The influence of physicochemical parameters on the distribution of dominant bivalve species in the ensenada do Baño (Ria de Ferrol) in Northwest of Spain

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ABSTRACT. This paper presents a synecological study of the dominant bivalve species in the Ensenada do Baño (Ría de Ferrol, NW Spain), and reports on relationships between the distribution of these species and physicochemical parameters (particle size, carbonate content, organic matter content, sorting coefficient and depth/ height with respect to tidal zero). We conclude that the most important factors governing species distribution are grain size and depth/height.

RÉSUMÉ. Une étude synécologique des bivalves dominants de l' Anse do Baño (Ría de Ferrol, NO Espagne) est présentée. Cette étude montre les relations entre leur distribution et les conditions physico-chimiques du milieu (granulométrie, teneur en carbonates et en matière organique, coefficient de sélection et profondeur). Cette étude a permis de mettre en évidence que les facteurs déterminant de la distribution des bivalves sont le gradient sédimentaire et la profondeur ou la hauteur par rapport au niveau 0 de la marée.

INTRODUCTION

In early studies on the biology of benthic faunas, an understanding of sedimentological parameters proved to be of utmost importance, due to their effect on the faunal composition of communities and to the close relationship between sediment variables and the ecological preferences of the different species. This is particularly true for infaunal species, which the nature of the sediment determines life style as well as trophic and reproductive habits.

In a number of studies, the primary goal has been to gather information on relationships between mollusc distributions and the physicochemical properties of the sediment. It has been observed that the relationship between mollusc distributions and the sedimentary environment is the result of a dynamic interdependence among physical, chemical and microbiological sediment factors (BADER, 1954). Important studies in this field include those of LANDE (1975), TUNBERG (1981) and CORNET (1985, 1986) on the distribution and ecology of bivalve communities of European Atlantic coast, and those of DRISCOLL & BRANDON (1973), FRANZ (1976), FRANZ & MERRILL (1980) on the American Atlantic coast in which benthic molluscan assemblages in relation to sediment were studied. Previous studies about distribution and ecology of molluscs of the coasts of northern Spain include those of FIGUERAS (1956), VIÉITEZ (1976), PLANAS & MORA (1984), LABORDA & MAZÉ (1987), MAZÉ & LABORDA (1988), BORJA (1988, 1991) and TRONCOSO & URGORRI (1992).

Despite of abundance of malacological studies on the Galician coasts, there is a scarcity of research on sinecology of molluscs. For that, we decided to extend the knowledge of this group, particularly in the Ría de Ferrol, where this group has been poorly studied. In the present study, we investigated relationships between bivalve distributions and physicochemical factors in the Ría de Ferrol. The study was carried out in the Ensenada de Baño (Baño Inlet), which contains a wide range of sediment types (including mud, muddy sand, shell gravel, coarse sand and maërl).

METHODS

The study area is located on the southern side of the Ría de Ferrol (NW Spain), between Punta do Faro da Palma (43°27'52"N; 08°16'49"W) and Punta Piteira (43°27'57"N; 08°15'37"W), and has an area of 0.5 km^2 and a maximum depth of 18 m (Fig. 1).

The inlet is oriented in direction NNE-SSW; the prevailing winds are southwesterlies for most of the year, except in summer when northeasterlies become dominant. The mean tidal range in the ria is 2,7 m, and tidal effects give rise to strong currents (up to 1,5 m/s in the ria's central channel). Outward movement of water from the ria provokes movement to the SE within the inlet, while movement into the ria provokes movement to the SSW within the inlet. These currents, which are stronger at the mouth of the inlet than at more distal points, are the dominant factor affecting sediment distribution within the inlet.

Mollusc were sampled between July 1991 and June 1992 at 40 intertidal and 35 subtidal stations (one sample per station). Sampling points were selected along 12 parallel transects drawn across the inlet at 100 m intervals, taking samples at the points that were judged by visual examination to show a change in nature, texture or substrate covering. In the subtidal zone, the samples were collected by scuba diving. At each point, a 0,25 m^2 square sample was taken, to a depth of approximately 20 cm, using a rectangular shovel. The tidal range at intertidal stations was 2.29 m. The intertidal samples were additionally collected at the ends of each transect and, in the inner intertidal zone, samples were also taken every 100 m along each transect (OLABARRIA *et al.*, 1996). All samples were subsequently wet-sieved through a series of sieves with 10, 2, and 0.5 mm mesh. Finally the sieved samples were transported to the laboratory to be sorted by the remounting technique (ROS, 1975).

Surface sediment samples were also collected from each sampling point, for granulometric analysis and for determination of organic matter and carbonate content by the method of GUITIÁN & CARBALLAS (1976) (Table 1).

For each species and each environmental factor, possible relationships between population density (number of individuals in the sample) and the level of that factor were investigated by Spearman rank correlation analysis (SOKAL & ROHLF, 1979) (Table 2).

RESULTS

Distribution of individual species with respect to sediment characteristics

The samples yielded a total of 7579 specimens of bivalves belonging to 52 species, of which 11 (*Mytilus edulis, Thyasira flexuosa, Mysella bidentata, Papillicardium papillosum, Parvicardium exiguum, Cerastoderma edule, Abra alba, Venus verrucosa, Dosinia exoleta, Venerupis senegalensis* and *Hiatella arctica*) represented 80.8% of the total, with *Mysella bidentata* being the most representative species (35.6%) (Table 3).

Mytilus edulis occurred most commonly in the intertidal zone (93.3%), of individuals, versus 6.7% in the subtidal zone reaching its highest densities in coarse sand bottoms located in the intertidal zone on the border of the inlet (Fig. 2A). The density of individuals in the intertidal zone was positively correlated with gravel, coarse sand, and carbonate contents, and negatively correlated with fine sand content (Table 2).

Thyasira flexuosa was found almost exclusively in the subtidal zone (99.4% of individuals), reaching its highest densities in the eastern area of the inlet (Fig. 2B), on fine sand bottoms with silt-clay contents of over 10% and organic matter contents of 1-2%. There was a strong positive correlation between the density of this species in the subtidal zone and fine sand and organic matter contents, and a strong negative correlation with coarse sand and carbonate contents (Table 2).

Mysella bidentata was the most abundant and widely distributed bivalve, with a broad distribution throughout the inlet and a large number of individuals in the subtidal zone (Fig. 2C). Correlation analysis did not reveal any relationship with physicochemical parameters in the subtidal zone, due to the widespread occurrence of this species on all types of bottom. In the intertidal zone, however, the density of this species correlated positively with coarse sand and gravel contents, and negatively with fine sand content (Table 2).

