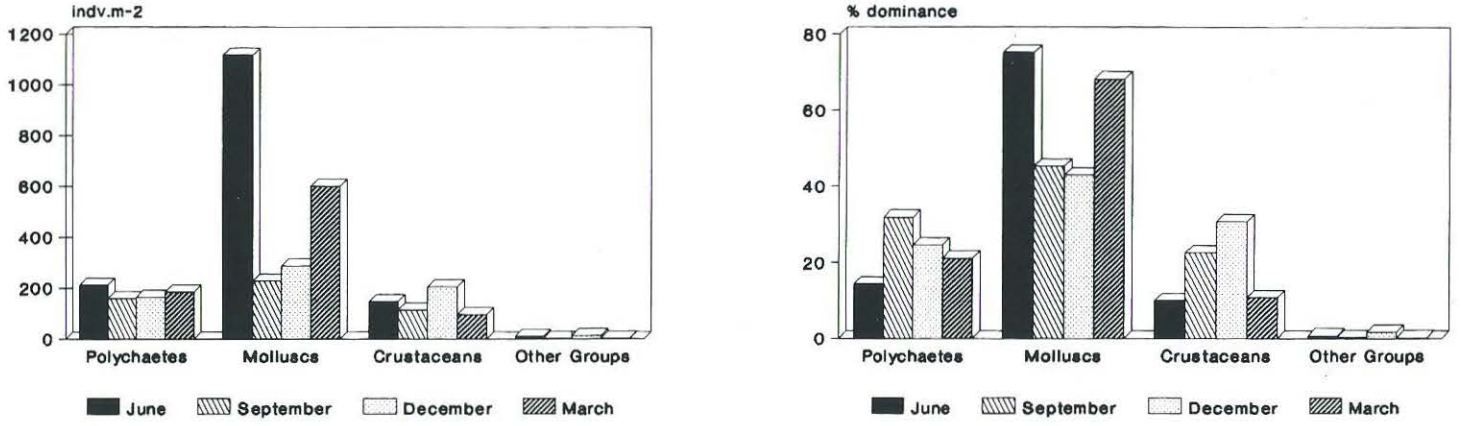

Fig. 3 : Abundance and dominance of polychaetes, crustaceans, molluscs and other groups in sublittoral sheltered sands of Ría de Foz during the sampling periods.

