MOLLUSCAN BIOCOENOSES AND THANATOCOENOSES IN THE RIA DE AROSA, GALICIA, SPAIN

by

G. C. CADÉE
Nederlands Instituut voor Onderzoek der Zee, Den Helder

CONTENTS

INTRODUCTION

The present study forms a part of a biological, oceanographical and sedimentological investigation carried out in the Ria de Arosa, northwestern Spain 1962-1964. This investigation was undertaken jointly by the Department of Geology and Mineralogy, University of Leiden and the Rijksmuseum van Natuurlijke Historie, Leiden, and financially supported by the Netherlands Organisation for the Advancement of Pure Research (Z.W.O.) Details of the aim and scope of these investigations have been set forth by Brongersma & Pannekoek (1966).

The present paper deals with the shell-bearing molluscs collected during these investigations and contains some remarks on skeletal remains of other organisms found in the sediments. A representative collection of all species of Mollusca obtained in the Ria de Arosa is kept in the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

I wish to express my sincere thanks to all the members of the Ria the Arosa expeditions, especially to dr. M. Brongersma-Sanders, dr. J. D. de

Jong and dr. W. Vervoort; to Ir. L. Otto and Mr. W. S. Koldijk, who made available respectively their oceanographical and sedimentological data to me; to my brother who assisted especially in collecting the molluscs. Deseo expresar aqui mi agradecimiento al Don Luis Losada Lago de Villagarcia de Arosa, quien generosamente puso a nuestro disposición su fábrica situada en el Punto Preguntoiro, cerca de Villagarcia para instalar un laboratorio temporal durante las investigaciones.

It is a pleasure to thank Mrs. I. Den Hartog-Adams who very carefully corrected the English text.

My thanks are also extended to Mr. W. C. Laurijssen for making the photographs, to Mr. W. Bergmans who made most of the drawings, and to Mrs. J. K. Stegeman-Geervliet for typing the manuscript.

I. DESCRIPTION OF THE AREA

Topography (see fig. 1).

The Ria de Arosa is the largest of the four "rías bajas", deep bays on the west coast of Galicia. The total length, from the island Salvora at the entrance to the estuary of the River Ulla at its upper end amounts to some 25 km in a straight line. The width is variable due to islands and embayments. The total surface of the ria is about 230 km^2 (L. Otto, pers. comm.) (compare the Ria de Vigo: 183 km^2, Saiz et al., 1957:40).

With respect to the bottom topography, the most conspicuous feature is the central channel which is 60 m deep near the entrance of the ria. The depth diminishes 7.5 km inwards to less than 50 m, but increases again to more than 60 m in the narrower part west of the Isla de Arosa. The inner part of the ria becomes silted up by the Ulla, the largest river discharging into the upper end of the ria. The outer part of the ria receives less sediment and as a consequence the bottom here is more irregular, the shoals are not masked by sediments. Some of these shoals rise above sea level to form small islands. The coastal features show wide variation, rocky cliffs alternating with sandy beaches. The rocks exposed on the coast are for the greater part granites, the rest, especially on the northwestern and northern shores, being gneisses and micaschists. In the protected bay behind the peninsula of El Grove there are extensive tidal flats with some salt-marshes along the margins.

Climate.

The climate can be characterized as temperate humid (Saiz et al., 1957:33).

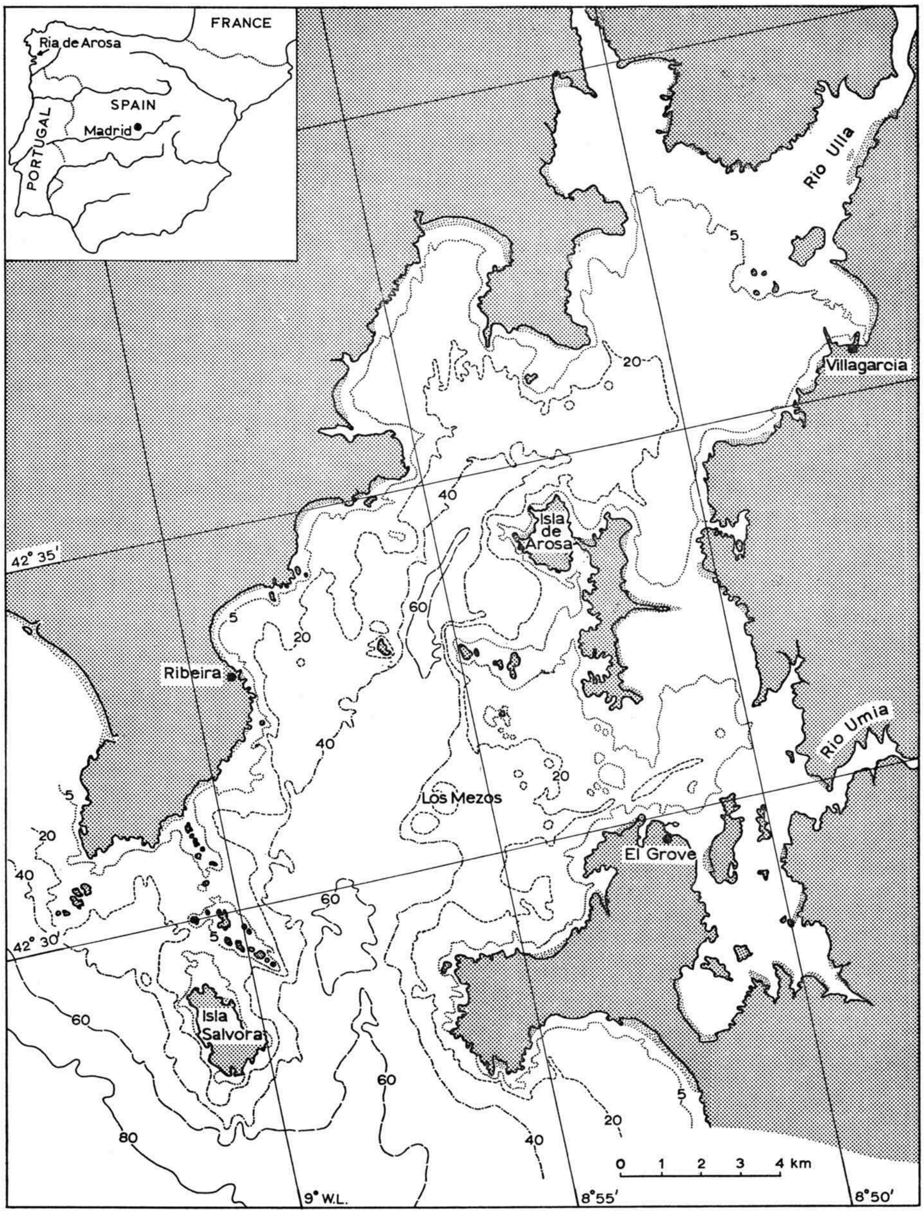


Fig. 1. Situation map and bathymetry of the Ria de Arosa.