Papillicardium papillosum occurred most commonly in the subtidal zone (96.7% of individuals). The highest densities were those observed in the outer subtidal zone (Fig. 2D), dominated by coarse sand and medium sand bottoms with organic matter contents of less than 1% in most cases. The density of this species in the subtidal zone was positively correlated with coarse sand content and depth, and negatively correlated with fine sand content (Table 2).

Parvicardium exiguum was commonest in the intertidal zone (86.4% of individuals). The highest densities were found in the mid-intertidal zone where there is a *Zostera noltii* meadow (Fig. 3A). The density of this species in the subtidal zone showed a significant though weak positive correlation with medium and fine sand contents, and a significant negative correlation with gravel and carbonate contents. In the intertidal zone, the density of this species was negatively correlated with tidal height (Table 2).

Cerastoderma edule was present only in the intertidal zone, and reached its highest densities in the inner intertidal zone (Fig. 3B), where the bottoms are mostly medium and fine sand with organic matter content ranging between 0.5 and 1%. Correlation analysis did not reveal significant relationships with the physicochemical parameters, except for a negative correlation with tidal height (Table 2).

Abra alba was most frequent in the subtidal zone (84.5% of individuals). However, it was widely distributed in the inlet (Fig. 3C), being most common on bottoms with particle size smaller than 0.5 mm and organic matter content greater than 1%. The density of this species in the subtidal zone correlated positively with the sorting coefficient and less strongly with organic matter content, and negatively with coarse sand

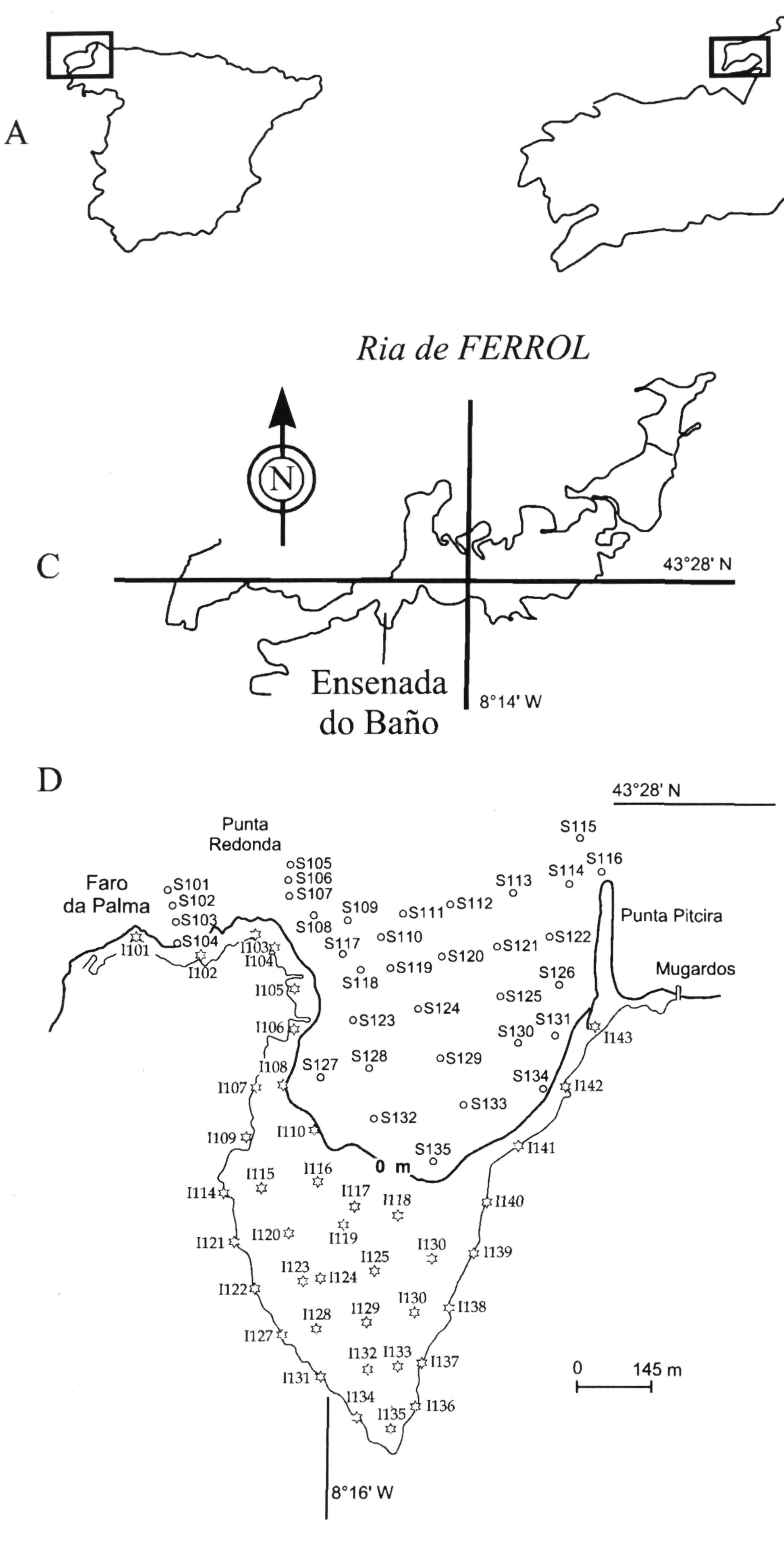

Fig. 1. Location of the study area and the sampling sites. A: Spain; B: Galicia; C: Ría de Ferrol; D: Ensenada do Baño.

content. In the intertidal zone, density showed a weak but significant positive correlation with silt-clay content (Table 2).

Venus verrucosa occurred largely in the subtidal zone (94.5% of individuals), and reached its highest densities on bottoms with coarse sediments and varying percentages of organic matter (Fig. 3D). The density of this species in the subtidal zone was negatively correlated with fine sand content. In the intertidal zone, however, a positive correlation was observed between the density of this species and both coarse sand content and the sorting coefficient (Table 2).

Dosinia exoleta occurred most commonly in the subtidal zone (96.8% of individuals), and reached its highest densities in the outer part of the inlet on coarse sand bottoms with variable organic matter content (0.4-1.7%) (Fig. 4A). The density of this species correlated positively with coarse sand content and to a lesser extent with carbonate content, and negatively with fine sand content (Table 2).

Venerupis senegalensis was slightly more frequent in the subtidal zone (61.8% of individuals), attaining its highest densities in the outer inlet. In the intertidal zone it was distributed homogeneously throughout the whole area. In both cases, it occurred on bottoms of varied physicochemical characteristics (Fig. 4B). In the intertidal zone, density was negatively correlated with tidal height (Table 2).