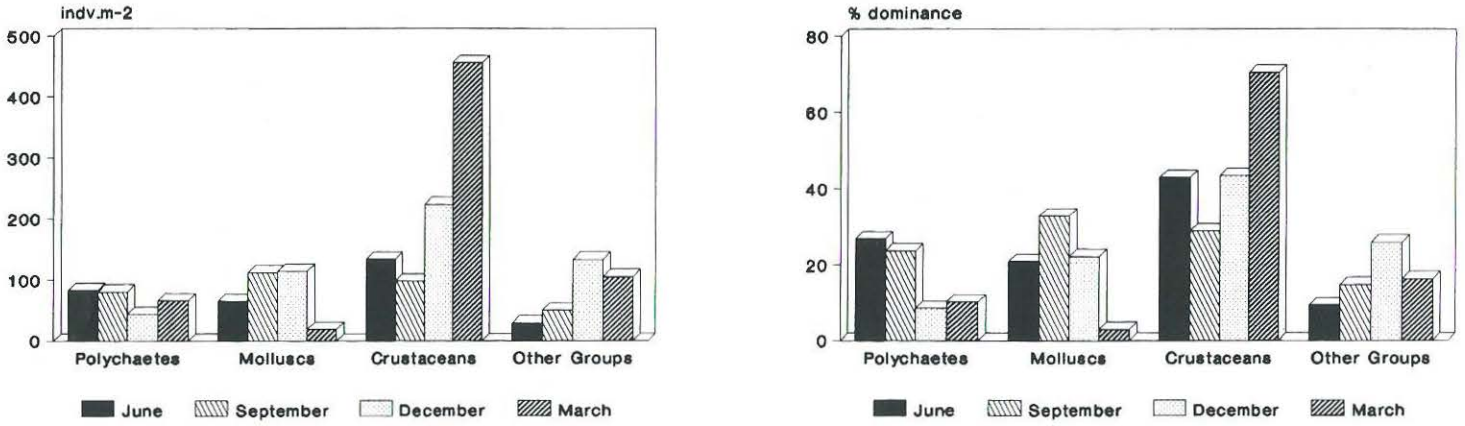

Fig. 4 : Abundance and dominance of polychaetes, crustaceans, molluscs and other groups in midlittoral sheltered sands of Ría de Foz during the sampling periods.

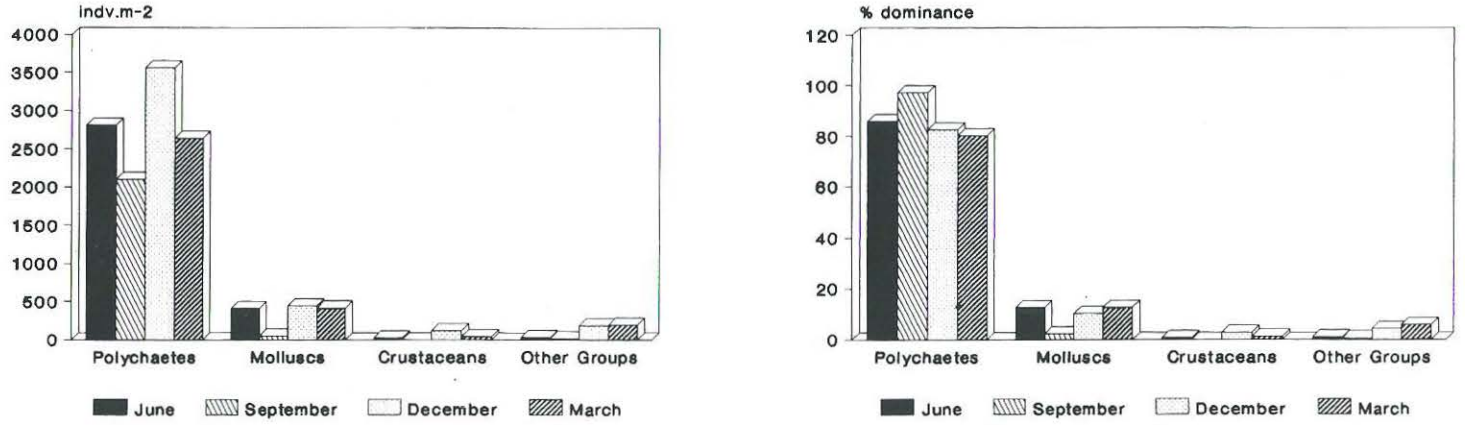

Fig. 5 : Abundance and dominance of polychaetes, crustaceans, molluscs and other groups in muddy sand flats of Ría de Foz during the sampling periods.

