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DISTRIBUTION AND ECOLOGY OF BENTHIC FORAMINIFERA IN THE SANTOÑA ESTUARY, SPAIN.

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ABSTRACT

The living and dead assemblages in the Santoña estuary were studied seasonally in order to determine the distribution and abundance of the benthic foraminifera in this area. Samples were collected from winter 1983 to summer 1985 to document the seasonal variation of the faunas and various ecological factors in the intertidal zone. Salinity is thought to be the main control of the living assemblages and two different biofacies characterising the upper and lower areas have been defined. *Ammonia beccarii* and *Haynesina germanica* are the most dominant forms throughout the estuary with *Miliammina fusca* as co-dominant in the upper estuary and *Quinqueloculina seminulum* as co-dominant in the lower estuary.

The dominant living species are also dominant in the dead assemblages but in the latter the agglutinated indigenous component is much more abundant. This compositional difference is thought to be caused by production rates and change in the environmental conditions within the estuary. The living and dead assemblages have been analysed and compared using the Fisher α diversity index, Triangular plot of wall types and Sanders similarity index.

Keywords: Benthic foraminifera, Ecology, Living assemblages, Dead assemblages, Estuarine environment, Holocene, Santoña, Spain.

RESUMEN

En la Ría de Santoña se han estudiado las asociaciones vivas y muertas de foraminíferos bentónicos con el objetivo de determinar su distribución y abundancia. Las muestras fueron recogidas desde el invierno 1983 hasta el verano 1985 con el fin de documentar la variación estacional de las faunas y de los diversos factores ecológicos en la zona intermareal. La salinidad ha sido considerada como el principal control de las asociaciones vivas y se han definido 2 biofacies que caracterizan las partes alta y baja del estuario. *Ammonia beccarii* y *Haynesina germanica* son las formas dominantes, con *Miliammina fusca* como especie asociada en la parte superior y *Quinqueloculina seminulum* como especie asociada en la parte inferior del estuario.

Las especies dominantes en las asociaciones vivas son también dominantes en las asociaciones muertas pero en estas últimas el componente autóctono aglutinante es mucho más abundante. Esta diferencia composicional parece estar causada por cambios en los niveles de producción y en las condiciones ambientales dentro del estuario. Las asociaciones vivas y muertas han sido analizadas y comparadas entre sí por medio del índice α de Fisher, el diagrama triangular de tipos de caparazón y el índice de similaridad de Sanders.

Palabras clave: Foraminíferos bentónicos, Ecología, Asociaciones vivas, Asociaciones muertas, Estuario, Holoceno, Santoña, España.

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INTRODUCTION

The Santoña estuary, located in the province of Cantabria, is one of the very few unpolluted intertidal areas on the industrial northern coast of Spain. Having in mind the actualistic principle of "the Recent as the key to the Past" this study has been carried out to increase the overall knowledge of estuarine foraminiferal faunas in general and to help in the palaeoecological interpretation of the fossil record in particular.

The only previous micropalaentological work on the studied area is that of Cearreta (1983). The author studied the benthic foraminiferal assemblages of the intertidal zone in the period 1982-1983 but, unfortunately, the sampling method was not very accurate and these assemblages must be understood as total (living plus dead) assemblages. Few other studies deal with nearby littoral and shelf areas, such as those of Colom (1941), Bilbao and Lamolda (1982), Pascual (1984), and Pascual and Orue-Etxebarria (1985, 1986) on the Basque Coast.

MATERIALS AND METHODS

Previous to the field collection, sampling localities were selected using the Marine Chart n.º 24 B from the Instituto Hidrográfico de la Marina de Cádiz (1960) corresponding to the Santoña estuary. The selection of the sites was made on the basis of previously suspected environmental changes both in space (salinity, substrate) and in time (seasons).

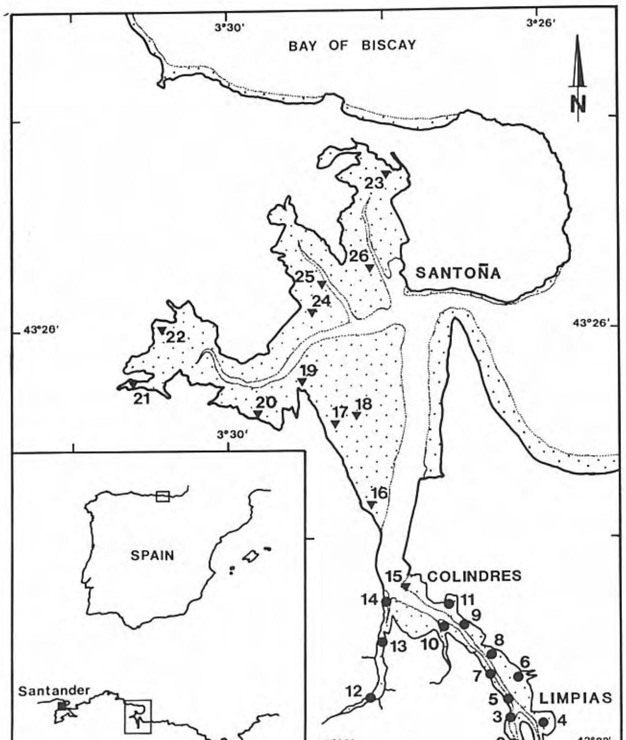

Figure 1. Geographical location and sampling sites (dots representing upper estuary and triangles representing lower estuary).

In this way, twenty six sampling localities were chosen being more concentrated in the upper estuary where there is more rapid horizontal environmental changes (salinity in particular) (Figure 1).

Five different seasonal samplings were carried out during low tides at approximately four monthly intervals corresponding to winter 1983 (December), spring 1984 (May), summer 1984 (August), winter 1984 and summer 1985. Two seasonal samplings were repeated (winter and summer) in order to compare the results from one year with those gathered the year before.

The sampling was limited to the intertidal zone. Foraminifera live in the top few centimetres of the sediment in the brown, oxidised, surface layer. A hard plastic ring was pressed down into this layer and the top 1 cm. of sediment contained inside of it was scraped off carefully and placed in a bottle containing an equal volume of ethanol. This process was repeated twice to sample 90 cm^2 (45 $cm^2 \times 2$) in order to avoid the patchy distribution of foraminifera and to allow a quantitative study. Furthermore, both sediment and water samples were taken to determine the substrate nature, pH, organic carbon, $CaCO_3$ and Sr content in the former, and the environmental salinity and Ca and Mg in the latter case. The water temperature and vegetation were also recorded.

In the laboratory, the foraminiferal sample bottle was shaken and the content poured into a 63 microns aperture sieve and washed with water to remove the clay. When clean the content of the sieve was tipped into a bowl and an equal volume of rose Bengal stain was added in the proportion of 1 gr. rose Bengal in 1l. distilled water. After one hour the sample was tipped into the sieve and washed again to remove the excess stain. Rose Bengal stains protoplasm bright red and therefore stained forms presumed to be alive at the time of collection can be easily differenciated from unstained empty tests (Walton, 1952). The sediment was then returned to the bowl and dried overnight in an oven at 60° C. When dried and cooled the sample was concentrated in foraminiferids using the flotation technique with trichlorethilene as described in Murray (1979). The concentrated sample was weighted and stored. This process was followed for each sample.

Around 300 living foraminifera from each sample and 300 dead tests from some of them were picked from a known fraction of the total sample and the results expressed as a number per unit of area of sediment (90 cm^2). All in all more than 70.000 living and dead foraminifera from the seasonal samples were studied under a stereoscopic binocular mocroscope using reflected light.