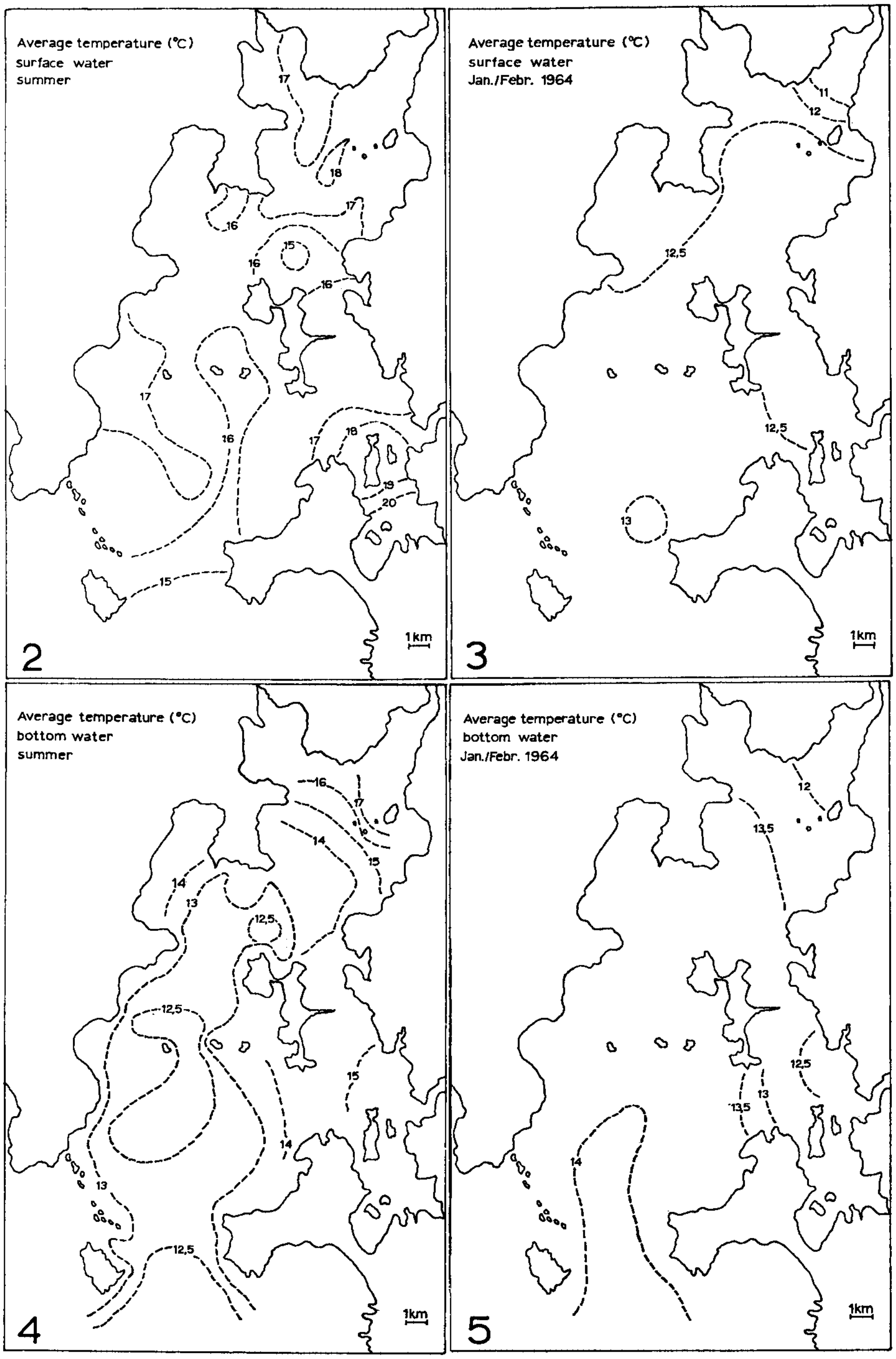


Fig. 2-5. Temperature of surface and bottom water in summer and winter.