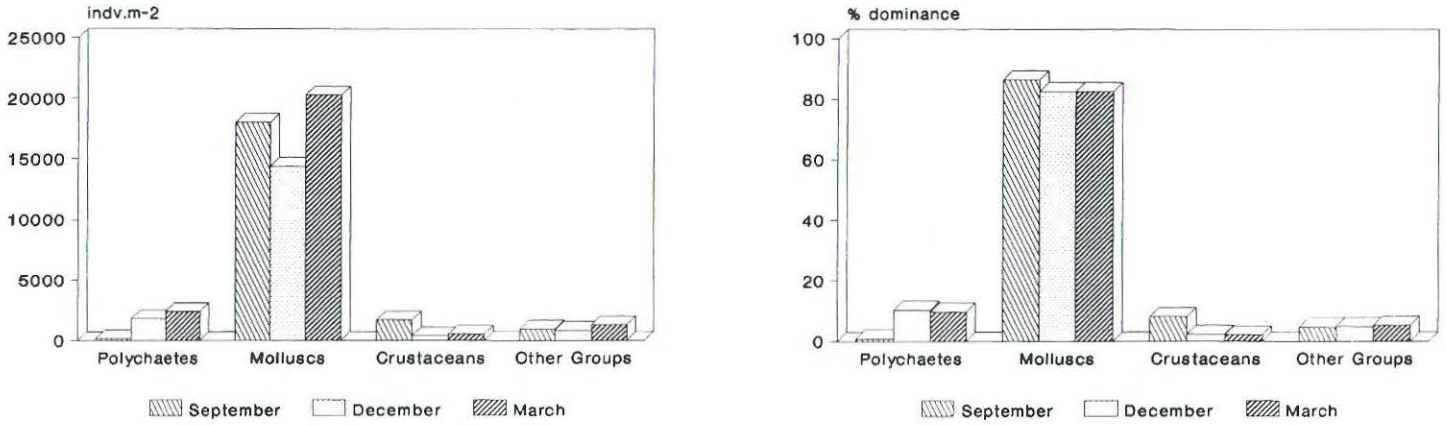

Fig. 6 : Abundance and dominance of polychaetes, crustaceans, molluscs and other groups in seagrass meadows of Ría de Foz during the sampling periods.

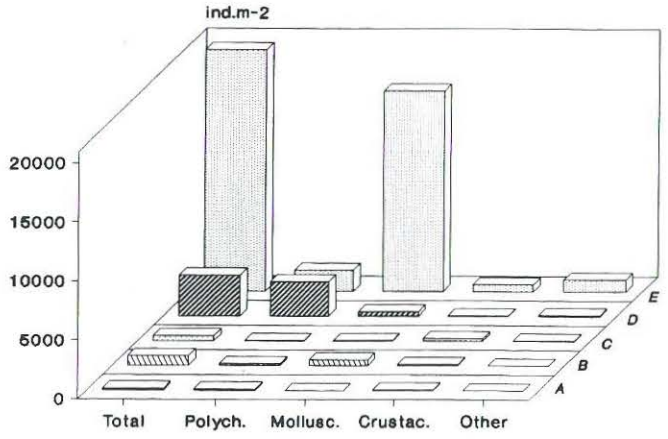

Fig. 7 : Mean density of macrofauna, polychaetes, crustaceans, molluscs and other groups in five habitats of Ría de Foz during all the study time. A : Beaches, B : Sublittoral sheltered sands, C : Midlittoral sheltered sands, D : Muddy sand flats, E : Seagrass meadows.

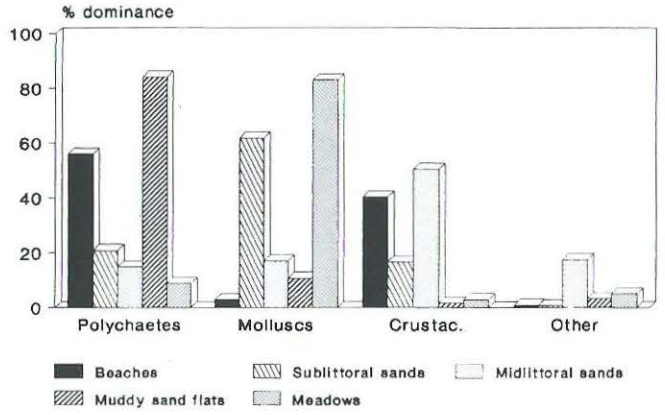

Fig. 8. Mean dominance of polychaetes, crustaceans, molluscs and other groups in five habitats of Ría de Foz during the whole study period.