Site	Q_{50}	S-C	S_o	CA	OM	D/H	Site	Q_{50}	S-C	S_o	CA	OM	D/H
S101	1.02	10.2	2.4	30.2	0.4	10.25	**I103**	1.30	10.6	>2.5	19.6	0.6	0,80
S102	0.71	20.3	2.7	31.1	0.5	7.25	**I104**	1.30	1.6	1.8	20.6	0.4	0,21
S103	0.41	20.7	1.7	33.3	0.4	4.25	**I105**	0.32	5.4	1.6	9.4	0.7	1,75
S104	0.15	35.3	6.0	18.2	1	1.03	**I106**	0.65	2.5	2.6	12.9	0.4	0,74
S105	2.31	20.2	4.8	34.7	0.7	11	**I107**	0.65	4.7	2.5	2.6	0.5	0,52
S106	0.53	27	8.4	8.9	1	9	**I108**	0.40	4.8	1.9	2.1	0.5	00
S107	2.90	20.6	6.4	32.4	1.9	5	**I109**	>2	3.8	>1.6	1.7	0.6	0,55
S108	3.00	14.2	2.2	34.7	1.2	4.3	**I110**	0.80	5	3.7	8.6	2	1,13
S109	0.09	45.7	9.6	29.3	1.5	7.2	**I114**	1.80	1.5	>1.3	1.7	0.2	0,84
S110	1.90	11.5	2.7	32.9	0.7	13.2	**I115**	0.28	6.2	1.8	1	0.5	0,70
S111	0.18	36.9	0.2	32	1.7	13	**I116**	0.45	17.5	5.0	0.3	1.4	0,74
S112	0.25	31.9	21.7	13.8	1.1	17	**I117**	1.40	11.4	3.7	26.7	0.6	0,10
S113	0.44	7.7	2.5	13.8	0.9	17	**I118**	0.38	4.4	2.9	16.3	0.3	0,98
S114	0.11	44.6	20.9	21.3	1.4	14	**I119**	0.18	5.5	1.6	0.8	0.6	1,91
S115	0.85	11.4	2.0	34.7	0.4	15.5	**I120**	0.13	8.7	1.5	0.3	0.9	0,16
S116	0.49	12.8	1.7	34.7	0.6	11	**I121**	1.80	4.4	>2.5	0.8	0.9	1,30
S117	0.65	12.5	2.1	4.9	0.3	2	**I122**	0.12	15.9	1.5	1.7	1.4	0,91
S118	0.34	27.3	9.5	24.9	1.5	4	**I123**	0.16	6.5	1.9	0.3	0.6	0,94
S119	1.75	13.2	2.6	17.3	0.4	8	**I124**	0.13	10.9	1.4	0.2	0.8	0,08
S120	1.39	14.6	3.4	18.4	0.6	13	**I125**	0.11	10.7	1.4	0.3	0.8	0,27
S121	3.00	6	2.5	27.6	0.9	18	**I126**	0.14	5.6	1.3	1	0.4	0,57
S122	1.21	23.4	7.5	30.2	0.6	16	**I127**	0.32	10	2.3	0.9	0.5	0,80
S123	1.55	13.2	>2.3	16.4	0.4	5	**I128**	0.34	6.6	2.2	0.3	0.8	0,38
S124	1.40	11.4	>3.3	30.2	0.7	10	**I129**	0.15	3.5	1.4	0.9	1	0,81
S125	0.16	40	10.0	35.6	0.9	13	**I130**	0.13	9	0.3	0.3	1.2	0,92
S126	>2.00	7.7	>3.9	22.6	1.3	10	**I131**	0.24	27.7	4.3	0.9	0.5	1,03
S127	0.09	13.3	>1.8	2.2	1.8	1.2	**I132**	0.13	6.6	1.4	0.2	0.7	1,67
S128	1.55	5.4	>3.5	6.3	0.3	4.5	**I133**	0.13	7.6	1.4	0.3	0.9	1,45
S129	0.13	37.9	8.5	17.3	1.8	9.8	**I134**	0.11	5.4	1.3	0.2	0.9	1,78
S130	0.06	49.8	9	25.8	1.5	12	**I135**	0.26	4.7	1.5	1	0.5	1,78
S131	0.03	53.1	8.5	16.3	2	7.6	**I136**	0.19	4.7	1.7	0.2	0.4	1,05
S132	0.23	10.4	1.6	1.3	0.6	1.5	**I137**	0.12	11	1.4	0.2	0.9	1,63
S133	0.06	46	5.2	6.2	2	5.8	**I138**	0.18	5.5	3.7	0.2	0.8	1,20
S134	0.75	13.1	>3.5	19	0.9	6.4	**I139**	0.36	7	3.9	0.9	0.7	1,59
S135	0.19	17	1.7	0.9	0.4	2	**I140**	0.13	27.9	7.2	0.9	0.6	0,84
I101	>2	0.9	1.1	12	0.2	0.35	**I141**	0.90	5.5	3.0	4.3	0.7	0,68
I102	0.35	5.9	1.8	1.4	0.4	2.29	**I142**	0.32	4.7	1.6	24.9	0.4	0,96
							I143	0.36	9.7	3.6	14.3	0.8	0,78

Table 1. Characteristics of the sampling sites. Q_{50} : median particle size (mm); S-C : silt and clay contents (% w/w); S_o : sorting coefficient; CA : carbonate content (% w/w); OM : organic matter content (% w/w); D : depth (m) with respect to tidal zero (subtidal sites); H : height (m) with respect to tidal zero (intertidal sites).

