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Macrozoobenthic community structure in the Ría de Foz, an intertidal estuary (Galicia, Northwest Spain)

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Abstract. The community structure of the macrobenthic (> 1 mm) fauna of an intertidal soft-bottom estuary, the Ría de Foz (Galicia, Northwest Spain) was investigated on 99 occasions during June, September and December 1984 and March 1985. The infaunal data were subjected to classification and ordination techniques. The analyses indicated that sediment characteristics (grain size, percentage silt-clay and organic-matter content) and tidal height are the most important factors governing the distribution and abundance of the intertidal communities. Three faunal assemblages were identified and examined in terms of species dominance, constancy and fidelity. In the clean sands of the outer estuary two main assemblages were distinguished; one, corresponding to the "boreal Lusitanian *Tellina* community", inhabited the middle and lower tidal levels; the other, typical of a biocoenosis of sands and slightly muddy mediolittoral sands, inhabited the upper tidal level. The third benthic assemblage occupied the muddy sands and mud of the inner estuary and displayed some features in common with the *Cardium edule-Scrobicularia* community described by Thorson.

Introduction

Although many studies have been made of commercially important benthic animals in the Galician rías (estuaries), the intertidal soft-bottom macrozoobenthos have, in general, been neglected by benthic researchers, and only during the last 15 yr have surveys of selected areas been carried out (Viéitez 1976, 1981, Anadón 1980, Viéitez and López Cotelo 1982, Penas and González 1983, Planas et al. 1984, Planas and Mora 1984a, b, Laborda 1986, López Serrano and Viéitez 1987, Viéitez and Baz 1988). No previous study has been made in the Ría de Foz (Galicia, Northwest Spain) and only a few investigators have sampled particular groups in the area (Van Maren 1975 and Acuña and Mora 1979, amphipods; Martínez-Ansemil 1984, oligochaetes), involving a total of nine species.

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 2800 m upstream. The whole ria is subjected to regular tidal fluctuation, and most of its bottom is situated at the intertidal level. Although receiving the outflow from the Masma River and two streamlets, 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.

Baseline studies in the top 15 cm layers of the sediment have been presented in another paper (Junoy and Viéitez 1989).

The present paper describes the soft-bottom intertidal macrozoobenthos, identifies a number of faunal assemblages on the basis of classification, ordination and statistical analysis, and considers the relationships between the distributional pattern of these assemblages and certain environmental factors. This study was undertaken previous to dredging and breakwater construction, in 1986, which have considerably affected the mouth of the ría by creating a new beach on the eastern border of the mouth.

Materials and methods

Sample collection and processing

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. A total of 99 samples was taken over June, September, and December 1984 and March 1985 at 41 intertidal stations. Fig. 1 shows the spatial and temporal distribution of the samples.

On each sampling occasion, sediment was removed from quadrats measuring 40 × 40 cm to a depth of 30 cm, sieved (1 mm),