Molluscs reached a density of 5 500 ind.m^{-2} (Sample 61), but no specimens were collected in two samples (Samples 32, 52). *Cerastoderma edule, Angulus tenuis* and *Peringia* (= *Hydrobia*) *ulvae* were the more abundant species. Polychaete density varied from 31 ind.m^{-2} (Sample 32) to 425 ind.m^{-2} (Sample 61), with *Nephtys cirrosa* and *Scolaricia typica* as more abundant species. Crustaceans exhibited a density of between 6 ind.m^{-2} (Sample 52) and 600 ind.m^{-2} (Sample 34), with two species of *Urothoe*, *U. brevicornis* and *U. poseidonis*, as the most abundant. As a consequence of these abundances, mollusc dominance varied from 42.9 % (December) to 75.16 % (June), polychaete dominance from 14.31 % (June) and 31.80 % (September) and crustacean dominance from 9.86 % (June) to 30.7 % (December).

Macrofaunal abundance varies from 25 ind.m^{-2} (Sample 11) to 1 106 ind.m^{-2} (Sample 87) in midlittoral sheltered sands. Although no crustaceans were collected in Sample 11, this group was the most abundant and reached a density of 825 ind.m^{-2} (Sample 87), with *Eurydice pulchra*, *Bathyporeia sarsi-pilosa* and *Haustorius arenarius* as the dominant species. Of the remainding macrofaunal species, *Cerastoderma edule* and *Ophelia bicornis* were especially notable for their abundance. Crustacean dominance varied between 28.8 % (September) and 70.5 % (March). Molluscs (32.08 %) and polychaetes (26.8 %) had their highest dominances during September and June respectively.

There was a notable increment in the macrofauna of the muddy sand flats, from 250 ind.m^{-2} (Sample 78) to 6 456 ind.m^{-2} (Sample 76). Polychaetes were the most abundant group, with densities of between 218 ind.m^{-2} (Sample 78) to 5 487 ind.m^{-2} (Sample 76). *Pygospio elegans*, *Capitella capitata*, *Spio martinensis-decoratus* and *Streblospio benedicti* were the most abundant species. Of the remaining macrofaunal species the density of *Scrobicularia plana* was particularly notable. Polychaetes comprised more than 69 % of the specimens in all the samples. Polychaete dominance varied from 80.2 % (March) to 97.1 % (September).

The highest macrofaunal density, from 14 462 ind.m^{-2} (Sample 86) to 29 062 ind.m^{-2} (Sample 98) occurred in seagrass meadowns. These abundances largely depended on the *Peringia ulvae* density, and mollusc density varied from 8 000 ind.m^{-2} (Sample 86) to 23 268 ind.m^{-2} (Sample 90). Other abundant species were the polychaetes *Capitella capitata* and *Pygospio elegans*, the amphipod *Melita palmata*, the isopod *Idotea chelipes* and indeterminate species of oligochaetes. Mollusc dominance was always more than 82 %.

Figure 7 shows the distribution of the mean density of polychaetes, molluscs, crustaceans and other groups and total macrofauna at the five habitats of the Ría de Foz during all the study period. Excluding the polychaetes, which showed the highest density in the muddy sand flats, the remaining groups showed their highest densities in the seagrass meadows. Mean macrofaunal density was 20 526 ind.m^{-2} at this habitat. Macrofaunal density was decreased from this region to the mouth of the ría, with a mean macrofaunal density of 3 499 ind.m^{-2} at muddy sand flats, 855 at sublittoral sheltered sands, 458 at midlittoral sheltered sands, and 192 ind.m^{-2} at beaches.

Polychaetes were dominant in muddy sand flats (84.14 %) and beaches (55.96 %), molluscs in seagrass meadows (83.07 %) and sublittoral sheltered sands (61.74 %) and crusta-

TABLE I

Species median density (D) and frequency (F) on samples of species collected at each habitat.