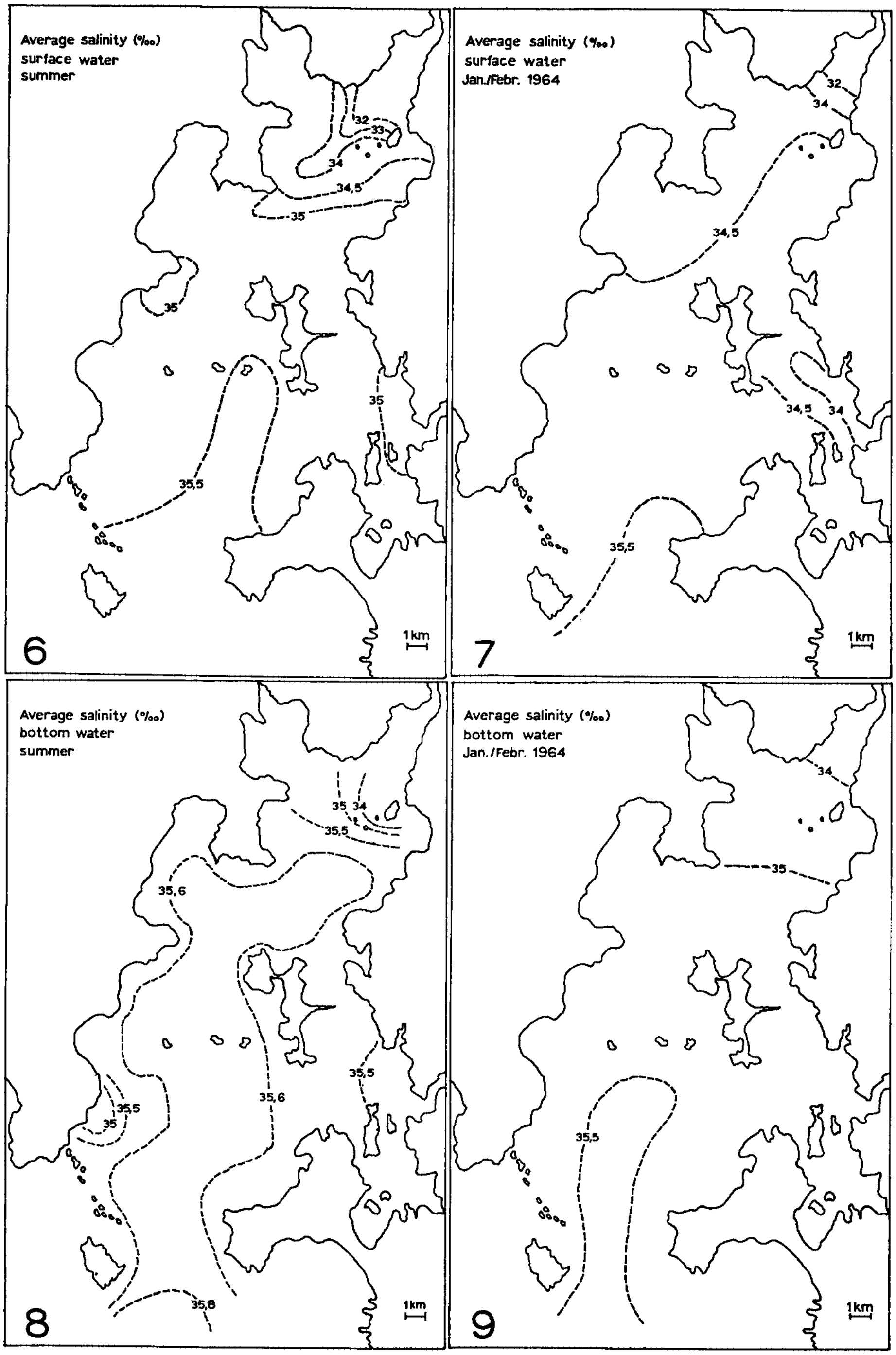


Fig. 6-9. Salinity of surface and bottom water in summer and winter.

The mean air temperature varies from 8° C in January to 20° C in July/August at Pontevedra. Precipitation reaches its minimum in summer and is high during the rest of the year. The mean annual precipitation is about 1500 mm. The wind blows in summer predominantly from northerly directions, in winter the wind is more variable.

More extensive weather data will be published by L. Otto.

Hydrography.

Tides and currents. — At Villagarcia (inner part of the ria) the tidal range amounts to 3.5 m at spring tide and 1.1 m at neap tide. Westerly winds cause an increase in the rise which sometimes amounts to 0.4 m, and easterly winds a similar decrease. The tidal currents attain a maximum rate of one knot (50 cm/sec), except in the narrow channels where they are somewhat stronger (Pilot, 1957: 102). According to measurements by L. Otto (pers. comm.) wind-driven currents may be more important in the ria than tidal currents. His measurements give a mean maximum current for the surface layer of 30 cm/sec and a range of 5 to 91 cm/sec (based on 16 measurements over the whole ria). In an intermediate layer from 10 to 30 m

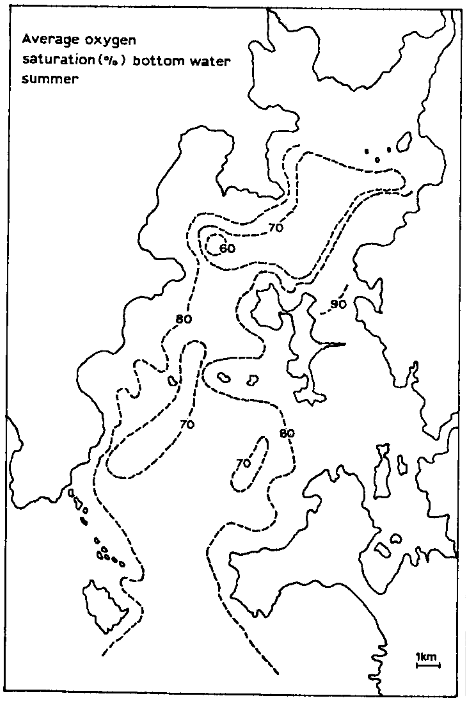


Fig. 10.

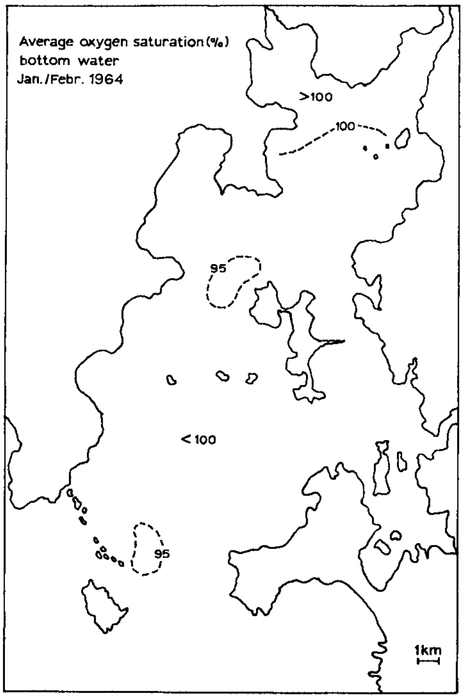


Fig. 11.

he found a mean maximum current of 20 cm/sec and a range of 8 to 57 cm/sec (12 measurements). In the bottom layer the current velocity will be still lower as indicated by the presence of soft fine sediments, but measurements were not made.