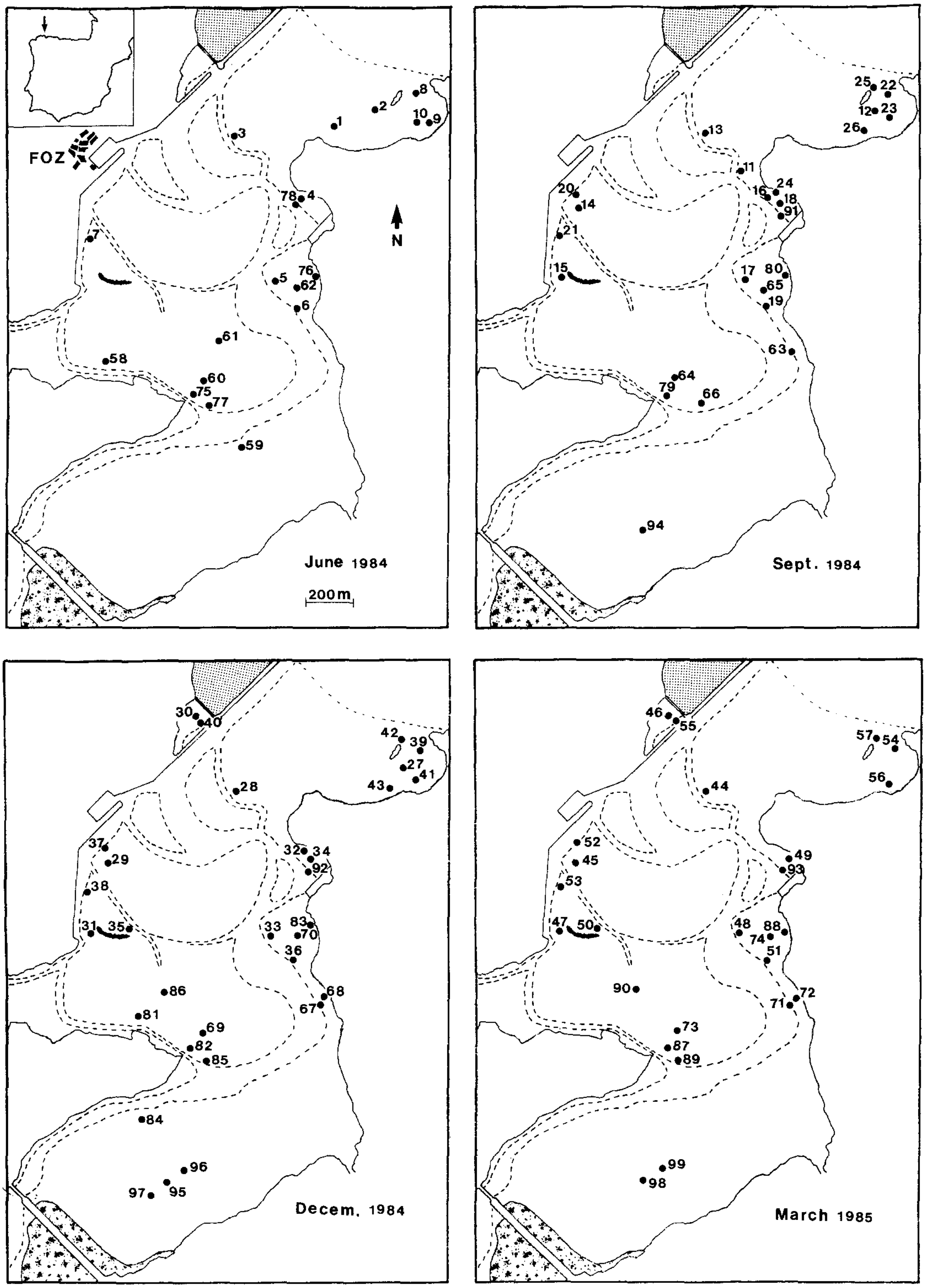

Fig. 1. Location of 99 samples taken in the Ría de Foz, Northwest Spain; inset shows coastline of Iberian Peninsula. Mouth of estuary is to the north, at the top of the maps. Sedimentary types were: Samples 1 to 57, medium sand; Samples 58 to 75, fine sand; Samples 76 to 90, muddy fine sand; Samples 91 to 99, mud

and preserved (10% formaldehyde in sea water). In the laboratory, faunal samples were sorted, enumerated and identified to species level whenever possible. Much doubt remained as to the correct identification of four species which displayed taxonomic characteristics intermediate between two other species, and these are here referred to as *Spio martinensis-decoratus, Eteone longa-flava, Sphaeroma rugicauda-monodi* and *Bathyporeia sarsi-pilosa.*

Data analysis

Data were first organized into a samples × species matrix. Species diversity and evenness were measured with the Shannon-Wiener function, H', and Pielou's evenness index, J', respectively (Shannon and Weaver 1963, Pielou 1966).

To reveal possible sample and species groupings, the data were subjected to numerical classification and ordination. Groups of similar samples (normal analysis) and similar species (inverse analysis) were produced by cluster analysis using the BMDP computer package. In both cluster analyses, the measure of similarity was the degree of correlation and the criterion for combining two clusters was the average similarity (Dixon 1983). Affinity assemblages were established among samples and among species and between samples and species using correspondence analysis. All raw data were transformed by $x = \log(x+1)$. Data treatment was by progressive omission of less important (in terms of dominance and/or frequency) species. Spearman's rank correlation coefficients were calculated between sample coordinates and the environmental parameters measured at sampling.

Species dominance, constancy (Dajoz 1971) and fidelity (Prenant 1927) were calculated for each classification group (sample group). Species which comprised >1% by number of the total specimens collected in any particular sample group were termed "dominant" for that sample group (Soyer 1970). Species present in more than half the samples in a sample group were termed "common"; those common species having a fidelity of more than 50% in a particular sample group were termed "characteristic" for that sample group. Exclusive species were only found among the samples from one sample group (fidelity = 100%).

Results

Faunal analysis, species diversity and abundance

The 99 samples analyzed yielded 39 457 individuals belonging to 93 species (considering nemerteans, oligochaetes and chironomids as one species each) of which polychaetes, crustaceans and molluscs together comprised 95.2% of the total individuals and 89.2% of the species (Table 1). One species, the gastropod *Peringia ulvae,* accounted for 57.1% of the total individuals collected. This species was present over the whole area, with its highest densities (>23 000 individuals m^{-2}) in mud sediments.

Of the 93 species, 35 were taken only occasionally, 39 occurred at a frequency of >10% (sampled in 10 or more samples), and 20 at a frequency of >20%. The 29 species considered in the multifactorial analysis comprised 90.0% of the total number of individuals. This indicates that only a small group of species determine the characteristics of the population (dominance, total abundance). This is a general feature of intertidal macrozoofauna.

Shannon-Wiener diversity-index values ranged from 3.48 (Sample 78) to 0.19 (Samples 2 and 96) and faunal evenness from 0.02 (Sample 96) to 0.82 (Sample 23). These two community parameters were positively correlated ($r = 0.60$; $p < 0.001$). Diversity displayed a significant negative correlation with the percentage of silt-clay in the sediment, and was negatively correlated with organic-matter content. Evenness exhibited significant positive correlations with median grain size and water oxygenation, and negative correlations with silt-clay content, and to a lesser degree, with organic-matter content and tidal level (Table 2).

The lowest population density was recorded for Sample 27, with 18 individuals m^{-2}; and the highest density for Sample 98, with 29·000 individuals m^{-2}. Mean densities were 190 m^{-2} in exposed sandy beaches at the mouth of the ria, 700 to 800 m^{-2} in sandy sites, 3 100 m^{-2} in muddy sand sites in more sheltered areas in the middle of the ría, and, 20 000 m^{-2} in the seagrass meadows of the inner ría. Population density displayed significant positive correlations with silt-clay and organic-matter content and negative correlations with median grain size and water oxygenation (Table 2). This explains the general increase in abundance towards the inner part of the ría, and lower abundancy in more exposed areas.