Species	Beaches		Sublitt. sh. sands		Midlitt. sh. sands		Muddy sand flats		Seagrass meadows	
	D ind.m^{-2}	F %	D ind.m^{-2}	F %	D ind.m^{-2}	F %	D ind.m^{-2}	F %	D ind.m^{-2}	F %
Cnidaria										
Actiinidae sp. A									3.1	12.5
Platyhelminthes										
Policladida sp A			0.2	3.2						
Nemertini										
Unidentified species	1.4	18.1	1.8	29.0	6.2	72.2	8.3	66.6	28.1	50.0
Annelida										
Scolaricia typica Eisig	39.7	50.0	34.2	77.4	9.7	50.0	3.4	22.2		
Paraonis fulgens (Levinsen)	10.2	45.4	1.4	19.3						
Malacoceros fuliginosus (Claparède)			0.8	3.2			11.1	33.3	2.3	37.5
Pygospio elegans Claparède			14.1	35.4	2.4	16.6	1731	100	431.2	62.5
Scolelepis mesnili (Bellan & Lagardère)	22.4	36.3	1.0	6.4						
Scolelepis squamata (Müller)	0.2	4.5	6.2	29.0	6.9	38.8	2.0	11.1		
Spio martinenesis-decoratus	0.8	13.6	13.1	64.5			268.7	77.7	0.7	12.5
Spiophanes bombyx (Claparède)			1.8	19.3						
Streblospio benedicti Webster			0.4	3.2			265.2	88.8	81.2	50.0
Magelona papillicornis Müller			0.6	6.4						
Poecilochaetus serpens Allen							1.0	11.1		
Dodecaceria concharum Oersted									0.7	12.5
Caulleriella sp.	0.5	4.5								
Capitella capitata (Fabricius)	3.1	13.6	7.0	16.1			295.8	88.8	912.5	62.5
Heteromastus filiformis (Claparède)			2.6	12.9	0.3	5.5	150.6	88.8	107.8	50.0
Mediomastus fragilis Rasmussen			0.4	3.2			4.8	22.2	21.0	25.0
Arenicola marina L.			2.4	16.1	0.3	5.5	5.5	66.6	29.6	37.5
Ophelia bicornis Savigny	1.7	18.1	3.8	9.6	39.5	61.1				
Ophelia neglecta Schneider	2.2	27.2			2.4	5.5				
Ophelia rathkei McIntosh			2.6	3.2	0.3	5.5				
Anaitides mucosa (Oersted)			1.0	12.9			10.4	55.5		
Eteone foliosa Quatrefages	1.4	18.1	0.8	6.4						

Eteone longa-flava			3.8	32.2			55.5	88.8	17.9	25.0
Mysta picta Quatrefages			0.8	12.9	0.3	5.5	4.8	33.3	11.7	25.0
Microphthalmus pseudoaberrans Campoy & Viéitez			0.2	3.2						
Hediste diversicolor (Müller)			0.2	3.2			75.0	77.7	131.2	75.0
Glycera alba Rathke	2.8	22.7	0.4	6.4			6.2	22.2		
Glycera tridactyla (Keferstein)			0.2	3.2			18.0	77.7	30.4	37.5
Nephtys cirrosa Ehlers	21.8	95.4	77.6	93.5	5.5	22.2	1.0	11.1		
Nephtys hombergi Savigny							30.5	88.8	1.5	12.5
Diopatra neapolitana delle Chiaje			0.2	3.2						
Lumbrineris impatiens (Claparède)	0.5	9.0	0.2	3.2						
Owenia fusiformis delle Chiaje			0.2	3.2						
Alkmaria romijni Horst							28.1	25.0		
Fabricia sabella (Ehrenberg)							0.7	12.5		
Manayunkia aestuarina (Bourne)							1.5	12.5		
Oligochaeta sp.							102.7	77.7	894.5	87.5
Mollusca										
Loripes lucinalis (Lamarck)					1.0	11.1				
Mysella bidentata (Montagu)			1.0	5.5						
Cerastoderma edule (L.)	0.5	4.5	250.2	90.3	64.2	72.2	60.4	88.8	92.1	75.0
Venerupis decussata (L.)					1.0	11.1			0.7	12.5
Donax vittatus (da Costa)	1.4	13.6			0.3	5.5				
Angulus tenuis (da Costa)	2.2	22.7	142.7	70.9	5.2	11.1	14.5	33.3		
Scrobicularia plana (da Costa)			0.6	3.2	0.3	5.5	252.7	88.8	143.7	87.5
Gibbula umbilicalis (da Costa)			0.2	3.2						
Littorina littorea (L.)									2.3	37.5
Littorina obtusata (L.)									32.8	62.5
Peringia ulvae (Pennant)	1.4	22.7	134.6	54.8	6.5	38.8	51.3	88.8	16780	100
Crustacea										
Callianassa cf. *thyrrena* (Petagna)							0.6	11.1		
Upogebia pusilla (Petagna)									0.7	12.5
Carcinus maenas (L.)	0.5	9.0	0.2	3.2			2.7	44.4	28.1	100
Portumnus latipes (Pennant)	0.2	4.5								
Crangon crangon (L.)	0.5	9.0	0.6	9.6			0.6	11.1		
Paragnathia formica (Hesse)			0.4	6.4	0.3	5.5			75.0	25.0
Cyathura carinata (Kröyer)			1.8	3.2	0.6	11.1	46.5	66.6	16.4	62.5