The obtained data have been analysed and compared using different mathematical methods and indexes as described in the following sections.

THE ENVIRONMENT

Before analysing in detail the foraminiferal assemblages the estuarine environment must be understood in order to carry out a truly ecological study of the faunas present in it.

An estuary can be defined as a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage (Pritchard, 1967).

The regional distribution of estuaries corresponds to the regional characteristics of continental shelves and, in general, on high-energy coasts with narrow shelves a ria coastline can be found having estuaries separated from the open sea by spits or beach deposits.

Estuaries are formed in the narrow boundary zone between the sea and the land and their life is generally short. Their form and extent is being constantly altered by erosion and deposition of sediment and drastic effects are caused by a small raising or lowering of sea level. At present, following the Pleistocene Ice Ages which overdeepened the river valleys and the subsequent Flandrian Transgression which flooded them, estuaries are both well-developed and numerous, but in geological terms this situation may not last long (Dyer, 1973).

LOCATION AND GENERAL PHYSIOGRAPHY

The Santoña estuary on the North coast of the Iberian Peninsula, Lat. 43° 27' N, Long. 3° 25' W, is 11 kms. long and 0.5 kms. wide in the upper estuary whereas it is 3 kms. wide in the lower estuary, having an area of 20 km^2. The seaward entrance has an effective width of only 0.4 kms. due to the northward growth of a sand spit formed as a consequence of the mutual action between longshore drift and the seaward current within the estuary. The estuary is formed by the final tidal part of the Asón River, faces north and discharges into the Bay of Biscay.

The entire dotted portion of Figure 1 is covered at high spring tide whilst at low water only the main channels are covered. The tides in the Bay of Biscay are of semidiurnal type with a 12 h. 25' period. The main spring rise is 3.99 metres and the mean neap rise is 3.03 metres, having a difference between high and low waters of 3.5 metres during spring tides and of 1.6 metres at neap tides. It is a very shallow intertidal estuary with an average depth of 3 metres over the tidal flats, 4.5 metres in the channels and about 10 metres at the mouth. The estuary as it exists today is almost totally infilled and large areas have been reclaimed especially all over the west side. It therefore represents a late stage in the estuary accretionary cycle. The main channel tends west in the upper estuary and east in the lower estuary as it might be expected due to the effects of the Coriolis Force on the broad lower area.

Because of its shape Santoña can be divided in two parts. Firstly, the narrow rectilinear upper estuary, where the fresh water coming from the river meets the incoming salt-water from the sea and which as a consequence presents brackish salinities. Secondly, the wide lower estuary with no direct river influence and so with normal-marine salinities during the whole year.

Between the high and low tide limits 4 physiographic subenvironments can be recognised. First, the Low Marsh which appears mainly in the west and north of the lower estuary. This low marsh is not well-developed and it is characterised by small clumps of short *Spartina* separated by soft muds. It is completely covered by all tides, except the lowest neaps. Second, the Tidal Flats which are the most extensive physiographic unit and are covered by all tides. They support a population of *Zostera* and some macroalgae, such as *Fucus, Ulva* and *Enteromorpha.*
The composition of the sediments varies depending on the distance to the mouth and the energy of the environment, having a higher sand content in the central areas of the lower estuary. Third, the Sand Spit limiting the east side of the lower estuary which together with the fourth unit, the Main Channels, are composed of unstable sands, have very scarce marine vegetation and the fauna consists of current-swept dead forms derived from both the tidal units within the estuary and the inner shelf (Cearreta, 1983). Because of this lack of living foraminiferal fauna only the two first physiographic units, low marsh and tidal flats, have been studied in the present work.

ENVIRONMENTAL FEATURES

Twelve water samples were taken seasonally from exposed intertidal pools at low tide. Temperature was also recorded using a thermometer. The chlorinity was determined by the standard silver nitrate method and the salinity calculated with the formula Salinity: 0.03 + 1.805 × chlorinity (Sverdrup, Johnson and Fleming, 1942) and expressed as the total concentration of salts in grams contained in one kilogram of water (McLusky, 1981).

If the water-temperature and salinity data are plotted together in a diagram the seasonal distribution is very clear (Figure 2). The temperature presents the lowest values in the winter, increases during the spring and reaches its maximum during midsummer. The temperatures oscilate between 8.5º17° C in winter, 14º19.5° C in spring and 19º34° in the summer.

As far as the salinity is concerned, the Santoña estuary shows a lower estuary (represented by "B"s) with normal marine values throughout the year, fluctuating from 30.82‰ to 42.16‰, and an upper es-

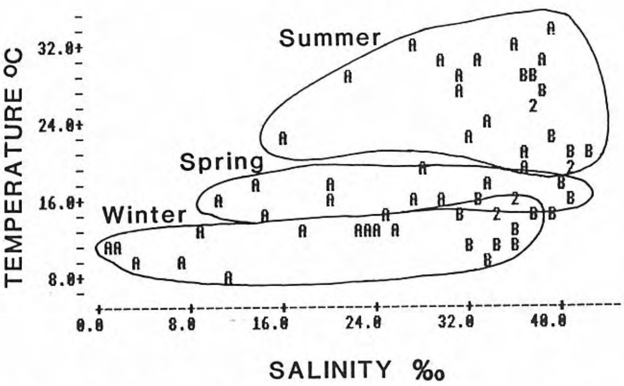

Figure 2. MINITAB LPLOT diagram showing the seasonal distribution of water-temperature and salinity ("A"s representing upper estuary and "B"s representing lower estuary).

tuary (represented by "A"s) having changing salinities depending on the season. As a consequence of the seasonal rainfall regime with a maximum during the winter, it is during this season that the upper estuary has very low salinities (0.61‰-25.43‰). During the spring it maintains its brackish waters (10.32‰-33.33‰) but during the summer, when the rainfall has its minimum, the upper estuary contains normal-marine waters (27.34‰-39.5‰) with smaller values just at the very head of the estuary where the river enters in. The existence of anormaly high salinity values in the summer is probably due to saline concentration in the intertidal pools as a consequence of water evaporation particularly important during this hot season. This seasonal distribution should be expected for a temperate area under Atlantic climate with high pluviosity and mild temperatures.

Twenty six samples were taken in winter 1983 and analysed to determine their grain size distribution. Organic content was digested with H_2O_2 and the remaining sample sieved through a 63 microns sieve to separate the sand fraction. The silt and mud fractions were determined using a Sedigraph 5000 D. The values obtained have been plotted on a triangular diagram of grain sizes (after Folk, 1974) and a very clear pattern can be seen (Figure 3). As it might be expected, as a consequence of the estuarine circulation pattern that determines the sediment movement and deposition, the lower estuary samples, represented by triangles, show a greater sand content due to the bigger influence of the sea. The Cantabrian is a high-energy coast with strong longshore currents which create the sandy beach coastline typical of this area. As a consequence a sand spit has been originated on the east part of the lower estuary which protects it from the direct action of the sea currents and waves. Nevertheless the continuous coarse material movement through the mouth of the estuary and the presence of this sand spit have a major influence on the lower estuary and determine the large sand content in the sediments.