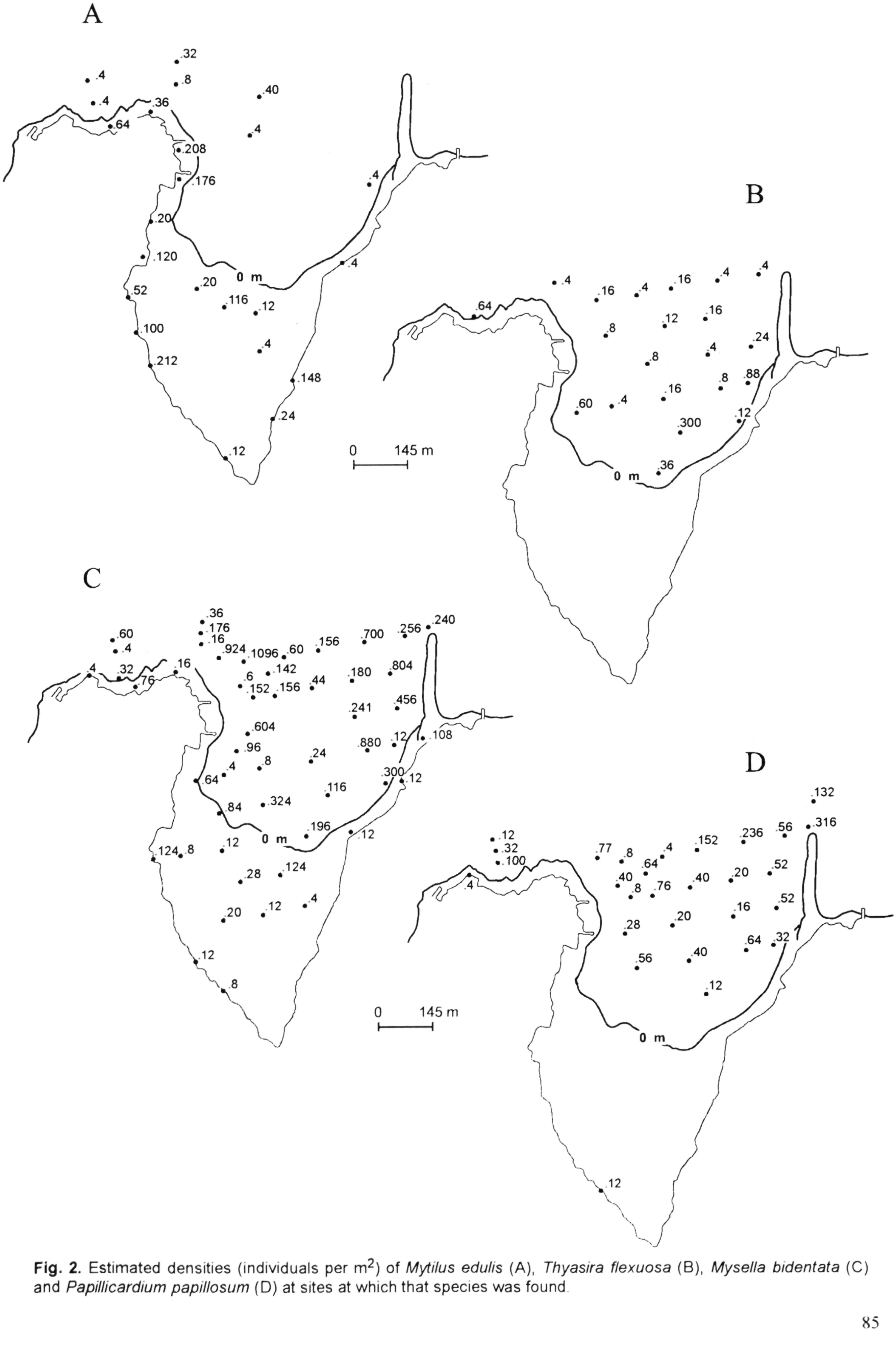

Fig. 2. Estimated densities (individuals per m^2) of *Mytilus edulis* (A), *Thyasira flexuosa* (B), *Mysella bidentata* (C) and *Papillicardium papillosum* (D) at sites at which that species was found.

Hiatella arctica was likewise slightly more frequent in the subtidal zone (65.5% of individuals), largely occurring on bottoms with a particle size greater than 0.5 mm, both in the subtidal and intertidal zone (Fig. 4C). The density of this species in the subtidal zone showed a slight positive correlation with gravel content and depth. In the intertidal zone the density of this species correlated positively with coarse sand, carbonate and gravel contents, and negatively with organic matter and fine sand contents (Table 2).

Among species relationships

In the subtidal zone, extensive overlap was observed among the distribution of *Hiatella arctica*, *Venus verrucosa* and *Venerupis senegalensis* (Fig. 5A), and similarly among the distribution of *Abra alba*, *Thyasira flexuosa* and *Mysella bidentata* (Fig. 5B), though note that the latter was very common throughout the subtidal zone. *Thyasira flexuosa* and *Dosinia exoleta* were not found together (Fig. 5B), since *D. exoleta* occurs on infralittoral gravel and *T. flexuosa* on muddy sands or muds. *Papillicardium papillosum* showed high densities (up to 150 individuals/m^2) on the deepest bottoms dominated by coarse sands.

In the intertidal zone, extensive overlap was observed between *Hiatella arctica* and *Venus verrucosa* and between *Parvicardium exiguum* and *Venerupis senegalensis* (Fig. 5A). *V. verrucosa* and *H. arctica* occurred in the same types of habitat (coarse sands and gravels), whereas *P. exiguum* and *V. senegalensis* both occurred on a wide range of bottom types. *Cerastoderma edule* occurred most commonly at intermediate tidal levels, with the highest densities at

SUBTIDAL

Species	G	CS	MS	FS	SC	OM	CA	S_o	D
Mytilus edulis	0.103 ^{NS}	-0.004 ^{NS}	-0.060 ^{NS}	-0.311 ^{NS}	-0.028 ^{NS}	0.033 ^{NS}	0.143 ^{NS}	-0.238 ^{NS}	0.048 ^{NS}
Thyasira flexuosa	**-0.359***	**-0.595****	0.067 ^{NS}	**0.619 ****	0.333 ^{NS}	**0.584****	**-0.412***	**0.430***	0.025 ^{NS}
Mysella bidentata	0.001 ^{NS}	-0.240 ^{NS}	0.198 ^{NS}	0.138 ^{NS}	0.082 ^{NS}	0.182 ^{NS}	-0.037 ^{NS}	0.198 ^{NS}	-0.196 ^{NS}
Papillicardium papillosum	-0.045 ^{NS}	**0.543 ****	0.071 ^{NS}	**-0.449****	-0.157 ^{NS}	-0.295 ^{NS}	0.164 ^{NS}	-0.002 ^{NS}	**0.443****
Parvicardium exiguum	**-0.425 ***	-0.278 ^{NS}	**0.385***	**0.356***	0.237 ^{NS}	0.1962 ^{NS}	**-0.3754***	0.053 ^{NS}	-0.048^{NS}
Cerastoderma edule	----------	----------	----------	----------	----------	----------	----------	----------	----------
Abra alba	-0.295 ^{NS}	**-0.378***	0.301 ^{NS}	0.153 ^{NS}	0.272 ^{NS}	**0.348***	-0.266 ^{NS}	**0.481****	-0.063 ^{NS}
Venus verrucosa	0.326 ^{NS}	-0.064 ^{NS}	-0.099 ^{NS}	**-0.382***	0.126 ^{NS}	0.199 ^{NS}	0.247 ^{NS}	0.152 ^{NS}	-0.038 ^{NS}
Dosinia exoleta	0.009 ^{NS}	**0.486****	0.126 ^{NS}	**-0.497****	-0.078 ^{NS}	-0.296 ^{NS}	**0.392***	-0.329 ^{NS}	-0.116 ^{NS}
Venerupis senegalensis	0.004 ^{NS}	0.102 ^{NS}	0.261 ^{NS}	-0.311 ^{NS}	-0.192 ^{NS}	0.053 ^{NS}	0.152 ^{NS}	-0.123 ^{NS}	-0.059 ^{NS}
Hiatella arctica	**0.382***	-0.034 ^{NS}	-0.102 ^{NS}	-0.195 ^{NS}	0.092 ^{NS}	0.160 ^{NS}	0.125 ^{NS}	0.073 ^{NS}	**0.471****