Eurydice pulchra Leach	2.2	22.7	13.5	22.5	142.0	94.4				
Dynamene bidentata (Adams)	0.2	4.5								
Sphaeroma rugicuda-monodi	11.0	31.8	0.6	9.6					0.7	12.5
Idotea chelipes (Pallas)			0.6	9.6			2.0	11.1	208.5	62.5
Idotea sp.	3.1	13.6	0.2	3.2						
Astacilla longicornis (Sowerby)			0.2	3.2						
Ione thoracica Montagu					1.0	11.1				
Bathyporeia pelagica (Bate)	10.7	36.3	0.2	3.2	0.6	5.5				
Bathyporeia sarsi-pilosa			17.5	25.4	51.7	66.6				
Haustorius arenarius (Slabber)	3.9	31.8	1.8	16.1	33.6	33.3				
Urothoe brevicornis Bate	22.4	59.0	53.8	87.0	0.3	5.5				
Urothoe poseidonis Reibisch			45.1	51.6	1.0	11.1	1.0	22.2		
Melita palmata Montagu			0.6	3.2			1.0	11.1	240.6	50.0
Chaetogammarus marinus (Leach)									1.5	12.5
Hyale nilssoni (Rathke)									50.7	75.0
Pontocrates arenarius (Bate)	8.8	13.6								
Gastrosaccus spinifer (Goës)	4.2	9.0	0.4	6.4						
Gastrosaccus roscoffensis Bacescu	0.2	4.5								
Paramysis bacescoi Labat			0.3	5.5						
Paramysis nouveli Labat			2.6	19.3			1.0	11.1	2.3	25.0
Cumopsis goodsiri (van Beneden)	8.8	22.7	1.4	19.3	1.4	19.3				
Iphinoe cf. *tenella* Sars			0.2	3.2	0.3	5.5				
Insecta										
Chironomidae sp. (larvae)							1.0	22.2	55.4	37.5
Diptera sp. A (larvae)			0.4	6.4	19.9	50.0	5.5	66.6	78.1	75.0
Diptera sp. B (larvae)			1.6	3.2	12.5	16.1				
Coleoptera sp. A			1.2	6.4	29.1	44.4			0.7	12.5
Phytosus spinifer Curtis			0.2	3.2	12.8	22.2				
Chordata										
Ammodytes tobianus L.	0.2	4.5	0.6	6.4						

ceans in beaches (40.2 %) and midlittoral sheltered sands (50.41 %). Other groups showed their highest dominance in midlittoral sheltered sands (17.48 %) (Fig. 8).

Table II shows the number of species and diversity and evenness indices of the five habitats. The highest number of species was recorded on sublittoral sheltered sands whereas beaches and midlittoral sheltered sands had the lowest species number. Excepting seagrass

TABLE II

Number of species of polychaetes, crustaceans, molluscs, other groups and total ; Shannon-Wiener diversity (H') and Pielou's evenness (J') indices ranges and means in each habitat of the Ría de Foz.