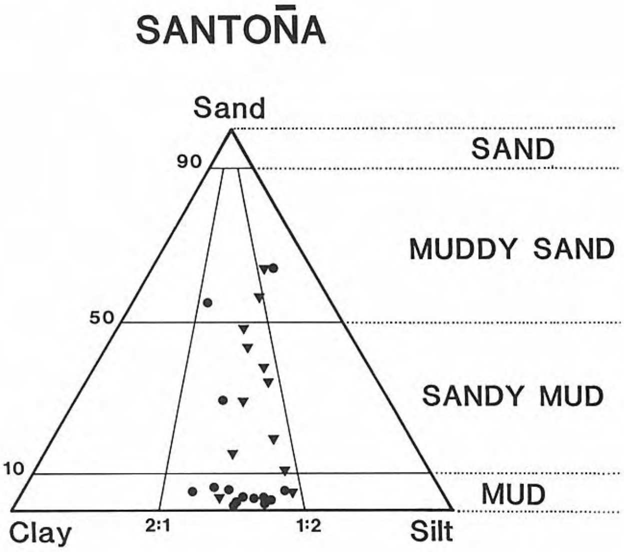

Figure 3. Sediment size analysis after Folk 1974 (dots representing upper estuary and triangles representing lower estuary).

However, the upper estuary sediments, represented by dots, show a higher river influence and consequently an overwhelming fine content. In general, it can be seen that the content of clay and silt is equally distributed in the sediments. Therefore, the estuary could be broadly divided into a mud dominated upper estuary and a sandy-mud dominated lower estuary.

FORAMINIFERAL ASSEMBLAGES

The basic problem of foraminiferal ecology is to determine the causes of the distribution and abundance of foraminifera. Three different approaches have been used to solve this problem: the mathematical, the laboratory an the field. The present study is primarily concerned with understanding the distribution and abundance of foraminifera in nature, that is, in the field.

Neither organisms nor species populations exist by themselves in nature but they are always part of and assemblage of species populations living together in the same area. A foraminiferal assemblage has a series of attributes that do not reside in its individual species components but have meaning only with reference to the community level of integration: species diversity, relative abundance of different species in the community, dominance of the ecologically successful species and structure of the assemblage in terms of wall type composition.

One characteristic of natural communities is change. The changes within the community may be temporal of spatial along environmental gradients. Most species are not in obligatory association with other especies, which suggests that assemblages are formed with many combinations of species and vary continuosly in space and time. The present ecological view of the nature of a community is individualistic and then, an assemblage is a collection of populations with the same environmental requirements rather than integrated units (Krebs, 1985).

Few marine environments offer such a fascinating picture of continuosly changing ecological conditions as an estuary. Superimposed on the alternating tidal flow over many cicles, there is a two-way net internal circulation in which water flows seaward near the surface and headward near the bottom (Nichols and Norton, 1969). The recognition of fossil estuaries and marshes is of interest to geologists because they mark the position of former shorelines. Modern intertidal areas are of interest to ecologists because they represent the transition from a terrestrial environment to a marine one (Murray, 1971).

Foraminifera, perhaps more that any other group of organisms, can be utilised in palaeoecological studies because they are basically simple physicochemical systems, they do not exert much biological pressure against the environment, and hence they are governed by the environment (Greiner, 1974). Benthic foraminifera are known to be highly responsive to subtle changes in the estuarine environment. Estuarine foraminiferal assemblages can be used to detect and delimit many oceanographic characteristics in estuaries, such as water masses, modal circulation pattern, open-ocean influences, sea-level changes, in addition to the modal salinity distribution (Scott, Schafer and Medioli, 1980).

Since 1952 a large number of studies have been carried out using rose Bengal to differenciate forms presumed to be alive at the time of sampling (stained forms) from those presumed to be dead (unstained forms). As Murray (1982) pointed out, from these stained samples the results can be divided into two categories. Firstly, living assemblages, assumed to be both in equilibrium with its environment and representative of a longer time period, and secondly, dead assemblages, inevitably built over a long period of time and drawn from the living assemblages through production and mortality of individual species, followed by post-mortem modification through transport and destruction.

In the present work, the living and dead assemblages, and the relationships between them have been studied with the object of building up a detailed picture of modern estuarine foraminiferal distributions and ecology in order to aid in the interpretation of the palaeocology of fossil faunas.

LIVING ASSEMBLAGES

Standing Crop and General Production

Standing crop is the number of living individuals present on a unit area of sea floor at any one time (Murray, 1973). The rates of organic production in the sea can be indicated, in a general way, by the standing crops of organisms over a period of time. High productivity is indicated by large standing crops and vice versa.

Most estuarine intertidal environments generally support very large standing crops of benthic foraminifera which undoubtedly are related directly to the amount of food present in the environment (Phleger, 1976). In the Santoña estuary, standing crop (90 cm^2) values changed enormously throughout the estuary and seasonally for the same location, and they ranged from a minimum of 8 individuals to a maximum of 16452 individuals. At the present time it is known that foraminifera are not homogeneously distributed but occur in patches of various sizes. This distribution is termed clumped and two reasons are given to explain it: microenvironment (abiotic variables: temperature, salinity, pH, food,... and biotic factors: interespecific and intraspecific interactions) and reproduction (sexual reproduction requires aggregation of foraminifera and asexual reproduction leads to centres of abundance) (Buzas, 1968; Matera and Lee, 1972; Murray, 1973).

Standing crop, although highly variable, exhibits a clear trend from large values in the upper, and particularly middle areas of the estuary, to smaller values in the lower estuary with a final increase near the mouth (Figure 4). This important peak of abundance of living foraminifera in the middle area may indicate relatively high rates of foraminiferal production and consequently high rates of organic production. This general negative gradient in density from the upper estuary to the mouth suggests that the foraminiferal "carrying capacity" of the system decreases in that direction (Ellison and Nichols, 1976). Scott, Schafer and Medioli (1980) defined an area called "transition zone" located in the middle to upper reaches of the estuary and formed as a result of the interaction between the marine and river influences. The effect of this zone is to create a turbidity maximum characterised by high amounts of suspended particulate matter as a result of opposing river and tidal currents being reduced. In addition to the turbidity, sedimentation rates and organic carbon content of the sediment are comparatively high in this zone. Then, these large foraminiferal densities, coupled with both high organic production and fine sediment content detected in samples from this area could indicate the presence of such turbidity, maximum in this zone of the Santoña estuary. Nevertheless, additional oceanographic studies should be necessary to support this fact suggested by the living benthic foraminifera.

The density of the living assemblages results from the ability of the organisms to live and reproduce in the environment. It may be assumed that any given environment is supporting the maximum possible standing crop of foraminifera, and that the number of individuals will decrease or increase in response to changes in food supply, biologic competition, predators or changes in the environment. Even though the standing crop (90 cm^2) values for different loca-

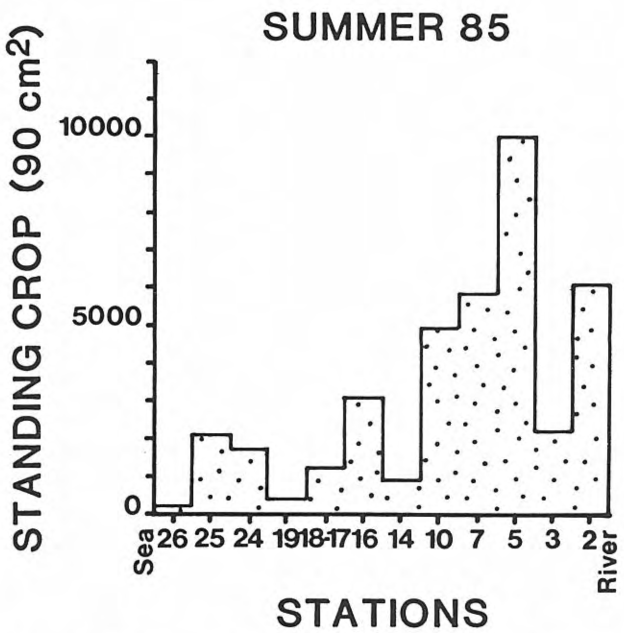

Figure 4. Longitudinal variation of the standing crop (90 cm^2) throughout the estuary.

lities in the estuary vary considerably, a small seasonal variation in the average standing crop exists over the period of study, particularly remarkable in the upper estuary, suggesting that the estuarine environment can support relatively uniform numbers of living foraminifera as a whole (Walton, 1955) (Table 1). Buzas (1970) noted that in the multispecies assemblage, individuals of various species somehow compensate for one another causing more homogeneity on the whole, and he suggested that such a response would be in keeping the most efficient utilization of habitat space and resources. Nevertheless, and as Murray (1968, 1973) pointed out, biomass measurements on foraminifera might be more reliable than standing crop values as an indication of sea floor fertility because they take into account size (juveniles, adults) as well as numbers. Monthly and annual biomass were determined for the most dominant species in an intertidal pool located in the upper estuary (Cearreta, 1988).