Table 1. Total number of individuals and species and percentage of total comprised by polychaetes, crustaceans, molluscs, and other groups sampled in Ría de Foz

Taxa	Individuals		Species	
	n	%	*n*	%
Polychaeta	9 419	23.8	40	43.0
Crustacea	2 590	6.5	31	33.3
Mollusca	25 647	64.9	12	12.9
Other groups	1 801	4.5	10	10.7
Total	39 457	100	93	100

Community structure

Fig. 2 classifies the samples into three groups, based on the dominance of 93 species. Samples in close proximity to each other in Fig. 2 cluster with each other, depending on sediment type, tidal level and geographical location. Three main sample groups can be distinguished. The largest main cluster is formed by 42 samples located in clean sand in the seaward part of the ría (Sample Group A), at the sublittoral level; a second main cluster by 29 samples taken in clean sand at the midlittoral level (Sample Group B); and a third main cluster by 26 samples which, with a few exceptions, were taken in sediments with >5% silt-clay content in the inner part of the ría (Sample Group C). Samples 57 and 91 had little similarity with any of the groups. Species dominance, constancy and fidelity to these three main sample groups are shown in Table 3.

Species groups resulting from inverse analysis are shown in Fig. 3. Species Groups A, B and C displayed their highest abundance and dominance in Sample

Table 2. Spearman's rank correlations between ordination axes and community index, and environmental variables in Ría de Foz. H': Shannon-Wiener diversity index; J': Pielou's evenness index. ***: $0.01 < p < 0.001$; **: $0.05 < p < 0.01$; *: $p < 0.05$; NS: not significant

Environmental variable	H'	J'	Density	Axis I	Axis II
Median grain size	0.19^{NS}	0.49^{***}	-0.67^{***}	0.68^{***}	-0.16^{NS}
Silt-clay	-0.40^{***}	-0.44^{***}	0.77^{***}	-0.59^{***}	-0.00^{NS}
Organic matter	-0.34^{**}	-0.31^{**}	0.67^{***}	-0.55^{***}	-0.03^{NS}
Tidal level	-0.25^{*}	-0.29^{**}	0.33^{***}	-0.33^{***}	0.70^{***}
Water oxygenation	0.15^{NS}	0.44^{***}	-0.45^{***}	0.55^{***}	0.05^{NS}
Salinity	-0.30^{*}	-0.03^{NS}	0.13^{NS}	0.13^{NS}	-0.38^{**}

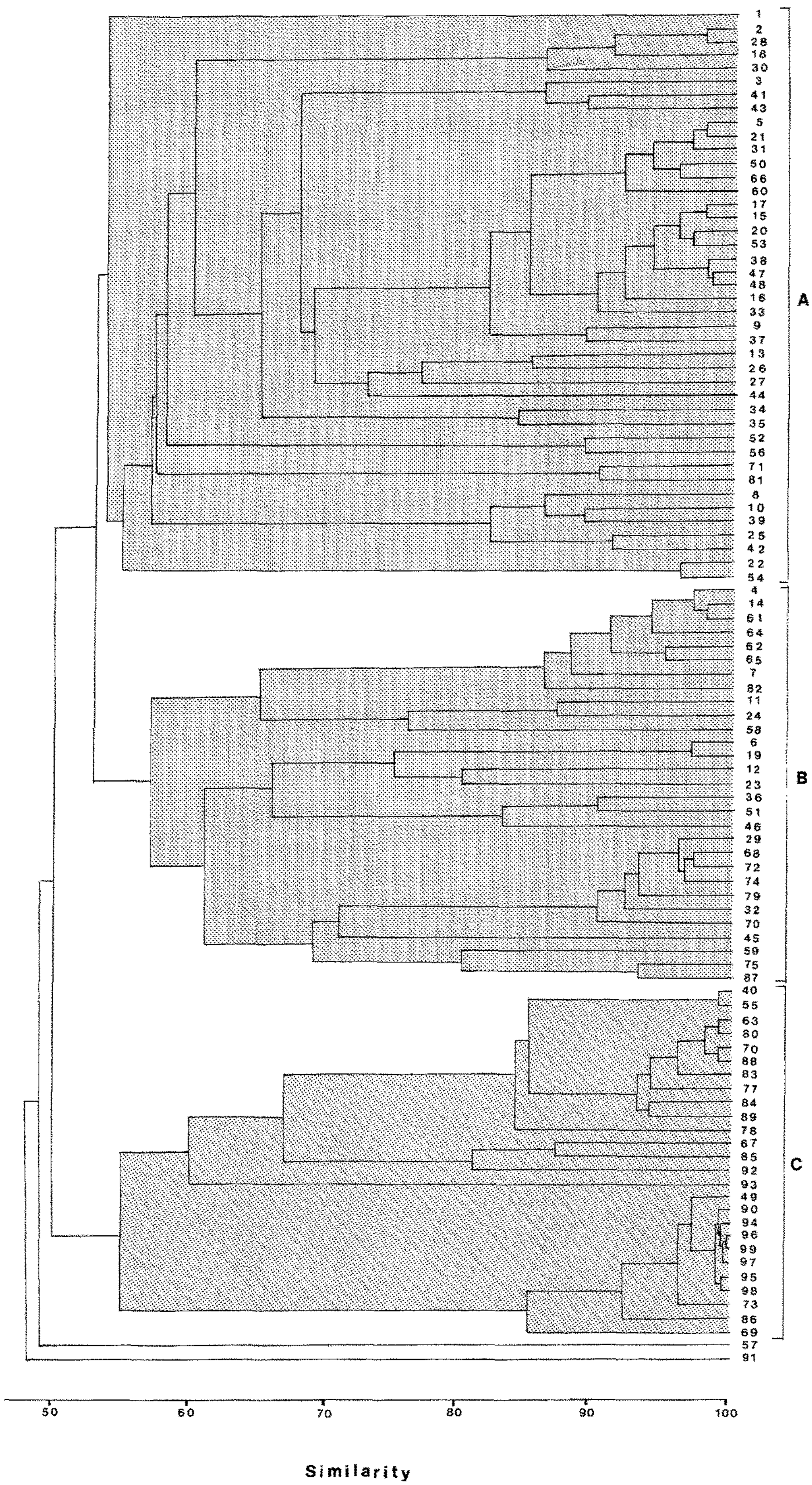

Fig. 2. Normal-cluster dendrogram of benthic samples showing three main sample groups

Groups A, B, and C, respectively. Species Group D consisted of less-frequently occurring species.