		Beaches	Sublitt. sh. sands	Midlitt. sh. sands	Muddy sand flats	Seagrass meadows
Species number						
	Polychaeta	13	28	10	19	17
	Mollusca	4	5	7	5	6
	Crustacea	14	19	11	9	10
	Other	2	7	6	4	6
	Total	33	59	34	37	39
Diversity H'						
	Range	0.19-3.12	0.86-3.43	0.81-3.10	1.37-3.48	0.19-2.16
	Mean	2.14	2.37	2.11	2.48	0.95
Evenness J'						
	Range	0.02-0.82	0.17-0.57	0.25-0.53	0.16-0.65	0.02-0.19
	Mean	0.51	0.35	0.38	0.30	0.08

meadows, where the diversity is reduced, this index is similar in all habitats with the maximum in the more stable sediments of muddy sand flats. Evenness fluctuated widely, from 0.08 on seagrass meadows to 0.51 on beaches.

DISCUSSION

The five habitats recognised in the Ría de Foz allow a comparison of the influence of different environmental factors on the distribution and abundance of the intertidal macrofauna. Beaches and sublittoral sheltered sands had a different exposure rate to wave action whereas they possessed similar sediment characteristics. A major environmental difference between sublittoral and midlittoral sheltered sands was the tidal level. Muddy sand flats and seagrass meadows had more fine sediments and more organic matter content than the three other habitats. The presence of macrophytes and greater silt-clay and organic matter contents differ between muddy sands flats and seagrass meadows.

Exposure to wave action determines an impoverished macrofauna compared with more sheltered sites (Dexter, 1983, 1988 ; Eleftheriou & Nicholson, 1975). The macrofauna of the beaches of the Ría de Foz, compared with those of sublittoral sheltered sands, has lower macrofaunal density and lower number of species but a slightly lower diversity and higher evenness. The major faunistic difference observed between these two habitats is the increase in mollusc abundance and dominance with increasing shelter, as observed in Scottish beaches (Eleftheriou & McIntyre, 1976). Other faunistic differences are the increase of populations of *Nephtys cirrosa* and *Urothoe brevicornis* on sublittoral sheltered sands, whereas *Paraonis fulgens*, species associated with exposed areas (Rasmussen, 1973, Castelli,

1985), and *Scolelepis mesnili* are more abundant and frequent on beaches. *Bathyporeia pelagica* is replaced in sub- and midlittoral sheltered sands by *B. sarsi-pilosa*, and *U. poseidonis* is missing from beaches.

The number of species and macrofaunal densities decrease as expected (McLachlan, 1977 ; Dexter, 1983, 1988) from sublittoral to midlittoral sheltered sands. The cirolanid isopod *Eurydice pulchra* and the haustoriid amphipod *Haustorius arenarius*, characteristic of the high tide zone on sandy beaches (Dahl, 1952 ; Faure, 1972, Dexter, 1983, 1988, 1989, Viéitez & Baz, 1988), have their highest densities and achieve high abundance and dominance of crustaceans on midlittoral sheltered sands. Two polychaete species, *Ophelia bicornis* and *Scolelepis squamata*, frequently recorded from high tidal level (Faure, 1972 ; López-Cotelo *et al.*, 1982 ; Harris, 1991), have their higher populations at this level where *Scolelepis mesnili* is missing, in accordance with the tidal segregation described by Bellan & Lagardère (1971). There are some populations of insects that, together with nemerteans, achieve an increase in the abundance and dominance of other groups compared with beaches and sublittoral sheltered sands.