Species Abundance and Estuarine Assemblages

During the sampling period 48 different species of benthic foraminifera were found living, although the maximum number of species at any one sampling station was 18 in the upper estuary and 23 in the lower estuary. As it may be expected the number of species oscillates greatly along the estuary with a general increasing tendency seawards. This longitudinal increase in the number of species from the upper to the lower estuary can be explained as a consequence of more stable marine conditions prevailing in the lagoonal lower estuary, particularly in terms of salinity variation.

On the basis of relative abundance (number of individuals of each species as a percentage or ratio of the total number of individuals) and/or frequency of appearance, all these 48 living species have been divided in four different categories (Table 2).

Twenty eight species are thought to be exotic to the Santoña estuary and brought in alive from the littoral area by tidal currents. They appear rarely in the estuary, particularly in the lower area, and normally they do not represent more than 0.3% of the living assemblage at any station. Another group of twelve species are constantly present throughout the estuary and therefore have been considered indigenous but they come to make up less than 1% of the living assemblages.

The remaining eight species represent the most abundant and important species in the living assemblages, with four of them, *Trochammina inflata*, *Jadammina macrescens*, *Elphidium oceanensis* and *Elphidium williamsoni*, being secondary species throughout the estuary, although they show different abundance in the upper and lower areas. Two species, *Miliammina fusca* and *Quinqueloculina seminulum*, are dominant or secondary species in different estuarine areas, and the final two species, *Ammonia beccarii* and *Haynesina germanica*, are the most abundant species throughout the estuary (Table 3).

In the Santoña estuary no foraminiferal zonation can be seen between the two physiographic units sampled, tidal flats and low marsh areas, and conse-

		Upper estuary			Lower estuary			
		MINIMUM	MAXIMUM	AVERAGE	MINIMUM	MAXIMUM	AVERAGE	AVERAGE
Winter	1983	39	11358	3231	144	9108	2917	3084
Spring	1984	82	8559	3212	198	16452	5059	4053
Summer	1984	100	12258	3466	116	8874	3648	3550
Winter	1984	459	8676	3623	306	9117	4276	3913
Summer	1985	76	9981	2931	8	14697	2749	2847

Table 1. Seasonal variation of the standing crop (90 cm^2).

		INDIGENOUS SPECIES			EXOTIC SPECIES	
		DOMINANT	SECONDARY	OTHERS	FOUND LIVING	ONLY DEAD
● Upper estuary ○ Lower estuary ★ Monthly ST#14 only		*Miliammina fusca* (●) *Quinqueloculina seminulum* (○) *Ammonia beccarii* *Haynesina germanica*	*Miliammina fusca* (○) *Trochammina inflata* *Jadammina macrescens* *Quinqueloculina seminulum* (●) *Elphidium oceanensis* *Elphidium williamsoni*	*Hormosina moniliforme* *Ammobaculites balkwilli* *Arenoparella mexicana* *Textularia earlandi* *Cornuspira involvens* *Quinqueloculina jugosa* *Quinqueloculina oblonga* *Fissurina lucida* *Bolivina pseudoplicata* *Brizalina* cf. *B. britannica* *Elphidium margaritaceum* *Haynesina depressula*	*Hormosina nana* *Hormosina scottii* *Haplophragmoides wilberti* *Cribrostomoides jeffreysii* *Ammoscalaria pseudospiralis* *Trochammina intermedia* *Deuterammina ochracea* *Deuterammina rotaliformis* *Eggerelloides scaber* *Quinqueloculina lata* *Massilina secans* *Miliolinella subrotunda* *Patellina corrugata* *Fissurina marginata* (★) *Fissurina* sp. *Buliminella elegantissima* *Brizalina variabilis* *Bulimina gibba/elongata* *Bulimina marginata* *Gavelinopsis praegeri* *Rosalina anomala* *Rosalina irregularis* *Cibicides lobatulus* *Asterigerinata mamilla* *Florilus pauperatus* *Elphidium excavatum* *Elphidium gerthi* *Elphidium* sp.	*Trochammina globigeriniformis* var. *pigmaea* *Spirorutilis wrighti* *Spirillina vivipara* *Astacolus crepidulus* *Lagena laevis* *Lagena tenuis* *Oolina melo* *Oolina squamosa* *Fissurina orbignyana* *Laryngosigma lactea* *Lamarckina haliotidea* *Brizalina difformis* *Fursenkoina fusiformis* *cassidulina carinata* *Cassidulina obtusa* *Cancris auricula* *Planorbulina mediterranensis* *Elphidium crispum* *Elphidium earlandi* *Elphidium macellum*
Nº OF SPECIES		3	5	12	28	20
AVERAGE % LIVING ASSEMBLAGE	Upper estuary	87.0	10.0	2.5	0.5	-
	Lower estuary	80.0	13.0	6.0	1.0	-
AVERAGE % DEAD ASSEMBLAGE	Upper estuary	72.0	18.0	7.5	2.0	0.5
	Lower estuary	61.0	23.0	9.0	6.0	1.0

Table 2. Classification and relative abundance of benthic foraminiferal species found in the living and dead assemblages of the Santoña estuary.

quently both have been treated together in the analysis of data. This phenomenon has been observed before in several other estuarine areas and apparently is due to the small development of the marshes in all these settings, having as a consequence, a dominance of hyaline forms (Phleger, 1970; Matera and Lee, 1972; Scott and Medioli, 1980; Scott and Martini, 1982).

UPPER ESTUARY	living assemblages		dead assemblages	
Ammonia beccarii	1	46.3	2	32.5
Haynesina germanica	2	33.9	1	34.7
Miliammina fusca	3	7.3	5	5.0
Quinqueloculina seminulum	4	3.5	7	2.2
Elphidium oceanensis	5	3.2	8	1.2
Elphidium williamsoni	6	1.4	9	0.6
Trochammina inflata	7	1.1	4	5.6
Jadammina macrescens	8	0.8	3	8.2
Hormosina moniliforme	-	0.7	6	5.0
LOWER ESTUARY				
Haynesina germanica	1	43.6	1	30.7
Ammonia beccarii	2	21.3	2	22.7
Quinqueloculina seminulum	3	15.2	4	7.7
Jadammina macrescens	4	4.4	3	9.9
Elphidium williamsoni	5	3.6	6	5.9
Trochammina inflata	6	2.3	5	6.0
Elphidium oceanensis	7	1.8	9	0.5
Miliammina fusca	8	1.5	8	0.8
Hormosina moniliforme	-	0.9	7	4.2

Table 3. Average relative abundance % and rank order of the main foraminiferal species.