The percentage of inertia explained by Axes 1 and 2 of the first eigenvalues of the correspondence analysis suggested that the most satisfactory treatment of the data would be obtained using 29 dominant species of the main sample groups (marked with asterisks in Table 3). Of these species, 17 occurred with a frequency >20%, 11 with a frequency >10%, and only one with a frequency <10%, in the total samples.

Fig. 3. Inverse-cluster dendrogram showing four species groups emerging from classification. Code letters as in Table 3

The coordinates of the first two axes, together accounting for 32.3% of the total variance, are plotted in Fig. 4. The results agree with those obtained by cluster analysis insofar as the biological data set divides into three main groups. Axis I (17.6% of total variance) was significantly correlated with the sediment parameters (median particle size, silt-clay and organic-matter content) and with the water oxygenation, while Axis II (14.7% of total variance) was significantly correlated with tidal level (Table 2).

The various techniques used to examine community structure at Ría de Foz all revealed a similar pattern. The results suggest the presence of three distinct benthic assemblages, illustrated in Fig. 5, and characterized as follows:

Table 3. Species dominance (dom.), constancy (con.) and fidelity (fid.) in each sample group. Code letters for each species are used in Figs. 3 and 4. Asterisks indicate species used for correspondence analysis . *Dynamene bidentata* and *Gastrosaccus roscoffensis* were collected only in Samples 57 and 91, respectively, two samples which had little similarity with any of the sample groups

Species	Code	Sample Group A			Sample Group B			Sample Group C		
		dom.	con.	fid.	dom.	con.	fid.	dom.	con.	fid.
Cnidaria										
Actiinidae sp. A	ACTSP							0.0	3.8	100
Platyhelmia										
Policladida sp. A	POLIC	0.0	2.3	100						
Nemertini										
Several unidentified species	NEMER	0.5	21.4	15.5	0.7	58.6	42.5	0.1	57.6	41.8
Annelida										
*Scolaricia typica**	SCOLA	15.0	61.9	41.0	2.7	62.0	41.1	0.2	26.9	17.8
*Paraonis fulgens**	PFULG	1.6	35.7	100						
*Malacoceros fuliginosus**	MFULI	3.5	7.1	18.8				0.0	30.7	81.1
Malacoceros tetracerus	MTETR	0.1	2.3	40.8	0.2	3.4	59.1			
Prionospio multibranchiata	PRMUL							0.0	3.8	100
*Pygosio elegans**	PELEC	0.9	14.2	10.9	1.8	27.5	21.1	10.9	88.4	67.8
*Scolelepis mesnili**	SMESN	3.6	23.8	86.0				0.0	3.8	13.9
*Scolelepis squamata**	SQUAM	1.0	9.5	14.3	1.7	41.3	62.4	0.0	15.3	23.2
*Spio martinensis-decoratus**	SPIOM	4.1	40.4	36.2	0.4	17.2	15.4	1.2	53.8	48.2
Spiophanes bombyx	SBOMB	0.0	2.3	11.6	0.1	10.3	50.6	0.0	7.6	37.6
*Streblospio benedicti**	STREB	0.2	2.3	3.9	0.0	3.4	5.7	1.9	53.8	90.2
Magelona papillicornis	MAPAP	0.1	2.3	40.8	0.0	3.4	59.1			
Magelona sp.	MAGSP							0.0	3.8	100
Poecilochaetus serpens	POECI							0.0	3.8	100
Dodecaceria concharum	DODEC							0.0	3.8	100
Caulleriella sp.	CAULL	0.1	2.3	100						
*Capitella capitata**	CAPIT	3.1	16.6	18.7	0.0	6.9	7.7	4.7	65.3	73.5
*Heteromastus filiformis**	HETER	0.2	4.7	6.5	0.0	6.9	9.4	1.1	61.5	84.0
Mediomastus fragillis	MEDIO				0.0	3.4	15.2	0.1	19.2	84.8
Arenicola marina	ARENM	0.4	9.5	14.4	0.1	10.3	15.6	0.1	46.1	69.9
*Ophelia bicornis**	OPBIC	0.1	7.1	12.3	4.1	51.7	87.8			
Ophelia neglecta	OPNEG	0.3	14.2	80.5	0.2	3.4	19.4			
Ophelia rathkei	OPRAT				0.4	6.9	100			
Anaitides mucosa	ANAIT	0.0	2.3	5.8	0.0	3.4	8.5	0.0	34.6	85.5
Eteone foliosa	ETFOL	0.3	11.9	100						
Eteone longa-flava	ETLON	0.6	16.6	19.7	0.1	13.7	16.3	0.4	53.8	63.8
Mysta picta	MYSTA	0.1	7.1	19.4	0.0	10.3	28.1	0.0	19.2	52.3
Microphthalmus pseudoaberrans	MICRO	0.0	2.3	100						
Hediste diversicolor	HEDIS	0.9	4.7	6.8	0.2	6.9	9.9	0.8	57.6	83.1
Glycera alba	GALBA	0.4	11.9	30.6				0.1	26.9	69.3
Glycera tridactyla	GTRID	0.0	2.3	5.3				0.2	42.3	94.6
*Nephtys cirrosa**	NCIRR	14.7	90.4	55.7	2.6	44.8	27.6	0.2	26.9	16.6
Nephtys hombergi	NHOMB	0.3	2.3	5.8				0.1	38.4	94.1
Diopatra neapolitana	DIOPA	0.0	2.3	100						
Lumbrineris impatiens	LUMBR	0.1	7.4	100						
Owenia fusiformis	OWENI							0.0	3.8	100
Alkmaria romijni	ALKRO							0.1	7.6	100
Lanice conchilega	LANIC							0.0	3.8	100
Fabricia sabella	FABRI							0.0	3.8	100
Manayunkia aestuarina	MANAY							0.0	3.8	100
Oligochaeta sp.*	OLIGO				0.0	3.4	5.0	3.8	65.3	94.9
Mollusca										
Loripes lucinalis	LOLUC							0.0	3.8	100
Mysella bidentata	MYSEL				0.0	3.4	100			
*Cerastoderma edule**	CEDUL	2.1	35.7	20.0	35.0	68.9	38.8	1.4	73.0	41.1
Venerupis decussata	VENER				0.0	3.4	47.2	0.0	3.8	52.7
Donax vittatus	DVITA	0.1	4.7	58.0	0.0	3.4	42.0			
Donax trunculus	DTRUN				0.0	3.4	100			
*Angulus tenuis**	ANGUL	17.3	64.2	49.3	6.9	27.5	21.1	0.4	38.4	29.5
*Scrobicularia plana**	SCROB	0.2	4.7	5.8	0.1	6.9	8.5	1.6	69.2	85.5
Gibbula umbilicalis	GIBUL	0.0	2.3	100						
Littorina littorea	LLITO							0.0	7.6	100
Littorina obtusata	LOBTU							0.1	19.2	100
*Peringia ulvae**	PERIN	1.0	35.7	21.6	3.9	44.8	27.1	66.2	84.6	51.2