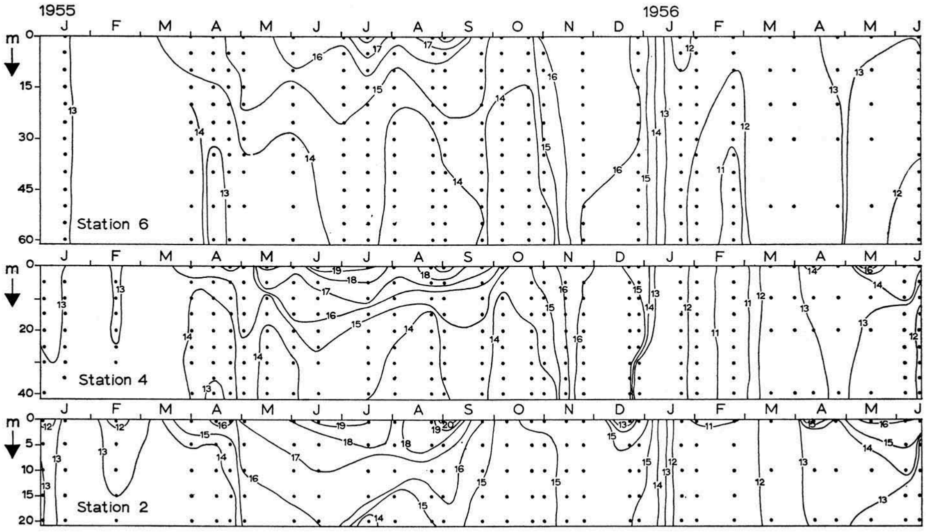


Fig. 12. Seasonal variation of the vertical distribution of the temperature in the Ria de Vigo (for location of stations, see fig. 14).

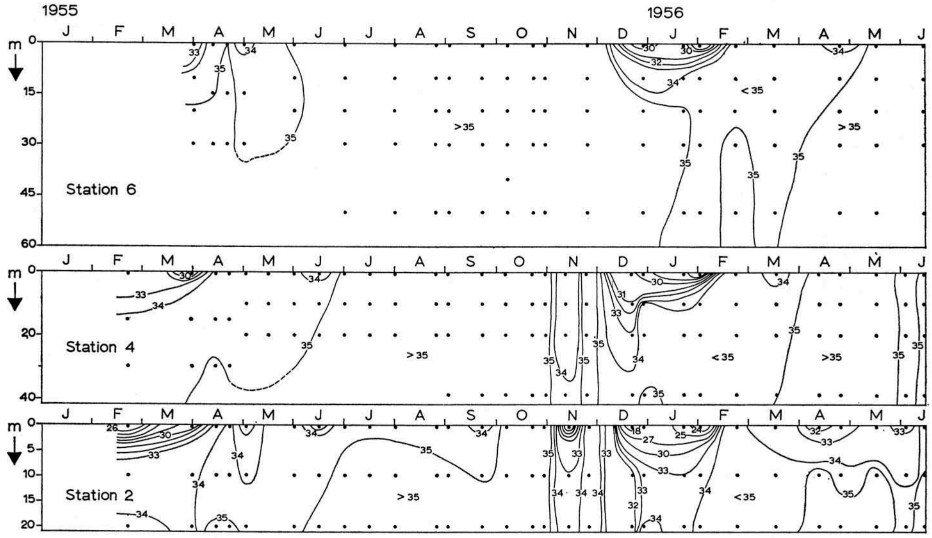


Fig. 13. Seasonal variation of the vertical distribution of the salinity in the Ria de Vigo (for location of stations, see fig. 14).

Temperature and salinity. — Figs. 2 to 9 give the average surface and bottom water data for summer and winter. These data can be compared with those from the hydrographically best known of the "rías bajas" in Galicia, the Ria de Vigo, published by Margalef et al. (1955), Duran et al. (1956), Vives & Lopez-Benito (1957) and Saiz et al. (1957), who give the fluctuations of hydrographical factors from January 1953 to June 1956.

In table I the data of the two rias are compared. They show a great similarity, but the winter data of the Ria de Arosa show a much higher salinity because they date from a dry winter period, with little river discharge. As the drainage area of the Ria de Arosa is about four times as large as that of the Ria de Vigo, 3560 km^2 and 958 km^2 respectively (L. Otto, pers. comm., and Saiz et al., 1957:40), it is possible that in wet periods, because of the greater river discharge, the surface salinity of the Ria de Arosa may be lower than in the Ria de Vigo.

Table I

		inner part the of ria				outer part of the ria				Atlantic ocean outside the rias			
		surface		bottom (20 m)		surface		bottom (40 m)		surface		bottom (80 m)	
		T°C	S^0/oo	T°C	S^0/oo	T°C	S^0/oo	T°C	S^0/oo	T°C	S^0/oo	T°C	S^0/oo
winter minimum	Ria de Arosa	12.5°	33	13.5°	35	13°	34.5	14°	35.5	—	—	—	—
	Ria de Vigo	10.1°	18.0	11.4°	32.6	12°	26.7	10.8°	34.3	11.8°	29.9	10.1°	34.9
summer maximum	Ria de Arosa	21.5°	35.0	13.0°	36.0	17.0°	35.5	13.0°	36.0	16.0°	35.7	12.0°	36.0
	Ria de Vigo	20.0°	35.6	16.6°	35.8	19.4°	35.6	16.0°	35.7	18.4°	35.8	16.0°	35.9

In both rias there is a decrease in temperature and salinity range from the surface to the bottom and from the inner part of the ria to the Atlantic waters outside.

Figs. 12 and 13 give the temperature and salinity of 3 stations in the Ria de Vigo (see map fig. 14) from January 1955 to June 1956, based on data of Duran et al. (1956) and Vives & Lopez-Benito (1957). They are given here because the differences between this ria and the Ria de Arosa are supposed to be small.

From these data the following conclusions may be drawn:

1. River influence is small in the ria during the greater part of the year, therefore the estuarine circulation (in the sense of Pritchard, 1952) will not be important in the ria.

2. The water mass in the ria is stratified during the greatest part of the year, showing homogeneity (due to convection currents and renewal of bottom water) in October-November and February-March.

3. Renewal of bottom water in summer takes place through the influx of

cold bottom water from outside the ria (May and July-August 1955; June 1956). This influx of bottom water is presumably caused by persistent northerly winds in summer, which push the surface water towards the ocean, giving rise to an "estuarine-like circulation" in the sense of Brongersma-Sanders (1965:370).

Shelf waters outside the rias are characterized by rather low surface temperatures in summer (data collected by the Spanish hydrographic vessel "Xauen" in 1950 and 1951). These low surface temperatures, especially close to the coast, are due to upwelling caused by the northerly winds in summer. Upwelling outside the rias and influx of cold bottom-water in the rias are of great biological interest: they give the fauna and flora a more northern character as compared with the north coast of Spain where no upwelling occurs (see also Fischer-Piette, 1955:108).