All these abundant species in the estuary are well known and typical estuarine and marsh species around the world (Murray, 1973) supporting the idea that a few highly adaptable and widespread foraminiferal forms occupy all the intertidal areas.

From the analysis of the relative abundances of the most important species it is possible to define two biofacies that characterise different areas in the estuary. The narrow and elongate upper estuary (stations 1-14) with brackish waters and high salinity variation, is characterised by a foraminiferal biofacies with *A. beccarii, H. germanica* and *M. fusca* as dominant species representing altogether an average 87% of the living assemblage. The lagoonal lower estuary (stations 15-26) is characterised by a constant normal marine salinity and a foraminiferal biofacies defined by *H. germanica, A. beccarii* and *Q. seminulum* as dominant living forms making up an average 80% altogether.

Undoubtedly the distribution of benthic foraminifera is caused by the collective action of many environmental factors but the marked changes in faunal composition from the upper to the lower estuary seem to indicate that foraminiferal distribution is mainly controlled by salinity gradients. Santoña is clearly dominated by the hyaline especies *A. beccarii* and *H. germanica*, and presents a co-dominant agglutinated element, *M. fusca*, in the upper estuary and a co-dominant porcellaneous element, *Q. seminulum*, in the lower estuary. One of the most notable features of the distribution of benthic foraminiferal assemblages in estuarine environments is the seaward change from an arenaceous fauna to a dominantly calcareous fauna (Weiss, 1976). Several abiotic factors (temperature, pH, substrate, nutrients, dissolved oxygen, ...) may influence the distribution of foraminiferal biofacies (Matera and Lee, 1972; Greiner, 1974; Scott, Schafer and Medioli, 1980) but the consistant correlation between faunal boundaries and different types of saline water is strong evidence of salinity control of the biofacies. An indicative case is the station 15 situated geographically at the end of the elongate upper estuary (Figure 1) but which exhibits a typical lower estuary biofacies. Opposite to it, on the west bank, it is station 14 which presents an upper estuary biofacies. This fact could be explained, according to Pritchard (1967) by the Coriolis Force that deflects the incoming salt water to the east side of the estuary, and would give additional support in the direction of saline control of the biofacies.

Moreover, the upstream "migration" of living *Q. seminulum* and the reduction in *M. fusca* content in the summer, when salinities in the upper estuary are almost normal marine as a result of a minimum rainfall during this season, gives further evidence of salinity as a main factor controlling distributions in the estuary. Nevertheless, as Buzas (1968) pointed out, although laboratory studies have demonstrated the importance of salinity for the growth and reproduction of foraminifera, field studies however, show that more biofacies can be recognised that can be explained by changes in this variable.

Clearly the most dominant species are those that most actively undergo asexual reproduction within the observed area. Obviously from the study of seasonal samples it is imposible to determine the periods of maximum reproduction for the main species in the estuary. However, juvenile individuals of all dominant species have been found along the estuary at all seasons, suggesting in this way that these four species reproduce continously throughout the year in Santoña although not with the same intensity. Reproduction is particularly active for *M. fusca* in spring and winter in the upper estuary, and for *Q. seminulum* in spring in the lower estuary and summer in both upper and lower estuary. The main reproductive periods are both spring and autumn for *A. beccarii* and *H. germanica* and autumn for *A. beccarii* (Cearreta, 1988).

Figure 5 shows in a diagramatic way the longitudinal and seasonal variation in the relative abundance of the dominant species within the estuary. The living assemblages of winter 1983 and 1984, and summer 1984 and 1985 exhibited 73% and 78% averaged similarity respectively and therefore their data were average and plotted as winter and summer to summarize the species and assemblages spatial and seasonal distribution in the Santoña estuary throughout the year.

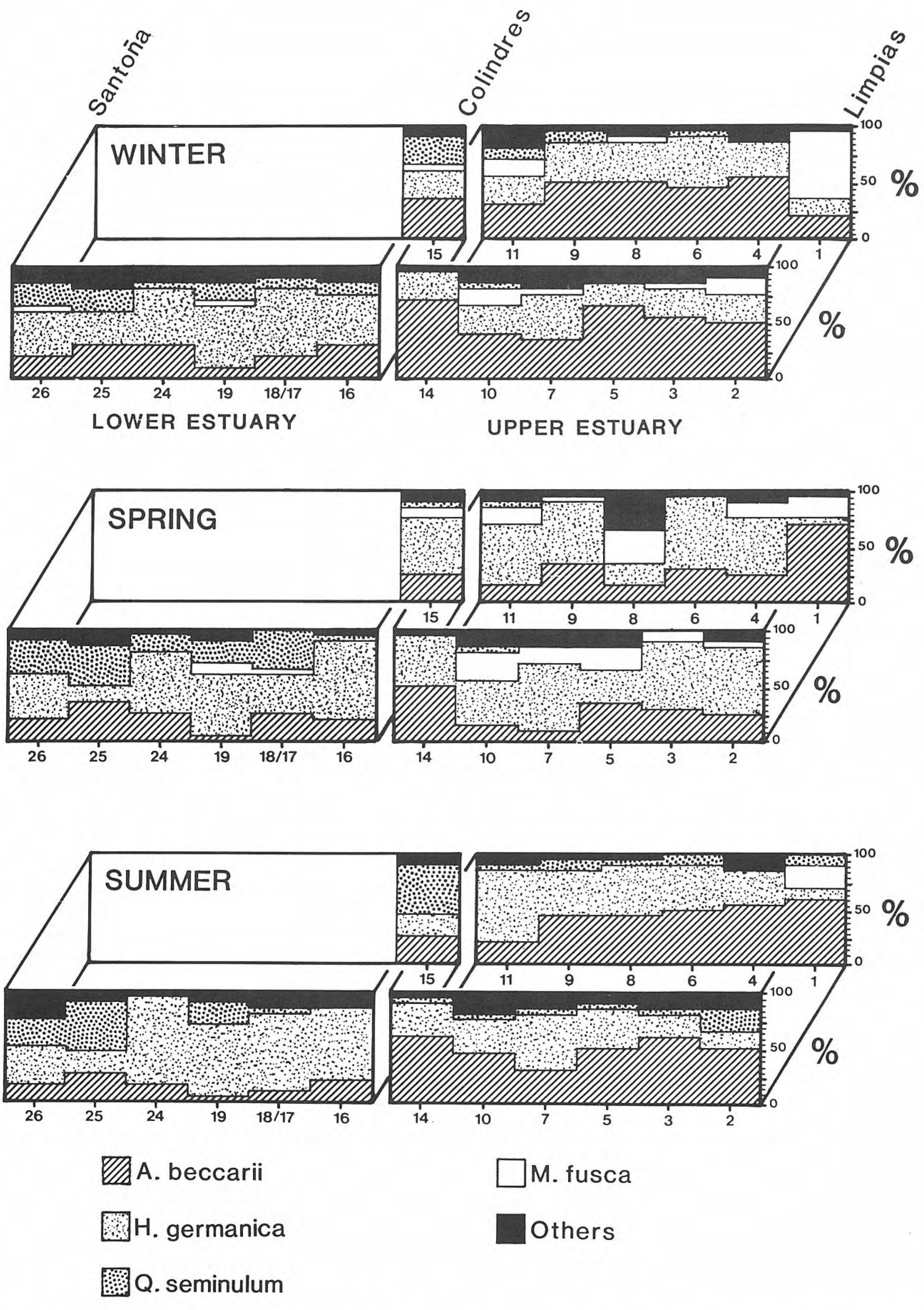

Figure 5. Longitudinal and seasonal variation in the relative abundance of the living dominant species throughout the year.