INTERTIDAL

Species	G	CS	MS	FS	SC	OM	CA	S_o	D/H
Mytilus edulis	**0.333***	**0.347***	-0.069 ^{NS}	**-0.431****	-0.128 ^{NS}	-0.086 ^{NS}	**0.397***	0.288 ^{NS}	-0.058 ^{NS}
Thyasira flexuosa	-0.132 ^{NS}	0.215 ^{NS}	0.173 ^{NS}	-0.104 ^{NS}	0.069 ^{NS}	-0.222 ^{NS}	0.048 ^{NS}	-0.008 ^{NS}	0.271 ^{NS}
Mysella bidentata	**0.321***	**0.468****	0.060 ^{NS}	**-0.357***	-0.117 ^{NS}	-0.284 ^{NS}	**0.388***	0.233 ^{NS}	-0.211 ^{NS}
Papillicardium papillosum	0.245 ^{NS}	0.086 ^{NS}	-0.020 ^{NS}	-0.174 ^{NS}	-0.087 ^{NS}	-0.158 ^{NS}	-0.083 ^{NS}	0.035 ^{NS}	-0.048 ^{NS}
Parvicardium exiguum	0.052 ^{NS}	0.136 ^{NS}	0.043 ^{NS}	0.000 ^{NS}	0.072 ^{NS}	-0.008 ^{NS}	0.119 ^{NS}	0.053 ^{NS}	**-0.373 ***
Cerastoderma edule	0.008 ^{NS}	0.094 ^{NS}	0.201 ^{NS}	-0.085 ^{NS}	-0.062 ^{NS}	-0.220 ^{NS}	-0.044 ^{NS}	0.250 ^{NS}	**-0.369 ***
Abra alba	0.003 ^{NS}	-0.031 ^{NS}	-0.214 ^{NS}	0.082 ^{NS}	**0.324***	0.185 ^{NS}	0.012 ^{NS}	-0.024 ^{NS}	-0.237 ^{NS}
Venus verrucosa	0.150 ^{NS}	**0.367***	0.023 ^{NS}	-0.178 ^{NS}	0.161 ^{NS}	-0.145 ^{NS}	0.259 ^{NS}	**0.344***	-0.078 ^{NS}
Dosinia exoleta	-0.193 ^{NS}	0.078 ^{NS}	0.201 ^{NS}	-0.119 ^{NS}	-0.037 ^{NS}	-0.119 ^{NS}	0.066 ^{NS}	0.014 ^{NS}	-0.152 ^{NS}
Venerupis senegalensis	0.244 ^{NS}	0.197 ^{NS}	0.011 ^{NS}	-0.205 ^{NS}	0.161 ^{NS}	-0.009 ^{NS}	0.304 ^{NS}	0.228 ^{NS}	**-0.577****
Hiatella arctica	**0.352***	**0.518****	-0.214 ^{NS}	**-0.397***	-0.054 ^{NS}	**-0.319***	**0.446****	0.130 ^{NS}	-0.192 ^{NS}

Table 2. Coefficients of rank correlation (T_s) between densities of the different species (number of individuals in the sample) and physicochemical factors (G : gravel content; CS : coarse sand content; MS : medium sand content; FS: fine sand content; SC : silt-clay content; OM : organic matter content; CA : carbonate content; S_o : sorting coefficient; D/H : depth/height with respect to tidal zero). NS : Not significant ($p > 0,05$), *: $p < 0,05$, **: $p < 0,01$

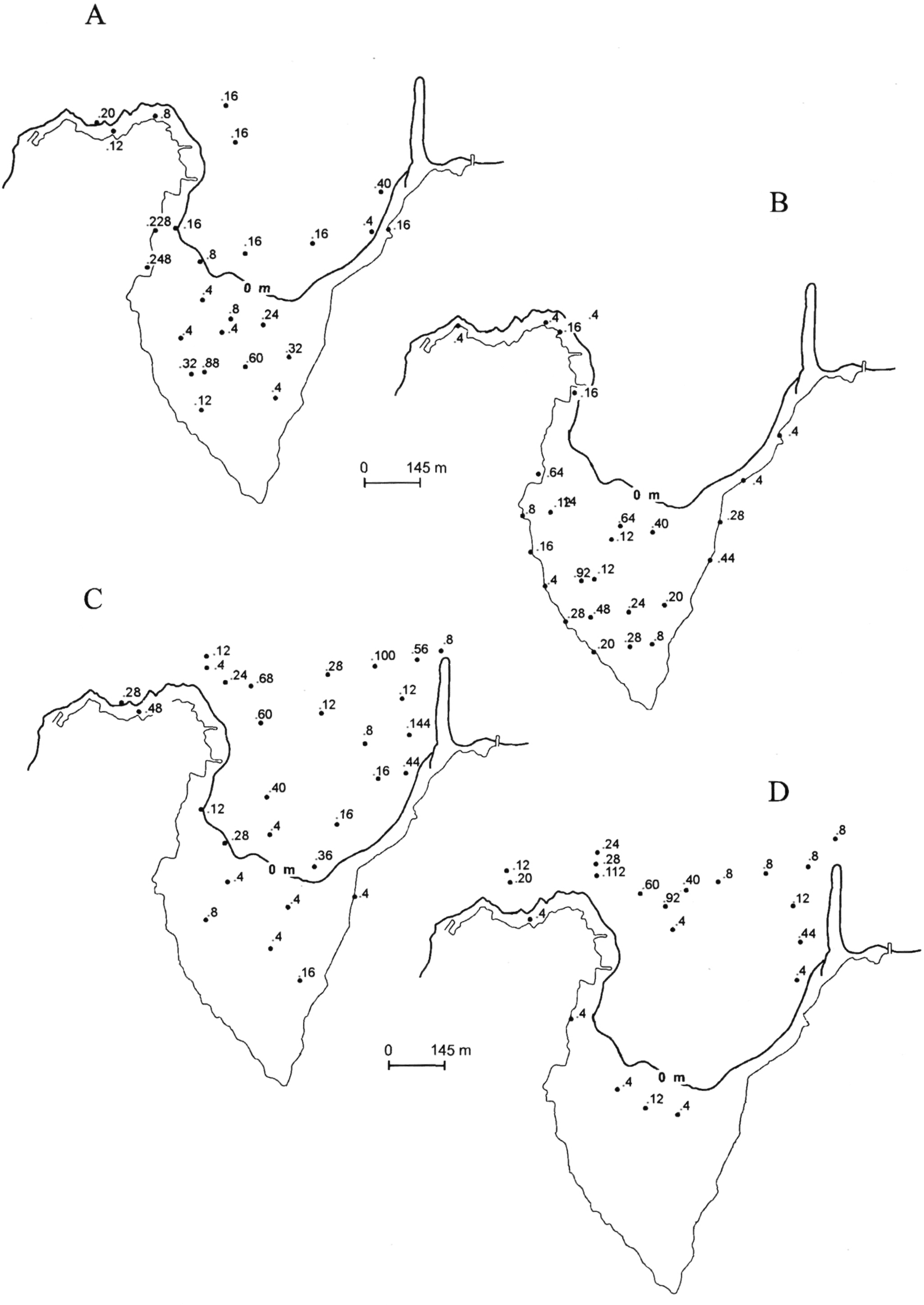

Fig. 3. Estimated densities (individuals per m^2) of *Parvicardium exiguum* (A), *Cerastoderma edule* (B), *Abra alba* (C) and *Venus verrucosa* (D) at sites at which that species was found.