Macrofaunal density on muddy sand flats is approximately four times greater than in the sublittoral sheltered sands, but there is a reduction in species number. This enhancement is principally caused by populations of spionid and capitellid polychaete species that live in both habitats and reach higher densities in sediments which are organically richer, namely ; *Pygospio elegans*, *Spio martinensis-decoratus*, *Streblospio benedicti*, *Capitella capitata* and *Heteromastus filiformis*. As noted by other authors (e.g. Clark & Haderlie, 1960 ; Clark *et al.*, 1962 ; Amoureux, 1968 ; Lagardère, 1972 ; López Cotelo *et al.*, 1982) *Nephtys hombergi* replaces *N. cirrosa* in the finer sediments. Crustacean populations have their minimum abundances, except for *Cyathura carinata*, a brackish-water species that needs stable substrates (Olafsson & Persson, 1986). Amongst the molluscs, *Scrobicularia plana* is the most abundant species. The enhancement of polychaetes, together with a decrease of crustaceans, has been described as associated with organic enrichment (Pearson & Rosenberg, 1978 ; Dauer & Conner, 1980).

On seagrass meadows there are extensive populations of the mud-snail *Peringia ulvae*. These populations achieve the highest macrofaunal density of the whole study area. According to Wolff (1973) this gastropod has high densities in sheltered areas with little water movement and less sediment instabiliy. The numbers of *P. ulvae* resulted in the lowest values of diversity and evenness of all the study area. There is a general decrease in polychaete populations that live on muddy sand flats, except those of *Capitella capitata* and *Hediste diversicolor*. This probably indicates that the amount of organic enrichment decreases oxygen concentrations to levels detrimental to more sensitive species whereas *C. capitata*, a species frequently cited as an indicator of organically polluted sediments (e.g. Reish, 1957 ; Grassle & Grassle, 1974) reaches its highest density. *H. diversicolor* has the highest density in *Spartina* patches, as observed by Jackson *et al.* (1985). Unlike the bare sediments of muddy sand flats, crustaceans have here their highest density, with *Idotea chelipes* and *Melita palmata* as the more abundant species. The oligochaetes, chironomids and larvae of Diptera (sp. A) are also more abundant and achieve the highest density of other groups.

CONCLUSIONS

The five habitats recognised in the Ría de Foz showed a different macrofauna abundance and composition. Exposure to wave action determined a general paucity of the macrofauna in the beaches, whereas number of species, macrofauna density and mollusc populations increased with the more protected condition of the sublittoral sheltered sands. Peracarid crustaceans, variously represented on the beaches and sublittoral sheltered sands, dominated the midlittoral sheltered sands. There was a notable increment of the macrofauna in the finer sediments of the inner Ría, with the polychaetes achieving their highest populations in the muddy sand flats. Comparing *Zostera* beds with bare sediments, it was found that the abundance of macrofauna was higher in seagrass meadows where *Peringia ulvae* had extensive populations.

Resumen : Se estudia la abundancia y la dominancia de cuatro grandes grupos taxonómicos (poliquetos, moluscos, crustáceos y otros grupos) de la macrofauna intermareal de sustrato blando en la Ría de Foz (Lugo, NW España). En esta ría pueden distinguirse cinco grandes hábitats, caracterizados por la naturaleza de sus sedimentos, el nivel mareal, el grado de exposición y la presencia o no de praderas de fanerógamas. La abundancia de la macrofauna se incrementa hacia el interior de la ría. En los sedimentos arenosos, la abundancia de la macrofauna depende principalmente del grado de exposición y del nivel mareal. En las playas expuestas de la boca de la ría, la densidad media es de 192 ejemplares.m^{-2}, siendo los poliquetos y los crustáceos los grupos dominantes. En la zona sublitoral de las áreas más resguardadas se incrementa la densidad de la macrofauna (855 ejemplares.m^{-2}), así como la importancia cuantitativa de los moluscos. En la zona mediolitoral de las áreas arenosas resguardadas la densidad media de la macrofauna es de 458 ejemplares.m^{-2}, siendo los crustáceos el grupo dominante. En los fondos de arenas fangosas, la densidad de la macrofauna es de 3 499 ejemplares.m^{-2} ; en estos lugares, los poliquetos alcanzan sus máximas abundancias. En las praderas de *Zostera noltii* del interior de la ría hay una abundante población del gasterópodo *Peringia ulvae*, y una densidad media de la macrofauna de 20.526 ejemplares.m^{-2}.

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