Diversity Index

It is apparent that estuarine intertidal environments are subject to more extreme ranges of conditions than any other marine environment. Dominance, relative abundance of species in communities and species diversity of communities are intrincately interrelated to the degree of specialization or generalization of the species in the community, generalists species being defined as those able to exploit a broader environmental range (Matera and Lee, 1972). The numerical relationship between the number of species and the number of individuals contained in an assemblage is defined as the diversity of that assemblage. In common with other marginal environments, few species are able to exploit the estuarine environment and often in large numbers. The foraminiferal diversity of estuaries is generally much lower than that observed in other marine environments.

Because samples do not contain the same number of individuals, in order to enable samples of different sizes to be compared a diversity index has been developed. The Fisher α index was first described by Fisher, Corbett and Williams (1943) and the value can now easily be determined by plotting the number of species against the total number of individuals (Murray, 1973). Only the samples from which at least 100 individuals were counted have been used because smaller samples are not considered sufficiently reliable for determination of the value.

There is a clear relationship between the diversity of a foraminiferal assemblage and the nature of its environment. In a general sense $\alpha = 5$ is a boundary separating normal marine environments ($\alpha > 5$) from abnormal environments ($\alpha < 5$). The values obtained for the living assemblages in the Santoña estuary oscilate from <1 to 3.5 in the upper estuary, and from 1 to 4.5 in the lower estuary over the period of study. Studies of the α index for other estuaries all over the world indicate very low values in the upper estuary ($\alpha < 3$) and low values in the lower estuary ($\alpha =$ 1-5) (Murray, 1973) suggesting that the results obtained in Santoña can be considered as characteristic of this estuarine environment. The wider range of values presented by the lower estuary can be attributed to the inmediate influence of open-ocean water invading through the mouth which brings littoral species into the living assemblages and allows a more diverse fauna to live because the conditions in that area are closer to normal marine.

Triangular Plot of Wall Types

Most ecologic studies of recent foraminifera have dealt with distributions of the various species or genera present in a particular area and with the correlation between those distributions and various environmental parameters. Greiner (1974) suggested that in order to extend ecological inferences of a particular faunal group to palaentologic situations, an understanding of environmental interactions with morphologic characteristics transcending specific or generic classifications should be sought.

The nature and structure of the wall of the shell is used to divide foraminifera into major groups. All modern foraminiferids with hard test fall into three types of wall structure: Hyaline, Porcellaneous and Agglutinated, and therefore can be represented on a triangular diagram (Murray, 1973).

The relative abundance distributions of the three wall types of benthic foraminifera are closely related to salinity distributions. The relationship on a local scale shows a gradient of maximum relative abundance for the three types, from agglutinated forms in low salinity waters, to hyaline forms in waters of intermediate salinities, to porcellaneous forms in waters of highest salinity. Each of the various types does not necessarily dominate the fauna at its maximum but only reaches its peak of relative abundance there for the estuary under consideration. The actual environmental factor controlling the distribution of foraminifera is the availability of calcium carbonate that depends to a great extend on salinity, temperature and depth of water. So agglutinated foraminifera are free of restriction to any estuarine area. Hyaline and porcellaneous foraminifera, on the other hand, require Ca CO_3 for the construction of

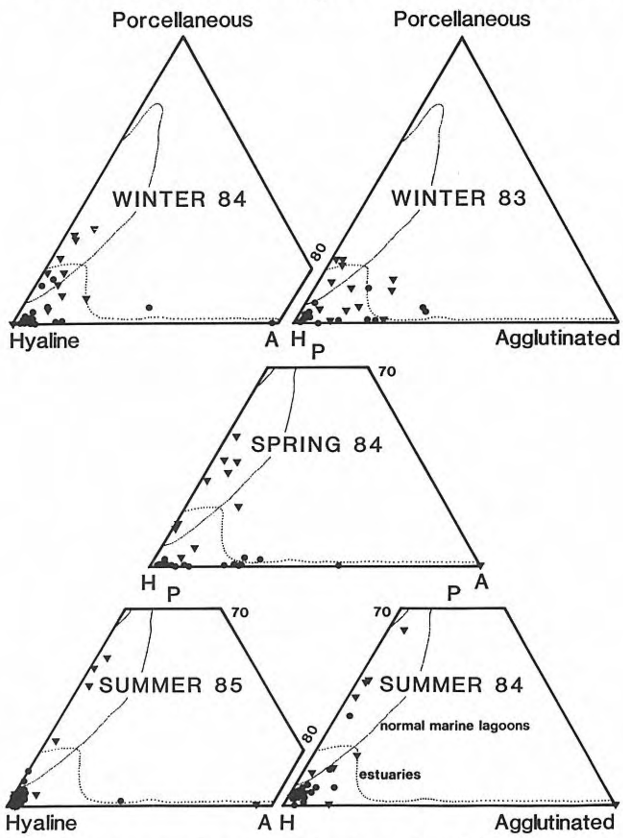

Figure 6. Seasonal variation in the ratio of the three wall types for the living assemblages (dots representing upper estuary and triangles representing lower estuary).

their tests, but the nucleating surface employed by the hyaline foraminifera allows them a great range of habitable environments, whereas porcellaneous forms are restricted to areas of readily available Ca CO_3 (Greiner, 1969, 1974).

Each living assemblage has been plotted, as a dot for the upper estuary and as a triangle for the lower estuary, representing the ratio of the three wall types in Figure 6. The composition of the shell wall is known to be linked to environment in a general way. The upper estuary assemblages, representing a brackish environment, show high abundance of hyaline and agglutinated components and a low content of porcellaneous forms. On the other hand, the lower estuary assemblages, representing a normal marine environment, are basically mixtures of hyaline and porcellaneous forms with small agglutinated component. If the fields defined for estuary and normal marine lagoon environments by Murray (1973) are superimposed on these triangular diagrams it is possible to observe that, in general, all the assemblages fall into these environmental fields, with a majority of upper estuary assemblages fitted in the field for estuaries and a majority of low estuary assemblages included in the field for normal marine lagoons.

DEAD ASSEMBLAGES

Although twenty six different stations were sampled in the Santoña estuary to determine the seasonal abundance and distribution of living benthic foraminifera only once, winter 1983, were all those samples analysed to stablish the relationship between the living and dead assemblages. For the following seasons, only six samples, three in the upper estuary and three in the lower estuary, were studied for their dead specimens content. This modus operandi is based on the belief that the dead assemblages integrate very efficiently all the small seasonal and spatial variations and therefore they are temporarily more homogeneous than the living assemblages.

Composition and Relative Abundance

Since 1952 and the introduction of the rose Bengal staining method, it has become recognised that in any one area the living and dead assemblages differ to a greater or lesser extent (Murray, 1976).

Examination of the dead assemblages reveals those differences, and their possible causes can be divided in two: production and post-mortem changes (particularly transport). Production, in its widest sense, includes all the new organisms produced during a unit of time regardless of whether or not they survive, because ultimately they are added to the dead assemblages. Production is a life process affecting the living assemblages, and particularly the indigenous species are subject to variations caused by it. The dead assemblages are built up over a period of time and therefore reflect the cumulative effects of the annual production (Murray, 1976). In Santoña each species reproduces at different rates and seasonal influences are fundamental in the intensity of the foraminiferal production (Cearreta, 1988). Consequently, the dead assemblages do not resemble in detail any seasonal living assemblage, and the rank order of abundance of particular species in the dead assemblage differs from that in the living.