Table 3 (continued)

Species	Code	Sample Group A			Sample Group B			Sample Group C		
		dom.	con.	fid.	dom.	con.	fid.	dom.	con.	fid.
Crustacea										
Callianassa cf. *thyrrena*	CALLI							0.0	3.8	100
Upogebia pusilla	UPOGE							0.0	3.8	100
Carcinus maenas	CARCI	0.1	7.1	11.7				0.1	53.8	88.2
Portumnus latipes	PORTU				0.0	3.4	100			
Crangon crangon	CRAGO	0.1	7.1	39.9	0.0	6.9	38.5	0.0	3.8	21.5
Paragnathia formica	PARAG	0.1	4.7	29.9	0.0	3.4	21.6	0.2	7.6	48.3
Cyathura carinata	CYATH	0.0	2.3	4.0	0.3	10.3	17.5	0.2	46.1	78.3
*Eurydice pulchra**	EURYD	0.5	14.2	14.0	14.4	75.8	74.6	0.0	11.5	11.3
Dynamene bidentata	DYNAM									
*Sphaeroma rugicauda-monodi**	SPHAE	1.7	16.6	59.9	0.0	3.4	12.4	0.0	7.6	27.6
Idotea chelipes	IDOCH	0.1	4.7	15.2	0.0	3.4	11.0	0.8	23.0	73.7
Idotea sp.	IDOSP	0.5	7.1	67.4	0.0	3.4	32.5			
Astacilla longicornis	ASTAC	0.0	2.3	100						
Ione thoracica	IONET							0.0	3.8	100
*Bathyporeia pelagica**	BPELA	1.7	21.4	86.1	0.0	3.4	13.8			
*Bathyporeia sarsi-pilosa**	BSARS	0.8	11.9	13.3	6.4	62.0	69.4	0.0	15.3	17.2
*Haustorius arenarius**	HAUST	0.8	21.4	38.3	4.0	34.4	61.6			
*Urothoe brevicornis**	UBREV	11.4	73.8	65.3	2.2	27.5	24.4	0.0	11.5	10.2
*Urothoe poseidonis**	UPOSE	5.4	21.4	29.5	2.4	24.1	33.3	0.0	26.9	37.1
Melita palmata	MELIT	0.0	2.3	13.4				0.9	15.3	86.6
Chaetogammarus marinus	CHAET							0.0	3.8	100
Corophium volutator	CVOLU							0.0	7.6	100
Corophium multisetosum	CMULT				0.0	3.4	100			
Hyale nilssoni	HYALE							0.1	23.0	100
Pontocrates arenarius	PONTO	0.6	4.7	100						
Gastrosaccus spinifer	GSPIN	0.6	4.7	58.0	0.0	3.4	4.2			
Gastrosaccus roscoffensis	GSROS									
Paramysis bacescoi	PABAC				0.0	3.4	100			
Paramysis nouveli	PANOU	0.3	4.7	15.6	0.1	10.3	33.9	0.0	15.3	50.4
*Cumopsis goodsiri**	CUMOP	1.6	23.8	100						
Iphinoe cf. *tenella*	IPHIN				0.0	6.9	100			
Insecta										
Chironomidae sp. (larvae)	QUIRO							0.2	23.0	100
Diptera sp. A (larvae)*	LDIPA	0.0	2.3	2.8	1.8	34.4	41.5	0.3	46.1	55.6
Diptera sp. B (larvae)*	LDIPB				1.1	37.9	100			
Coleoptera sp. A*	COLEO	0.0	2.3	6.3	2.7	31.0	83.2	0.0	3.8	10.3
*Phytosus spinifer**	PHYTO				1.1	20.6	100			
Chordata										
Ammodytes tobianus	AMMOD	0.2	7.1	100						