Oxygen. — Figs. 10 and 11 give the average oxygen saturation of the bottom water in summer and winter in the Ria de Arosa. These data may be compared with those from the Ria de Vigo where oxygen data were collected from July 1955 to June 1956 (Vives & Lopez-Benito, 1957: 102-104). Fig. 14 is based on these data, again we suppose them to be rather similar in the Ria de Arosa. As the water samples for oxygen data of the bottom water were always taken some metres above the bottom, oxygen values may be lower close to the bottom, where a microstratification may exist. These data indicate a saturation or slight supersaturation for the surface layer from March to September; apparently due to high oxygen production by phytoplankton. Mixing with undersaturated deeper water and less oxygen production evidently accounts for the undersaturation of surface water during the rest of the year.

Bottom water is always undersaturated: consumption of oxygen is always higher than its production. The lowest oxygen values (20% saturation) were measured during a period of "Red Water", a dinoflagellate plankton bloom in August-September in the Ria de Vigo (Vives & Lopez-Benito, 1957:117; Margalef, 1956b). The absence of precipitation and wind, and as a consequence minimum exchange of water with the ocean, are thought to be favourable for these blooms in the Ria de Vigo (Margalef, 1956b). The combination of these factors also prevents the bottom water from being renewed, which results in a low oxygen saturation value, and perhaps an absence of oxygen in the water nearest to the bottom.

"Red Water" occurred in the Ria de Vigo in September 1953 and August-September 1955 (Margalef, 1956b); according to local residents it is also known in the Ria de Arosa.

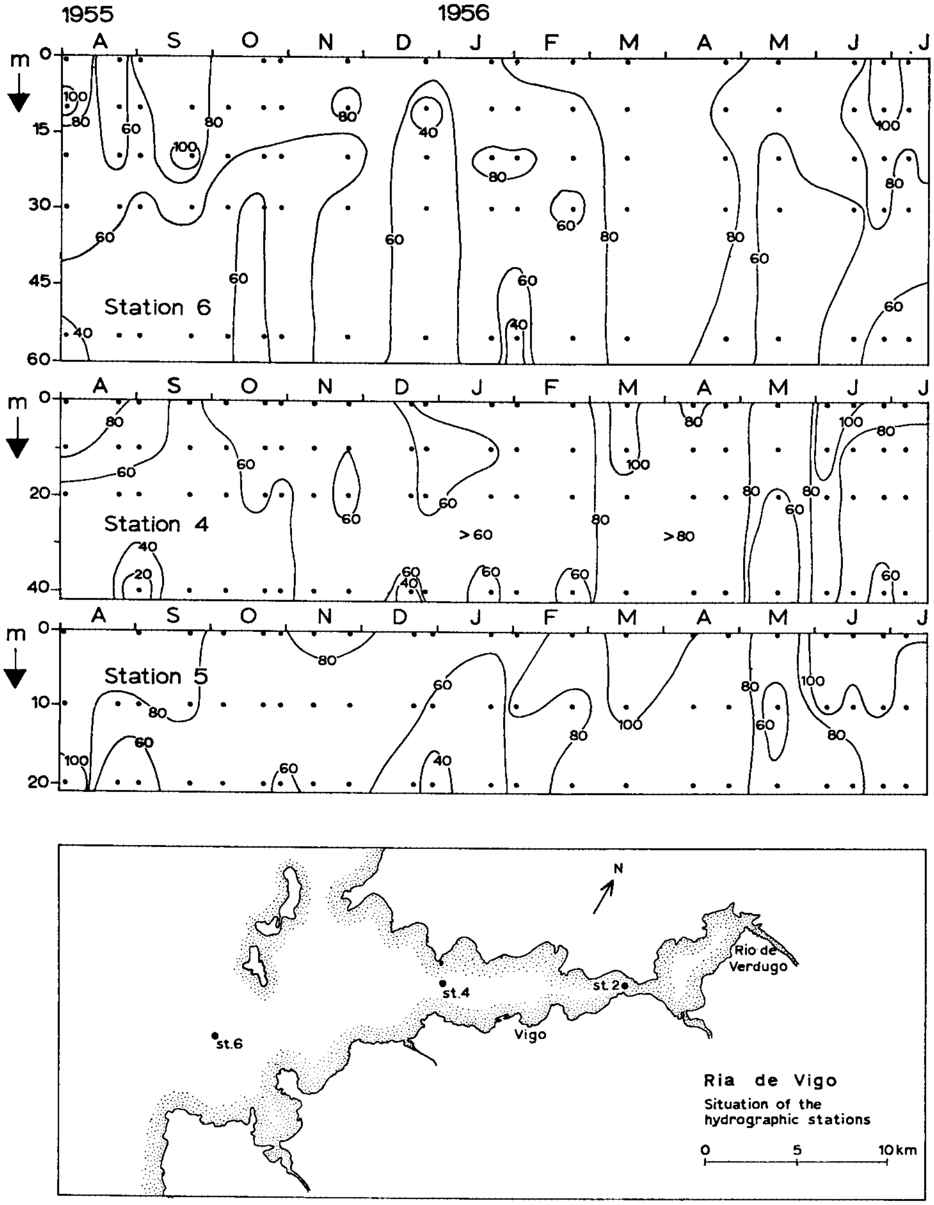


Fig. 14. Seasonal variation of the vertical distribution of oxygen saturation in the Ria de Vigo and location of the stations.

Turbidity. — The mean Secchi-disc visibility was found to be 5 to 6 m in the ria, the lower values occurring in the inner part. This indicates that the water in the ria is rather clear. In the North Sea off the coast of the Netherlands such values are found only at distances of at least 20 km offshore (Sweers, 1965: 5-1). The Ria de Arosa data are similar to those reported from the Ria de Vigo (Duran et al., 1956). Measurements of suspended material gave low values, mostly lying between 5 and 10 mg/l (compare Dutch coastal waters where suspended matter usually amounts to more than 10 mg/l, while values of 50 mg/l are no exception: Postma, 1961).

The hydrography of the area will be dealt with in detail by L. Otto in a future publication.

Sediments.

Grain-size. — Fig. 15 is based on grain-size data kindly supplied by Mr. W. Koldijk. The map shows the distribution of sediments, which is normal for basins, viz.: coarser sediments in a marginal zone along the coast, silt-clay sediments in the central part. Besides shells and organic debris, only a little sediment is deposited on the shelf off the ria.