In the upper estuary the two most dominant living species are still the most abundant in the dead assemblages, but *H. germanica* shows now the highest percentages, with *A. beccarii* being the second abundant species. They are followed by *J. macrescens* and *T. inflata* that are much more abundant in the dead assemblages, with *M. fusca* removed to the fifth position. An important new element is *Hormosina moniliforme* that as living is just another indigenous species, but it exhibits the same abundance than the co-dominant living species *M. fusca* in the dead assemblages.

In the lower estuary, *H. germanica* and *A. beccarii* occupy the same positions as dominant dead species as they did in the living assemblages, with *J. macrescens* being now more important than the co-dominant living species *Q. seminulum* in the dead assemblages. The species *T. inflata*, *E. williamsoni* and *H. moniliforme* are substantially more abundant in the dead than in the living assemblages (Table 3).

Possible post-mortem changes include transport of test away from assemblages (loss) or into assemblages (mixing), loss by solution or other destructive processes, and mixing by bioturbation or through non-sedimentation accompanied by an environmental change (relict assemblages) (Murray, 1984).

Estuarine environments are commonly areas of fairly active sediment accumulation. There are 3 different sources of sediments in a partially-mixed estuary: clay-grade materials transported down river in suspension that accumulate in the turbidity maximum area as a consequence of the water circulation pattern, sand and fine material removed from the nearshore areas and transported in as bed-load or in suspension respectively by the tidal currents, and finally, reworked sediments from within the estuary (Wang and Murray, 1983).

No fossil forms have been found in the samples and therefore the dead assemblages are composed of two elements: indigenous forms, showing a broad size range from juveniles to adults, and exotic specimens. The exotic component introduced in suspension is made up of small, thin walled forms like *Lagena*, *Oolina*, *Fissurina*, *Brizalina*, ... and juveniles of larger shells like *Cibicides*, *Rosalina*, *Asterigerinata*, ... that settle out at slack water high tide and are distributed along the estuary. The tests transported as bed-load, on the other hand, are most commonly found in the sandy lower estuary areas and comprise robust shells of *Cibicides*, *Elphidium*, *Planorbulina*, *Massilina*,... In general exotic specimens have been found all over the estuary and no substantial difference has been observed between low and high tide marks, probably due both to the small size of the estuarine area and the low development of the low marsh unit.

In the Santoña estuary while 48 species have been found in the living assemblages, an additional 20 forms were exclusively encountered as dead tests. From all these total 68 species recorded only 20 forms, showing different degrees of dominance, are considered truly indigenous of the estuary, whereas the other 48 species are thought to be exotic forms brought in from littoral and inner shelf areas by the tidal currents, both as living and as dead tests as a consecuence of their overall equal density (Murray, 1976) (Table 2).

The very effective landward movement of foraminifera can be demonstrated not only by the presence of small exotic species transported in suspension on the mudflats and low marshes along the estuary, but also by the presence of bed-loaded, robust, abraded empty shells of *C. lobatulus* and *M. secans* at station 1, located in the sandy uppermost tidal area of the estuary, more than 9 kms. away from the mouth.

Diversity Index

In any one area of sea floor, the dominant species are usually the same from sample to sample. The secondary and other indigenous species may be common to some samples but missing from others, and the exotic species are almost invariably irregularly distributed, and it is not unusual for each sample to have some rare species which are absent from all the others. The main reasons for this are firstly, the known patchiness on sea floor, with large patches of dominant species and ramdom distribution of rare species (Buzas, 1968), and secondly, the irregular time distribution of the rare species. These features have important consecuences for the dead assemblages because they are cumulative from a long period of time, and therefore, all the temporal species will be present increasing the diversity of the dead assemblages (Murray, 1976).

Studies of modern estuaries have shown that they are characterised by low-diversity assemblages of living benthic foraminifera. The dead assemblages are commonly more diverse and this has been attributed both to transport into the estuary of marine species from the sea and the cumulative contributions through time of rare short-lived species. As faunal dominance is related to species diversity, dominance decreases in the dead assemblages.

The α values obtained for the dead assemblages in the Santoña estuary ranged from 1.5 to 4.5 in the upper estuary, and from 1.5 to 10.5, although most of the obtained values are<5, in the lower estuary over the period of study.

Triangular Plot of Wall Types

Both production differences and post-mortem changes are likely to alter the relative position of the dead assemblages on the triangulart plot.

At all seasons the dead assemblages exhibit a dominance of hyaline and agglutinated components with a very low content of porcellaneous. The most striking feature is the decrease in porcellaneous element and the increase in agglutinated tests in relation to the living assemblages. As a consequence, the lower estuary stations that defined a normal marine lagoonal area on the triangular plot with their living assemblages, are fitted now in the field of estuaries together with the upper estuary assemblages.

Several authors have noticed that although calcareous species are characteristically present in the living assemblages of intertidal areas, sometimes they are much less commonly preserved in the dead assemblages as a result of the reducing conditions prevailing in the sediments due to the abundance of decomposing organic material. In the present study only the superficial oxidised layer of sediment was sampled and, on the other hand, hyaline forms are still dominant in the dead assemblages. Therefore, dissolution of calcareous tests cannot be invoked as a post-mortem process to explain this low abundance of dead porcellaneous tests. Probably the most reasonable explanation would be a change in the environmental conditions, affecting particularly the lower estuary, that derived the development of *Quinqueloculina* as a new dominant element in the living faunas. This change could be connected with the destruction of vast marsh areas due to land reclamation during recent years (1960-1970), that could provoke an increase in the sediment accumulation on intertidal areas affecting in this way the balance between the two water masses in the estuary. This could explain as well the high percentages of the agglutinated marsh forms *Jadammina* and *Trochammina* in the dead assemblages in comparison with their low abundance as living specimens. This environmental alteration has taken place too recently to be reflected yet in the dead assemblages. Only the study of some borehole material from different areas in Santoña could help to determine the evolution of this estuarine basin and it should clarify this point.

COMPARISON OF LIVING AND DEAD ASSEMBLAGES

It is possible to compare the living and dead assemblages at each sampling point using the similarity index. This is calculated in the following manner. The results for the living and dead assemblages are expressed as percentages, each summed to 100%.

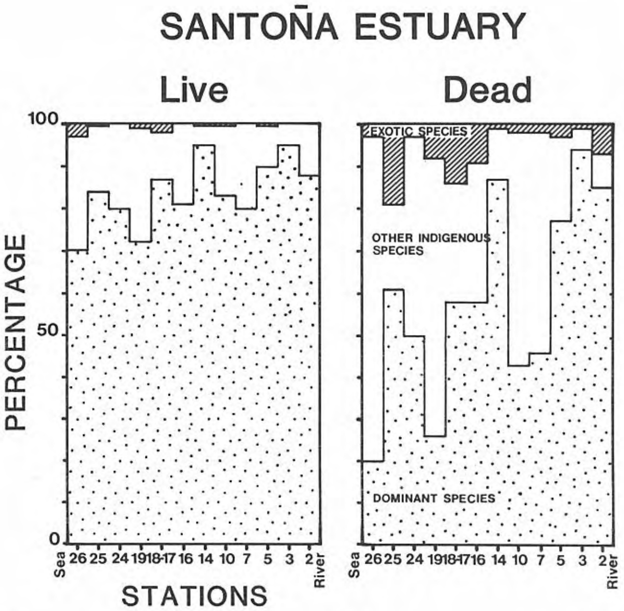

Figure 7. Living and dead assemblages composition along the estuary in winter 1983.