Group A. Marine assemblage located in the sublittoral zone in medium and fine sands with low organic-matter content. It was represented by 42 samples taken from the beaches and sandbanks of the outer ría. From these samples, a total of 59 species were collected: 29 polychaetes, 19 crustaceans, 6 molluscs and 5 "others". The number of species varied from 14 (Samples 30, 42 and 71) to 2 (Samples 2, 27). Common species were the polychaetes *Scolaricia typica* and *Nephtys cirrosa*, the bivalve *Angulus tenuis*, and the amphipod *Urothoe brevicornis*. *N. cirrosa* and *U. brevicornis* were characteristic for Group A. All the common species were dominant and comprised 58.4% of the total specimens collected in this assemblage. Other infaunal dominants were the polychaetes *Paraonis fulgens*, *Malacoceros fuliginosus*, *Scolelepis mesnili*, *S. squamata*, *Spio martinensis-decoratus* and *Capitella capitata*, the molluscs *Cerastoderma edule* and *Peringia ulvae*, and the crustaceans *Sphaeroma rugicauda-monodi*, *Bathyporeia pelagica*, *Urothoe poseidonis* and *Cumopsis goodsiri*. Of these species, *Paraonis fulgens* and *Cumopsis goodsiri* were collected only in samples of this assemblage and are thus exclusive species. Diversity ranged from 0.19 (Sample 2) to 3.12 (Sample 43); evenness varied from 0.04 (Sample 2) to 0.72 (Sample 10).

Group B. This assemblage was represented by 29 samples located in the midlittoral zone with sediment characteristics similar to those of Group A. The number of species varied from 17 (Samples 58, 64) to 2 (Sample 11), with a total of 52 species collected: 20 polychaetes, 18 crustaceans, 8 molluscs and 6 "others". Characteristic species for this assemblage were the polychaete *Ophelia bicornis* and the crustaceans *Eurydice pulchra* and *Bathyporeia sarsi-pilosa*. Other common species were the polychaete *Scolaricia typica*, the bivalve *Cerastoderma edule*, and the

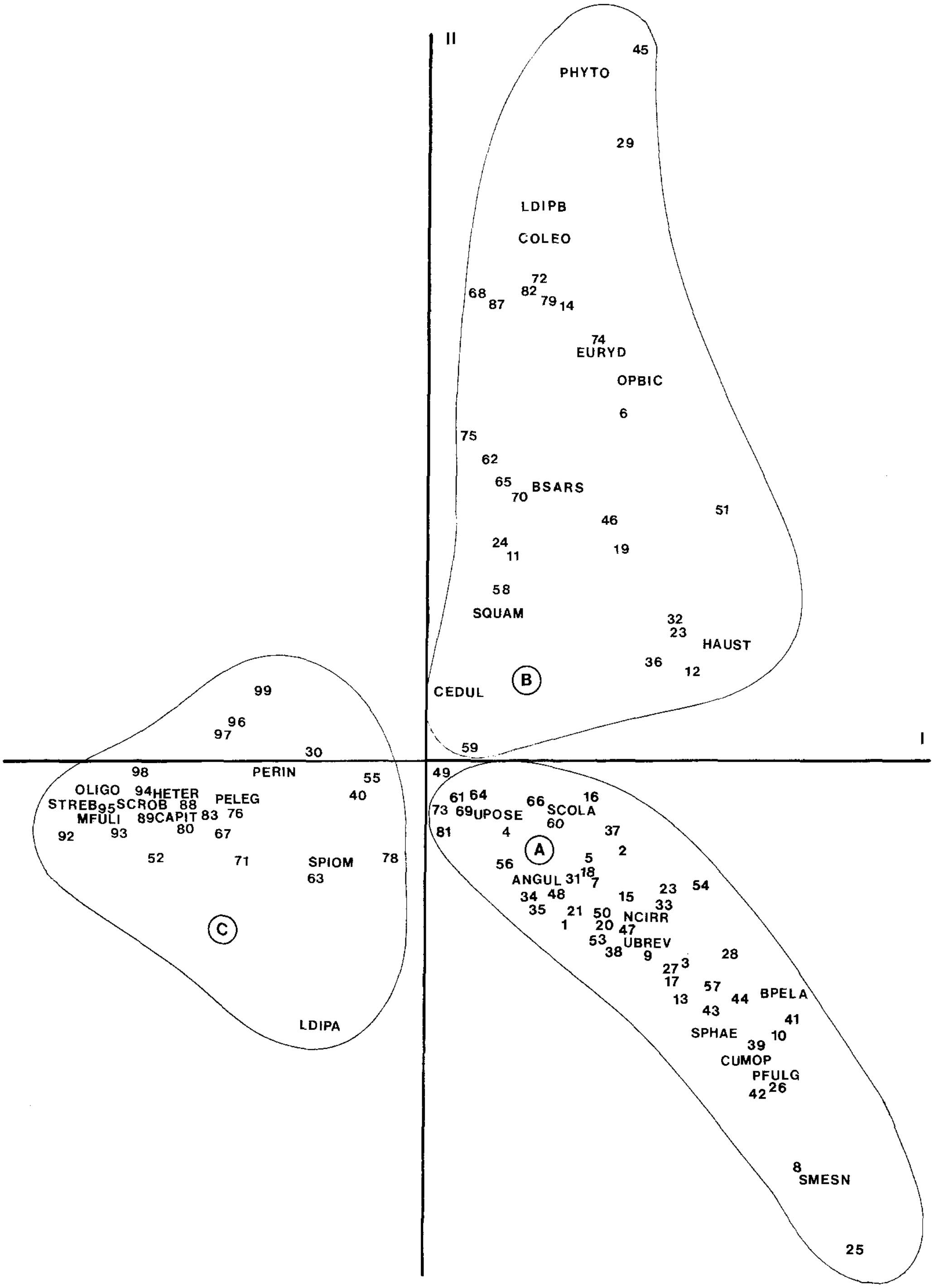

Fig. 4. Samples and species from Ría de Foz on Axes I and II of correspondence analysis, revealing division into three main groups. Some samples were omitted for clearer presentation. Code letters as in Table 3