As currents are never strong in the ria, wave action seems to be of major importance in the distribution of sediments, especially in preventing the settlement of the silt-clay fraction in the marginal zone. Ocean waves and swell can enter the ria through the southern entrance only, because the northern entrance is shallower and numerous isles and reefs form here a natural breakwater. A prediction of wave heights in the Ria de Arosa for dockworks in the inner part of the ria gave the following results: a wave generated by a south-west storm and 10 m high at the entrance to the ria will decrease to 7 m after travelling 4 km in the ria, to 5 m after travelling 7 km, to 2 m after travelling 13 km and to 1 m after travelling 16 km. Waves generated by a storm in the ria itself do not attain heights of 1 m or more, because the fetch is too small.

These data show that the inner part of the ria is better protected from waves than the outer part. This is reflected in the sediments: in the inner part of the ria silt and clay-rich sediments occur in a much smaller depth than in the outer part (about 5 m and 20 m resp.). In a very well protected embayment in the northern part of the ria the sedimentation of silt-clay sediments begins below 3 m. Sediments in the inner part of the ria are also softer (contain more water), than those from the outer part, perhaps as a consequence of this more sheltered character of the inner part of the ria.

Sediments deposited in the Ria de Vigo were demonstrated by Margalef

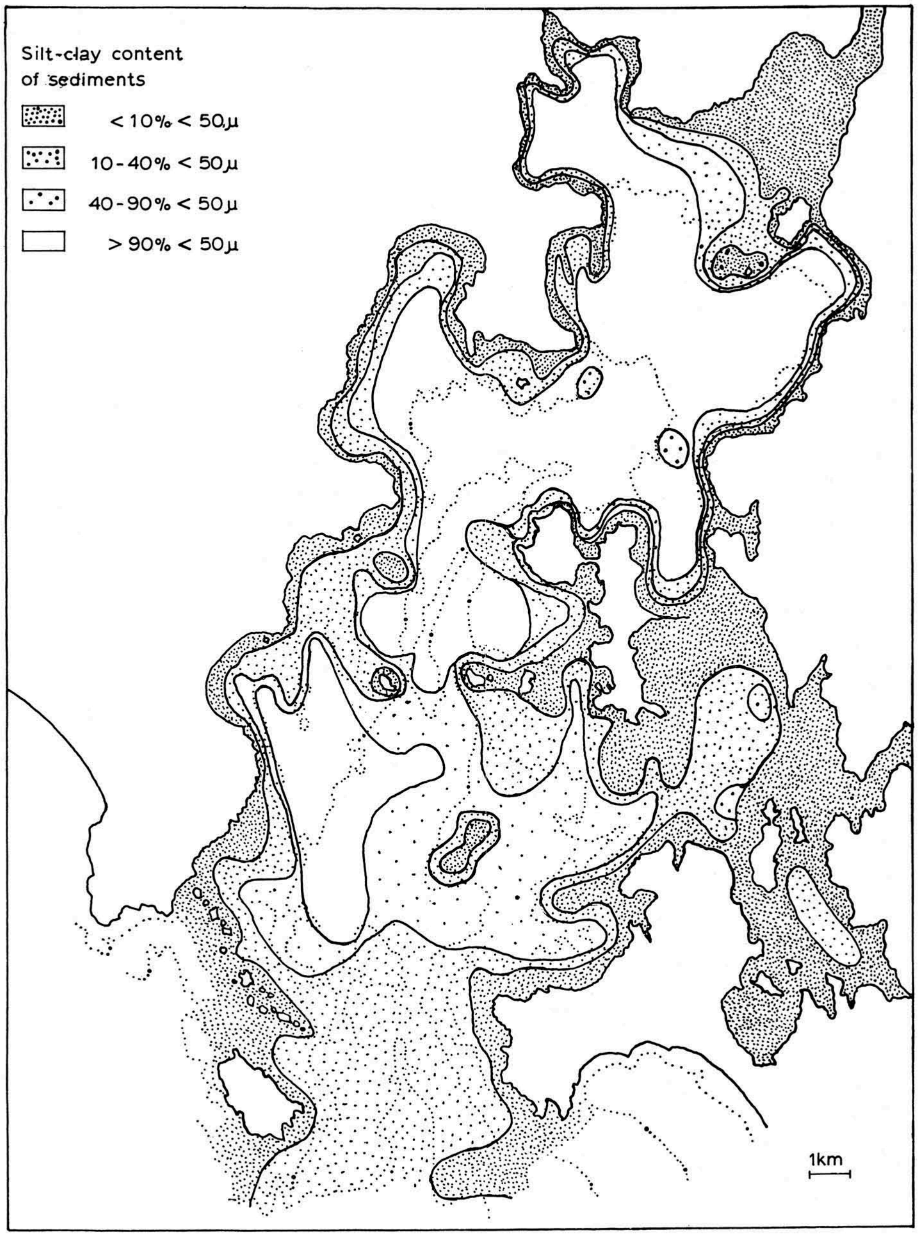


Fig. 15. Silt plus clay content of the sediment.

(1956a) to be of Holocene age. Margalef studied a sediment core of 7.8 m taken off Vigo. It is supposed that during the lower sea level in the different glacial stages the rias were above sea level and cleared of sediments (Pannekoek, 1966: 294).

Organic carbon content. — 46 surface silt-clay sediment samples, all from the central part of the ria, were analysed. The analyses were made with a "Coleman carbon hydrogen analyzer" kindly made accessible to me by Prof. H. Postma, in the Nederlands Instituut voor Onderzoek der Zee (Netherlands Institute of Sea Research), Den Helder. The samples were dried as soon as possible, usually within a day of sampling, at approximately 100° C. in order to stop bacterial activity. $CaCO_3$ was removed with 0.1 N HCl.

In the Coleman carbon hydrogen analyzer a weighed quantity of powdered sediment (about 50 mg) is placed in a platinum boat in a pyrex tube with Cuprox. The sample is burned at a thermostatically controlled temperature of about 700° C. Oxygen, purified by an absorption tube with anhydrous Mg-perchlorate and Ascarite, is passed through the tube. All combustion products except CO_2 are removed in absorption tubes with MnO_2 and anhydrous Mg-perchlorate. The CO_2 is then collected in an Ascarite tube which is weighed before and after burning of the sample, from the increase in weight the C content of the sample can be calculated. All analyses were duplicated. The results are shown in figs. 16 and 17. Organic carbon in the Ria de Arosa silt-clay sediments ranges from 1.63 to 6.98%. In the inner part of the ria the mean values are higher (4-6%) than in the outer part (2-4%). The decrease from the rivermouth to the entrance of the ria is very regular.