The results of both assemblages for the same sample location in a particular season are then compared on a species by species basis. For each species the lower of the two percentage values is taken and these are summed to give the similarity index (Sanders, 1960). The values are by definition<100% and in practice any value of >70% indicates a high degree of similarity for these low diversity assemblages.

Throughout the intertidal area the values obtained are moderate and very similar for all seasons (average 65%), with slightly higher similarities in the upper estuary (average 67%). The difference between the living and dead assemblages can be attributed in part to seasonal changes in the fauna related to salinity conditions (changing production rates) and also to transport of forms into the estuary from the sea.

Certain relationships between the distribution and abundance of empty tests and living specimens may provide insights into processes of estuarine sedimentation (Nichols and Ellison, 1967). One aspect of the relationship between foraminifera and tidal effects is the distribution of assemblages along the length of the estuary. Obviously the living assemblages are formed basically of indigenous species, and although the dead assemblages are made up of a mixture of indigenous and exotic forms, the former predominate. The data show a clear decrease in the abundance of the dominant species and a relative increase in the rest of indigenous species and exotic forms towards the sea, for both the living and dead assemblages in the Santoña estuary. If the living and dead distributions are compared a reduction is apparent in the dominant species component and an increase is detected in both the rest of indigenous forms and the exotic tests in the dead assemblages (Figure 7).

Wang and Murray (1983) determined that the overall abundance of transported species depends on the tidal regime, with a moderate proportion of exotic foraminifera (up to 35%) characterising partially-mixed (mesotidal) estuaries. Santoña is a mesotidal estuary and shows a variable percentage of exotic species with a maximum of 19.5% detected near the mouth, and an average of 7% in the lower estuary and 2.5% in the upper estuary over the period of study.

SUMMARY AND CONCLUSIONS

Foraminifera comprises but one element of the benthic community in the dynamic stressful estuarine system, large in number but small in total biomass. Although faunal boundaries and population sizes fluctuate seasonally and longitudinally along the environmental gradient from the river to the sea, the species composition of foraminiferal faunas is relatively distinct and stable and therefore the distribution and abundance of these faunas should provide useful ecological information about the estuarine ecosystem (Ellison and Nichols, 1976). In the Santoña estuary both the distribution and abundance of living benthic foraminifera seem to be determined by the mixing of two different water masses that meet within the estuary. The salinity gradients created along the estuary control the foraminiferal biofacies that define two estuarine areas, and the availability of nutrients and materials supplied by these riverine and marine water masses support the high density of foraminifera in Santoña, particularly in the upper estuary where they meet.

Although 68 different species of benthic foraminifera were found in the estuary, 71% of those are considered exotic forms, with 42% of these exotics found only as dead tests. Both living and dead assemblages are made up basically of the dominant species with higher percentages both in the upper estuary and the living assemblages. The secondary and the other indigenous species are more important in the lower estuary where conditions are more stable and their percentages increase substantially in the dead assemblages. The abundance of the exotic forms increases in the lower estuary and particularly in the dead assemblages but even so they always represent a minimum component of the assemblages.

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PLATE I

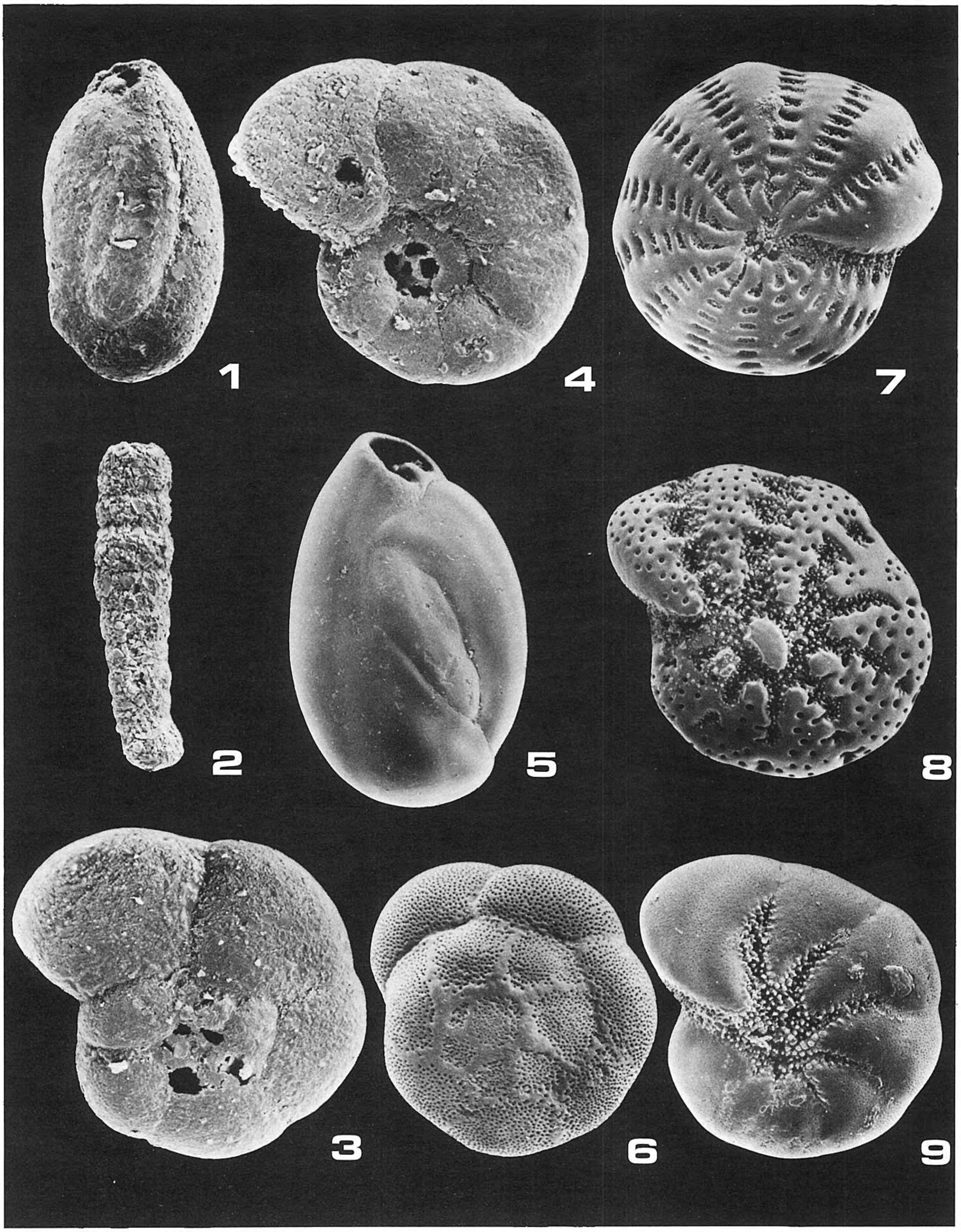

Plate I.- **1.** *Miliammina fusca* (Brady), × 145; **2.** *Hormosina moniliforme* Siddall), × 110; **3.** *Trochammina inflata* (Montagu), × 390; **4.** *Jadammina macrescens* (Brady), × 145; **5.** *Quinqueloculina seminulum* (Linne), × 235; **6.** *Ammonia beccarii* (Linne), × 185; **7.** *Elphidium oceanensis* (d'Orbigny), × 250; **8.** *Elphidium williamsoni* Haynes, × 130; **9.** *Haymesina germanica* (Ehrenberg), × 215.

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