nemerteans. All the common species were dominant and comprised 63.4% of the total specimens collected in this assemblage. Other infaunal dominants were *Pygospio elegans*, *Scolelepis squamata*, *Nephtys cirrosa*, *Peringia ulvae*, *Angulus tenuis*, *Haustorius arenarius*, *Urothoe brevicornis*, *U. poseidonis*, Diptera sp. A (larvae), Diptera sp. B (larvae), Coleoptera sp. A and *Phytosus spinifer*. The arthropods Diptera sp. B and *P. spinifer* were exclusive to this assemblage. Diversity ranged from 0.81 (Sample 11) to 3.43 (Sample 58); evenness varied from 0.17 (Sample 61) to 0.82 (Sample 23).

Group C. Geographically identified with the inner and most protected parts of the ría, this assemblage was represented by 26 samples, almost all located in sediment with a >5% silt-clay fraction and moderate to high organic-matter content. From these samples, a total of 61 species was collected: 29 polychaetes, 18 crustaceans, 8 molluscs and 6 "others". The number of species varied from 26 (Sample 98) to 4 (Sample 93). There were nine dominant species: *Pygospio elegans*, *Spio martinensis-decoratus*, *Streblospio benedicti*, *Capitella capitata*, *Heteromastus filiformis*, Oligochaeta sp., *Cerastoderma edule*,

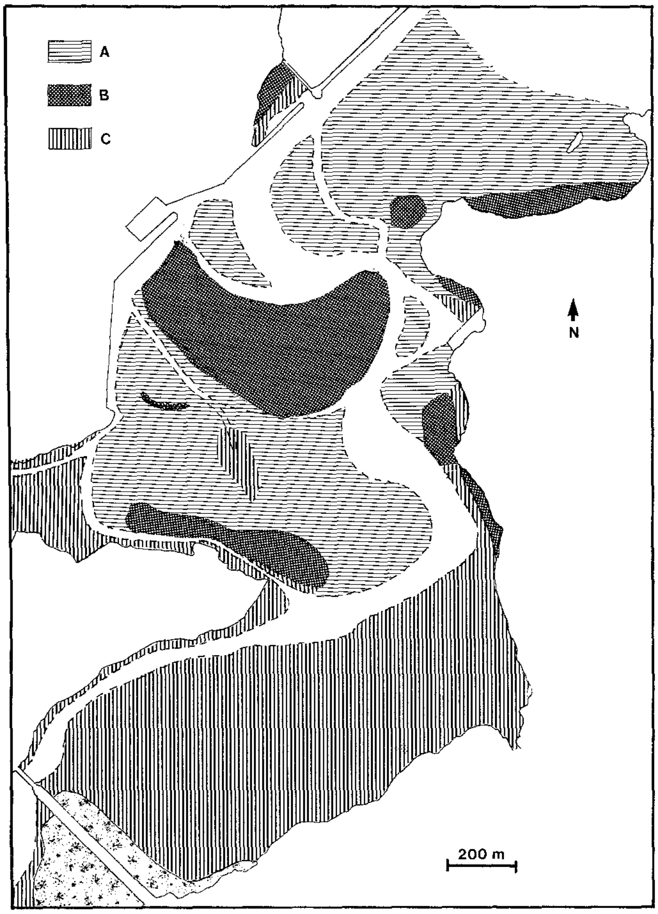

Fig. 5. Distribution of three distinct infaunal assemblages in Ría de Foz. Group A: marine sublittoral zone, medium and fine sands, low organic-matter content (characteristic species: *Nephtys cirrosa* and *Urothoe brevicornis*); Group B: midlittoral zone, sediment as for Group A (characteristic species: *Ophelia bicornis, Eurydice pulchra* and *Bathyporeia sarsi-pilosa*); Group C: inland zone, >5% silt-clay fraction, moderate to high organic-matter content (characteristic species: *Pygospio elegans, Streblospio benedicti, Capitella capitata, Heteromastus filiformis, Eteone longa-flava*, Oligochaeta sp., *Scrobicularia plana, Peringia ulvae*, and *Carcinus maenas*)

Scrobicularia plana and *Peringia ulvae*. The last species comprised 66.2% of the total specimens collected in this assemblage, the remaining dominant species 30.7%. In addition to the dominant species, common forms included the nemerteans, *Eteone longa-flava, Hediste diversicolor*, and *Carcinus maenas*. With the exception of the nemerteans, *Spio martinensis-decoratus, H. diversicolor*, and *C. edule*, all common species were characteristic for Group C. There were many exclusive species (see Table 3), collected only in the Group C samples. The most frequent of these were the polychaetes *Glycera tridactyla* and *Nephtys hombergi* and the oligochaetes. Diversity ranged from 0.19 (Sample 96) to 3.48 (Sample 78); evenness varied from 0.02 (Sample 96) to 0.66 (Sample 93).