There is also a relation between grain-size and organic carbon content: the sediments richer in clay are in general also richer in organic carbon. There are, however, some exceptions. Samples close to the mouth of the Rio Ulla have high organic C (6%) in somewhat coarser sediments (20-30% clay). This must be due to plant fragments which were found sometimes in great quantities close to the rivermouth.

These data agree very closely with those from the Ria de Vigo. Fernandez del Riego (1956) found a range of organic carbon content from 0.72-6.99%, the highest values occurring in the inner part of the ria. Margalef (1958) studying pigment contents of silt-clay sediments of the entire Ria de Vigo, found the same regular decrease from the rivermouth to the entrance. He also concluded that these pigments in the sediment had a marine phytoplanktonic origin because of the similarity with the pigments of the plankton.

As phytoplankton is generally seen as the main source of organic matter in sea (Bordovskiy, 1965:9) it is of interest to remark that Vives &

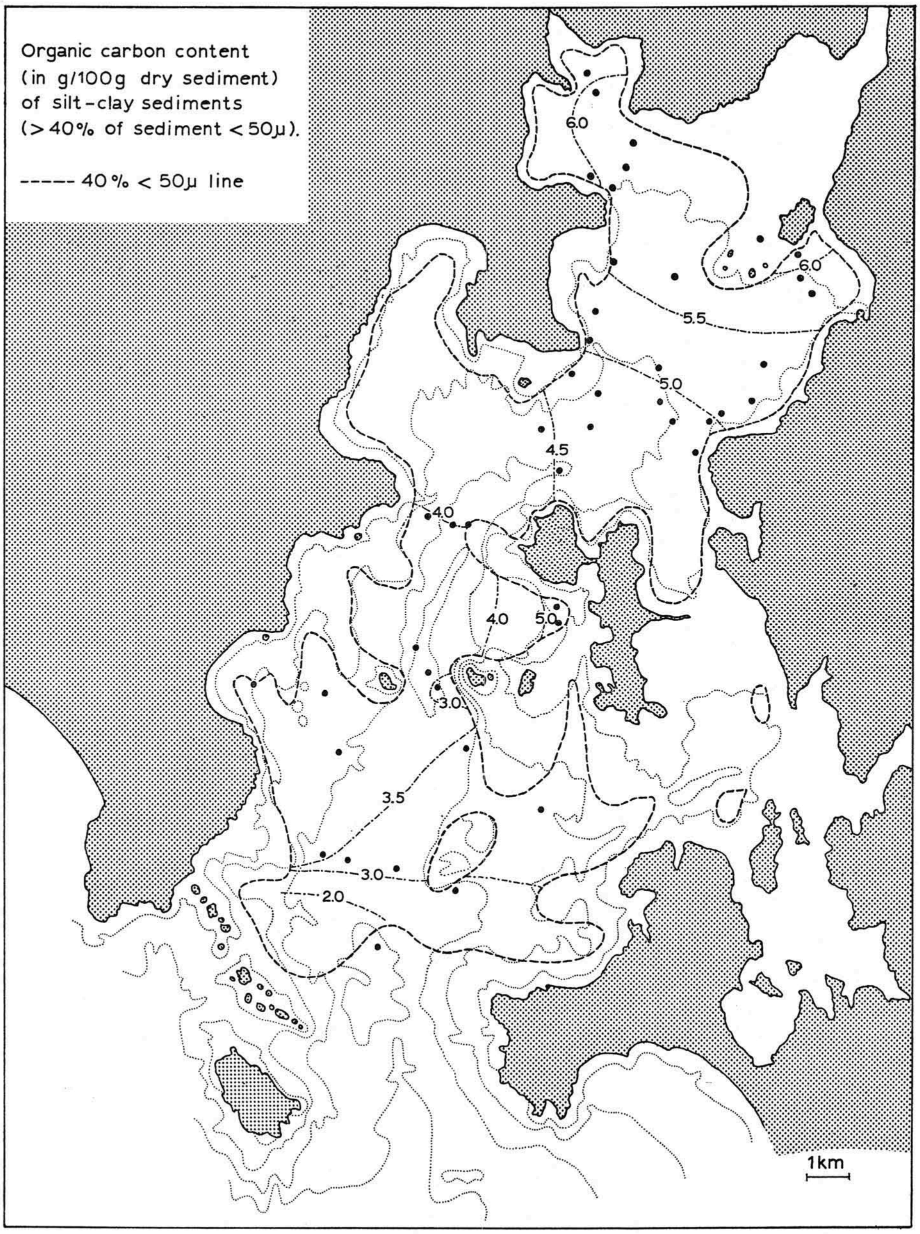


Fig. 16. Organic carbon content of the silt-clay sediments.

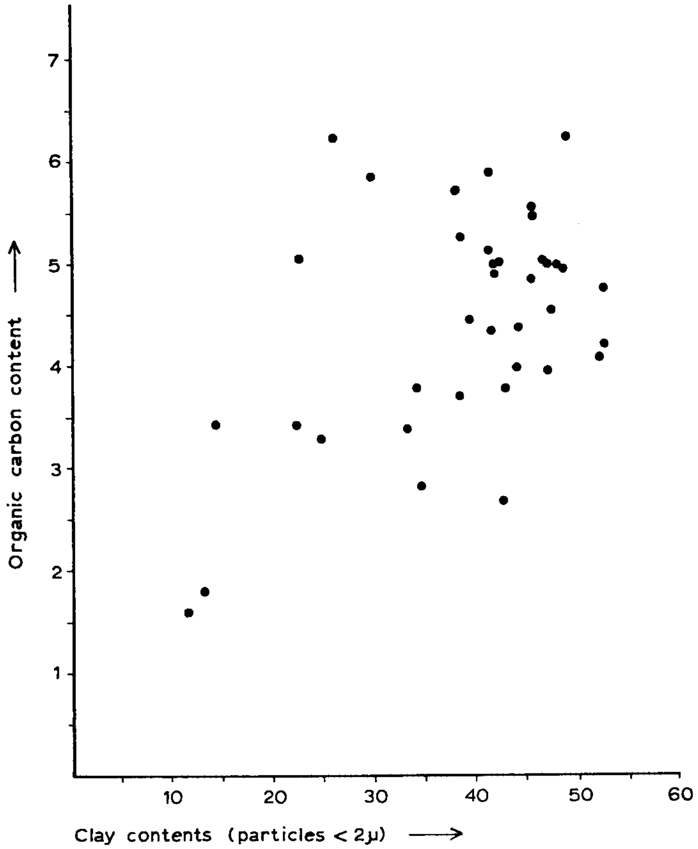


Fig. 17. Relationship between organic carbon and clay content of the sediment.