between 0.10 m and 0.94 m. *Mytilus edulis* was found in coarse sands and gravels, at densities of up to 100 individuals/m^2.

Generally speaking, the factors most strongly influencing bivalve distribution were grain size and depth, though carbonate content was also an important factor (possibly related to the positive correlation observed between carbonate contents and particle size; $T_s = 0.478$, $p < 0.01$). Anyway *M. bidentata*, *C. edule* and *V. senegalensis* seemed to be less specific in their choice of sediment types.

Species	RA %	Species	RA %
Nucula nitida Sowerby, 1833	0.20	*Parvicardium nodosum* (Turton, 1822)	0.73
Arca tetragona Poli, 1795	0.04	*Cerastoderma edule* (Linnaeus, 1758)	**2.68**
Striarca lactea (Linnaeus, 1758)	0.03	*Spisula elliptica* (Brown, 1827)	0.01
Mytilus edulis galloprovincialis Lamarck, 1818	**19.50**	*Lutraria lutraria* (Linnaeus, 1758)	0.03
Musculus subpictus (Cantraine, 1835)	1.22	*Phaxas pellucidus* (Pennant, 1977)	0.01
Pecten maximus (Linnaeus, 1758)	0.33	*Moerella donacina* (Linnaeus, 1758)	0.37
Anomia ephippium Linnaeus, 1758	1.4	*Moerella pusilla* (Philippi, 1836)	0.01
Pododesmus squamula (Linnaeus, 1758)	1.5	*Gobraeus tellinella* (Lamarck, 1818)	1.02
Monia patelliformis (Linnaeus, 1767)	0.1	*Gobraeus depressa* (Pennant, 1777)	1.01
Ostrea edulis Linnaeus, 1758	0.41	*Scrobicularia plana* (da Costa, 1778)	0.04
Crassostrea gigas (Thunberg, 1793)	0.01	*Abra nitida* (O.F.Müller, 1776)	0.22
Pisidium casertanum (Poli, 1791)	0.01	*Abra alba* (Wood, 1802)	**2.27**
Loripes lacteus (Linnaeus, 1758)	0.18	*Venus verrucosa* Linnaeus, 1758	**1.73**
Lucinoma borealis (Linnaeus, 1767)	0.13	*Gouldia minima* (Montagu, 1803)	0.81
Myrtea spinifera (Montagu, 1803)	1.02	*Dosinia exoleta* (Linnaeus, 1758)	**2.06**
Lucinella divaricata (Linnaeus, 1758)	0.02	*Tapes decussatus* (Linnaeus, 1758)	0.03
Thyasira flexuosa (Montagu, 1803)	**3.9**	*Venerupis rhomboides* (Pennant, 1777)	1.12
Lasaea rubra (Montagu, 1803)	0.04	*Venerupis saxatilis* (Fleuriau de Bellevue, 1802)	1.01
Kellia suborbicularis (Montagu, 1803)	1.21	*Venerupis senegalensis* (Gmelin, 1791)	**5.63**
Montacuta substriata (Montagu, 1808)	0.01	*Chamelea striatula* (da Costa, 1778)	0.44
Mysella bidentata (Montagu, 1803)	**35.62**	*Clausinella fasciata* (da Costa, 1778)	0.75
Digitaria digitaria (Linnaeus, 1758)	0.19	*Timoclea ovata* (Pennant, 1777)	0.04
Goodallia triangularis (Montagu, 1803)	0.03	*Corbula gibba* (Olivi, 1792)	1.02
Acanthocardia paucicostata (Sowerby, 1841)	0.01	*Hiatella arctica* (Linnaeus, 1767)	**1.80**
Papillicardium papillosum (Poli, 1795)	**4.59**	*Nototeredo norvegica* (Splenger, 1792)	0.11
Parvicardium exiguum (Gmelin, 1791)	**2.53**	*Thracia papyracea* (Poli, 1791)	1.11

Table 3. List of the species detected in the present study showing overall relative abundance (i.e. percentage of the total number of individuals found in all samples).

DISCUSSION

Interpretation of spatial variations in the abundance of benthic species is difficult, in view of the large number of environmental factors which may act on benthic communities. PEARSON & ROSENBERG (1978) studied the factors involved in structuring the marine benthos, and highlighted the importance of food availability as a determinant of community structure. They concluded that depth, latitude and water current speed are the factors which have the strongest effect on food availability. PETERSON (1979) reported that the factors affecting abundance in the benthos may be divided into density-dependent factors (such as competition, predation, and adult-larva interactions) and the physical properties of the sediment.

In our study area, the most important environmental factors affecting the distribution of bivalves were particle size and depth/ height. The current regime was not investigated, though it is clearly determinant of the distribution of sediment types.

The dominant species in the intertidal area, *Mytilus edulis, Parvicardium exiguum* and *Cerastoderma edule*, showed a relationship with physicochemical factors that was consistent with their autoecology. *M. edulis*, which feeds on suspended detritus and phytoplankton, is found primarily on coarse sediments that allow it to attach itself by its byssus (TEBBLE, 1966). In the present study, the density of this species correlated positively with coarse sediment content and negatively with fine sand content. Both *P. exiguum* and