Discussion and conclusions

This coenotypic model suggests that two major factors determine the distribution pattern of the macrozoobenthos in the Ría de Foz. The first is related to sediment properties such as particle size, silt-clay and organic matter content, with a gradient along the longitudinal axis of the ría ranging from clean sandy sediments in the outer ría to muddy sediments with moderate to high organic content in the inner ría. The second factor, relevant only in sandy sediments, is related to the degree of moisture in the sediment which is regulated by the tidal level, and is responsible for intertidal zonation.

The sediment properties, which result from many factors, determine environmental conditions of the benthic habitat (Gray 1974, Rhoads 1974, Keegan et al. 1977, Fresi et al. 1983). In the Ría de Foz, most of the numerically dominant species occur over a wide variety of sediment types, responding to sedimentary gradients with changes in abundance. Of the 29 dominant species used in the correspondence analysis, 5 were restricted to sandy substrates and have been commonly collected from sand substrates in other areas: the polychaetes *Paraonis fulgens* and *Ophelia bicornis*, the haustoriid amphipods *Bathyporeia pelagica* and *Haustorius arenarius*, and the cumacean *Cumopsis goodsiri*. With the exception of the oligochaetes, species characteristic of sediments with a high content of organic matter were widespread throughout the study area. Among these species, the polychaetes *Streblospio benedicti, Capitella capitata*, and *Heteromastus filiformis* have been considered as opportunistic (Grassle and Grassle 1974). The mud-snail *Peringia ulvae* was the most abundant and commonly collected species.

Investigations in sandy shores have concluded that tidal level is an important factor governing the distribution of intertidal species (López Cotelo et al. 1982, Penas and González 1983, Raffaelly and Boyle 1986, Viéitez and Baz 1988). Intertidal zonation of species on sandy shores has been observed by many authors (Stephen 1929, 1930, Bally 1983, Dexter 1983, Wendt and McLachlan 1985, Tarazona et al. 1986). Universal zonation schemes based on biological (Dahl 1952) and physical (Salvat 1964) factors have been proposed and discussed (Bally 1983, McLachlan 1983, Wendt and McLachlan 1985). In the sandy sediments investigated in the Ría de Foz, we observed a distinction between the upper tidal level and middle and lower tidal levels, that agreed with the midlittoral and sublittoral zones of Dahl's scheme. In Foz, the midlittoral ("retention zone" in Salvat's system) was characterized by the polychaete *Ophelia bicornis* and the crustaceans *Eurydice pulchra* and *Bathyporeia sarsi-pilosa*. The sublittoral ("resurgence and saturation zone" in Salvat's system) was characterized by the polychaete *Nephtys cirrosa* and the amphipod *Urothoe brevicornis*. Similar zonation patterns have been observed in other sandy shores of the Iberian Peninsula (Laborda 1986, Dexter 1988, Viéitez and Baz 1988).

The density of the macrofauna in the Ría de Foz supports the idea that more exposed areas contain a lower number of individuals (McIntyre 1971, McLachlan et al. 1981, Dexter 1972, 1983, 1988), whilst organic enrichment of more sheltered areas promotes an important enhancement of the macrofauna, with some species, such as *Pygospio elegans, Capitella capitata* and *Peringia ul-*

vae, exhibiting high numerical densities. The diversity and evenness calculated in Ría de Foz are similar to those for other intertidal areas of the Iberian Peninsula. Both statistics showed a general tendency to decrease with increasing silt-clay and organic-matter content of the sediment, as reported by other authors (Sanders 1968, Copeland and Bechtel 1971, López-Jamar 1981, Gray and Pearson 1982, Planas and Mora 1984b, Rodríguez Castelo and Mora 1984).

Most of the macrobenthic species of the Ría de Foz were not restricted to a particular habitat, but showed a high degree of overlapping in their distribution. This accorded more with the concept of communities being distributed as a near-continuum and responding to environmental gradients (Mills 1969) than to the concept of communities as units of characterizing species (Thorson 1957). Nevertheless, the abstraction of species groups from such continua facilitates description and comparison and enables the three benthic assemblages distinguished in the Ría de Foz to be compared with known Atlantic and Mediterranean benthic communities.

Group A is characterized by marine species corresponding to the "boreal Lusitanian *Tellina* community" of Stephen (1930) and Thorson (1957). This community has been widely investigated in many Spanish intertidal clean-sand environments (Viéitez 1976, 1981, Anadón 1980, Laborda 1986).

The characteristic and common species of Group B are similar to those cited by Pérès and Picard (1964) and, more extensively, by Pérès (1967) as typical of "biocoenosis of sands and slightly muddy mediolittoral sands". This community has only been reported from the Iberian Peninsula (Lapamán Beach) by Viéitez and Baz (1988), who submit that such communities may be more widely distributed in midlittoral sands but that data are lacking because clean beaches have thus far been rarely investigated.

The characteristic species of Benthic Assemblage C are, in general, well known as typical for soft sediments rich in mud and organic matter (Pérès 1967, Wolff 1973, Planas and Mora 1984b). Comparison of Group C with the different marine benthic communities described to date reveal that it displays some features of the *"Cardium edule-Scrobicularia* community" in Thorson's (1957) system. Species from this community have been widely reported as being typical of organic-polluted estuaries (Viéitez 1976, 1981, Anadón 1980, Penas and González 1983, Planas and Mora 1984a, b, Planas et al. 1984).

Two conclusions can be drawn from this study. First, the distribution of intertidal macrozoofauna and benthic assemblages are roughly determined by the sedimentary gradient and, in sandy sediments, by the degree of moisture in the sediment. Second, the overall faunal composition, species distribution and community structure in the Ría de Foz are comparable to those reported for other estuaries and intertidal sandy shores along the Spanish coast.

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