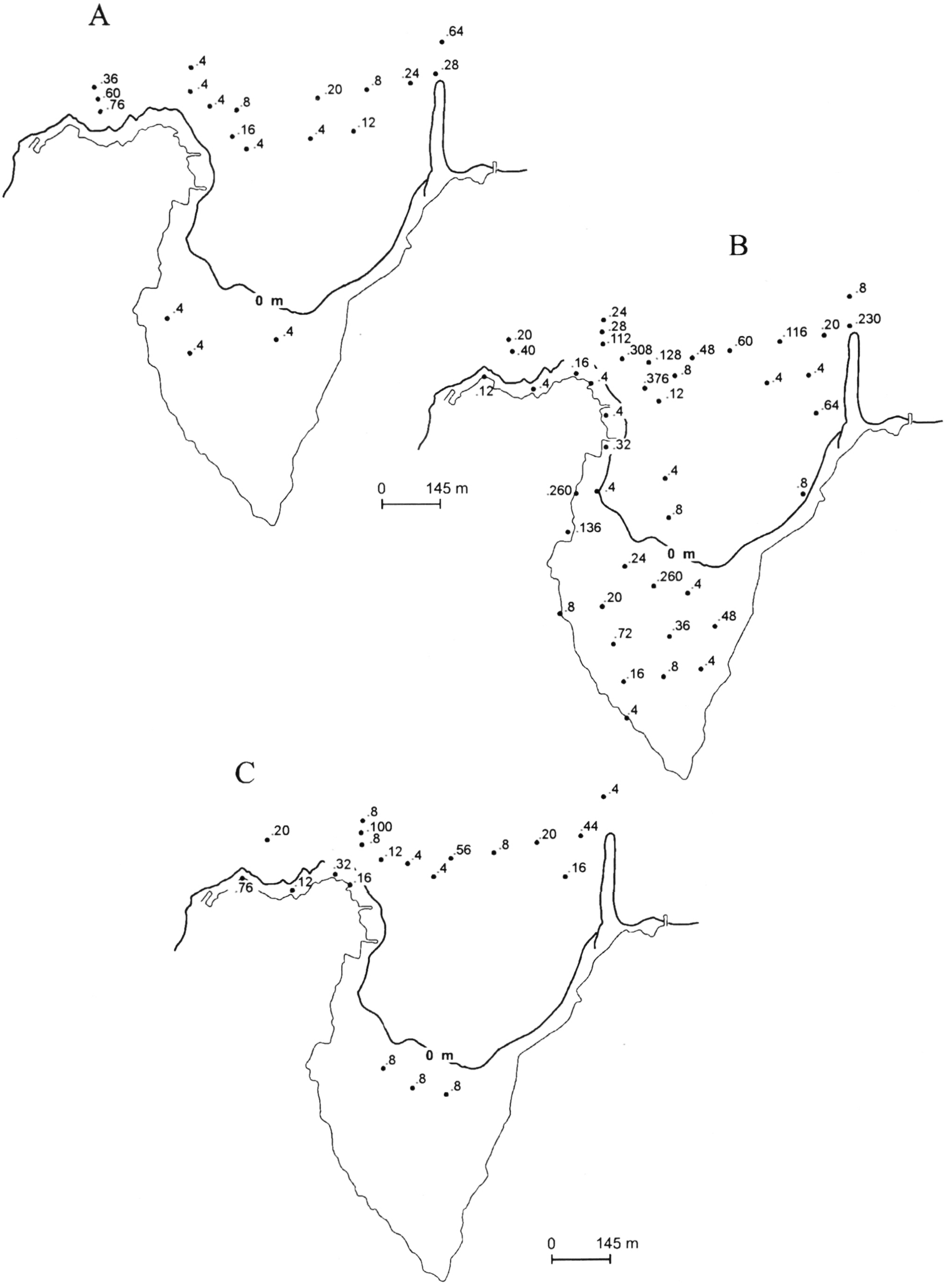

Fig. 4. Estimated densities (individuals per m^2) of *Dosinia exoleta* (A), *Venerupis senegalensis* (B), and *Hiatella arctica* (C) at sites at which that species was found.

C. edule are highly tolerant of variations in salinity, and are typically indifferent to the type of substrate (TEBBLE, 1966); the most important factors governing their distribution are the emersion time and water current speed, both related to food availability (FIGUERAS, 1956), since they are filter-feeders that can only feed when submerged (LABORDA, 1986). In the present study we found that the densities of both species in the intertidal zone were negatively correlated with height with respect to tidal level zero, while there were no significant correlations with the other environmental parameters. *Venerupis senegalensis* was also abundant in the intertidal domain, with the most important factor in its distribution being height: like most venerids, it is adapted to the lower levels of the intertidal zone or to the subtidal zone. The importance of tidal level and zoning has been discussed at length by other authors (WOLFF, 1973; RAFAELLI & BOYLE, 1986; JUNOY & VIÉITEZ, 1990). The distribution of this species did not show any clear relationship with sediment characteristics, in accordance with previous reports: TEBBLE (1966), for example, found that this species that inhabits all kinds of bottoms (sand, sandy gravel, silty gravel, and silty sand), while in Kilkieran Bay in Ireland, KEEGAN (1974) reported the presence of this species in a great variety of biotopes, including bottoms with clean sand, silty sand, maërl and on rare occasions even conchiferous gravel. However, a study by MORA (1980) in the Ría de Arousa (in southern Galicia), found this species to be limited to clean sand and gravel.

Of the dominant species in the subtidal zone, *Mysella bidentata* had a broad distribution throughout the inlet, with high densities of individuals. The density of this species in the subtidal zone showed no correlation with any of the physicochemical parameters in accordance with the fact that it is a highly ubiquitous species, able to exploit a wide variety of environments, from sandy to those with high contents of fine particles. It is also characterized by its feeding behavior, which changes depending on developmental stage: juveniles are deposit-feeders while adults are filter-feeders (OCKELMANN & MUUS, 1978). *Thyasira flexuosa* showed a strong positive correlation with fine sand and organic matter contents; similarly, other authors such as LÓPEZ-JAMAR *et al.* (1987) have reported that this species inhabits silty sediments with a relatively high organic matter content. This species has morphological adaptations that prevent clogging of the branchial filter by large particles in suspension (ALLEN, 1958). Endosymbiont bacteria, which probably contribute to its diet, are found in the gills (DANDO *et al.*, 1985). In our study area, the density of *Abra alba* correlated positively with the sorting coefficient (which indicates that it appears in poorly sorted sediments, with a wide diversity of particles) and to a lesser extent with organic matter content. GLÉMAREC (1973) reports on the presence of this species in heterogeneous silty facies. According to DAUVIN & GENTIL (1989), it is plentiful in silt and sand sediments, tolerates physicochemical changes in the sediment very well, and is rapidly adaptable (strategist r). LANDE (1975) highlights the presence of this species in heterogeneous sediments, and CORNET (1985) states that it can live on highly varied bottoms, and that substrate granulometry is not a decisive factor, although it requires a layer of suspended detritus in the water-sediment interphase as a source of food (GLÉMAREC, 1964).

Venus verrucosa, Dosinia exoleta and Hiatella arctica are species that live on bottoms characterized by coarse sand, silt gravel or conchiferous gravel (TEBBLE, 1966). In our study area, they occurred largely on coarse sand and gravel, and the densities of these species were negatively correlated with fine sand content.

The observed correlations between the densities of the different species and particle size and organic matter content appear to be related to feeding behaviour. For example, the densities of *T. flexuosa* and *A. alba*, which are burrowing detritus feeders, correlated positively with organic matter and fine sand contents, whereas the remaining species (with the exception of *M. bidentata* which may change its feeding mechanism depending on its developmental stage) fed on particles in suspension, so that their distribution correlates positively with sediments having a larger particle size. According to CORNET (1986), filter-feeders take over from detritus-feeders species when the proportion of fine particles decreases. LEVINTON (1977) reports that deposit-feeders dominate in ecosystems with fine, soft sediments and that their presence is linked to the silt-clay fraction, although this latter has not been verified in our study area. By contrast, filter-feeders dominate in sandy sediments (SANDERS, 1958) and their distribution may be governed more by hydrodynamic processes, which determine sediment characteristics, than by the characteristics of the sediment itself.

The marked overlap in the distribution of *A. alba* and *T. flexuosa* is as expected given that these species characteristically form part of a well-defined subtidal zone community (see THORSON, 1957). *Mysella bidentata*, which likewise showed considerable overlap with these two species, is not characteristic of this community but is ubiquitous and broadly distributed in our study area. *Hiatella arctica, V. verrucosa* and *V. senegalensis*, similarly showed overlapping distributions, and all three occurred at high densities on a maërl bed near Punta Redonda. This bed is made up of *Lithothamniom corallioides* and *Phymatolithon calcareum*, on a shell-gravel bottom with a small amount of silt. According to URGORRI *et al.* (1992), these bottoms offer stable substrates which provide good shelter for many species of small molluscs including the juveniles of certain species, so that the maërl acts as a hatchery.

The similar distributions in some areas of *P. exiguum* and *V. senegalensis* may be explained by the fact that these species are characteristic of the intertidal facies occupied by *Zostera noltii* within the limited community of *Macoma balthica* (THORSON, 1957).

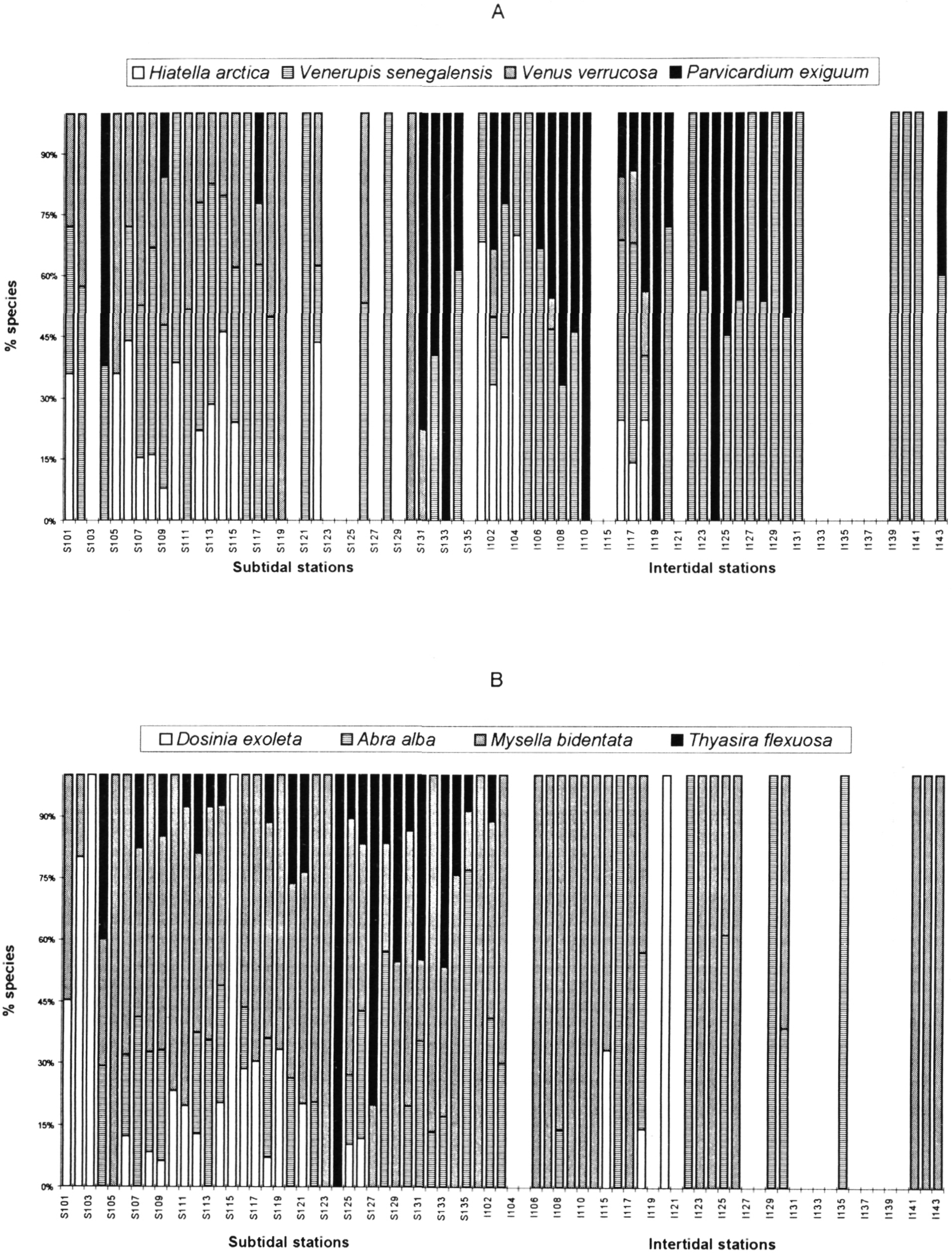

Fig. 5. Plots illustrating the overlaps in the distributions of *Hiatella arctica*, *Venus verrucosa*, *Venerupis senegalensis* and *Parvicardium exiguum* (A) and *Abra alba, Mysella bidentata*, *Thyasira flexuosa* and *Dosinia exoleta* (B). The horizontal axis shows sample number. The vertical axis shows relative abundance, here defined as the number of individuals in that sample expressed as a percentage of the maximum number of individuals per sample recorded for that species.

This has likewise been reported by CURRÁS & MORA (1991) in the Ría de Ribadeo (likewise on the north coast of northwest Spain), where *P. exiguum and V. senegalensis* were found on muddy sand or sandy mud bottoms covered by *Z. noltii*. This phanerogam gives rise to a more diversified habitat, and its rhizomes and roots compact the sediment and provide protection from predators (ECKMAN, 1987). Both population densities and species richness are thus typically higher.

Finally, *H. arctica* and *V. verrucosa* showed closely overlapping distributions since both occurred in the dumping area of the dredging operations carried out in the channel of the ría. The dumped material is characterized by coarse gravel and conchiferous gravel, which are typical habitats for these species.

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