Fraga (1961) found phytoplankton production to be 3 to 4 times larger in the inner part of the Ria de Vigo than in the outer part. According to Bordovskiy (1965) a rather rapid sedimentation and a poor bottom fauna (thus low consumption of organic matter) give the best possibilities for preservation of organic matter in sediments. A poor bottom fauna is found when oxygen is low or absent near the bottom.

The high organic carbon content of the inner part of the Ria de Arosa as compared with the outer part, may be explained by a higher phytoplankton production in the inner part, a greater supply of plant fragments, a lower density of benthos (see below), a higher rate of sedimentation and a higher clay content.

These organic carbon data were collected in order to obtain a better understanding of the ecological differences between the silt-clay part of the inner bay and the outer bay, as we found a marked difference in fauna between the two (see below). A higher organic carbon content of the sediment will result in a greater demand of oxygen for decomposition. If this higher oxygen demand can not be balanced by a more rapid supply this will result in a lower oxygen saturation near the bottom.

As the inner part of the ria is more sheltered, mixing will be comparatively poor; moreover the inflowing bottom water loses part of its oxygen when flowing towards the interior part. Therefore, the oxygen saturation close to the sediment will presumably be lower in the inner than in the outer bay.

Zero values of oxygen were not measured in the bottom water; in the inner part of the ria a thin veneer of rustbrown oxygenated sediment occurred on top of the black mud smelling of H_2S. Margalef (1958:97) suggested that the differences in the fauna of the inner part of the Ria de Vigo from that of the outer part were due to a lower oxygen saturation of the bottom water in the inner part.

Summary.

The most important hydrographic features of the ria are its fully marine character and its stratification, which occurs during the geater part of the year. In fig. 18 this is illustrated by some bathythermograph pictures. A well defined thermocline is seen at about 50 feet (= 18 m); below this depth water of uniform temperature is found. At about 20 feet (= 6 m) a second thermocline is seen; this marks the limit of the usually well mixed surface layer. This layered structure is also reflected in the zonation of the sediments of the ria: fine sediments being absent from a zone corresponding with the well mixed layer, increasing in the less mixed intermediate layer (6-18 m) and forming almost the whole of the sediments below the thermocline. It will not be surprising to find this stratification also reflected in the fauna.

II. METHODS

Molluscs were sampled at more than 300 stations (see fig. 19). The positions were fixed with a sextant, measuring angles between lighthouses, buoys and landmarks. Depth was measured by echo-sounding.

Different types of dredges and Van Veen grabs of 0.05 and 0.2 m^2 were used.

The collected material was sieved on 1 and 2 mm sieves; living molluscs larger than 2 mm were sorted out aboard. From most stations a sample of the material retained by the 1 mm sieve was stored in 70% alcohol. A sample of the material retained by the 2 mm sieve (mostly consisting of empty shells) was put in plastic bags.

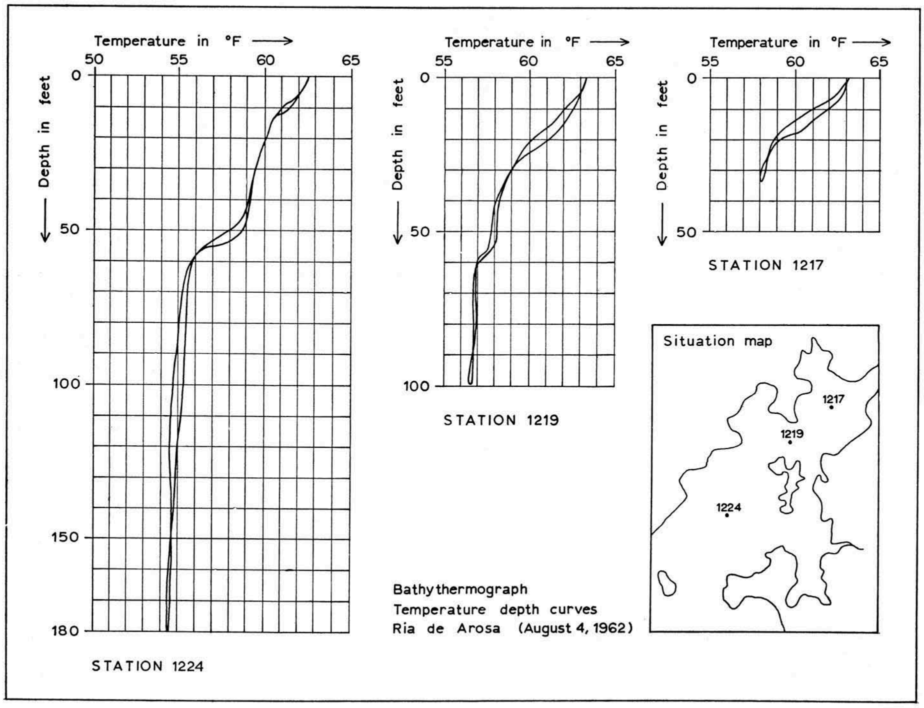


Fig. 18. Bathythermograph temperature depth curves from 3 stations in the Ria de Arosa.

Samples of material larger than 2 mm were qualitatively analysed and a selected set of samples was also quantitatively analysed. Samples of material between 1 and 2 mm were treated with Rose Bengal (Walton, 1952), this stains protoplasma and makes it easier to pick out the molluscs collected alive. These samples were analysed only qualitatively. Distribution maps were prepared for the more common molluscs and distribution patterns of the living and dead shells were compared. These distribution maps were compared with the ecological data mentioned above.

Discussion of methods.

At all stations a sample of empty shells large enough to include all the more common species was taken. It is obvious that the sample size was not the same in all areas investigated.

Generally more than 200 specimens were identified per sample. The number of species found as a rule is dependent on the sample size, therefore sample size may influence the distribution pattern if this is only based on qualitative data. This method nevertheless was chosen instead of a purely

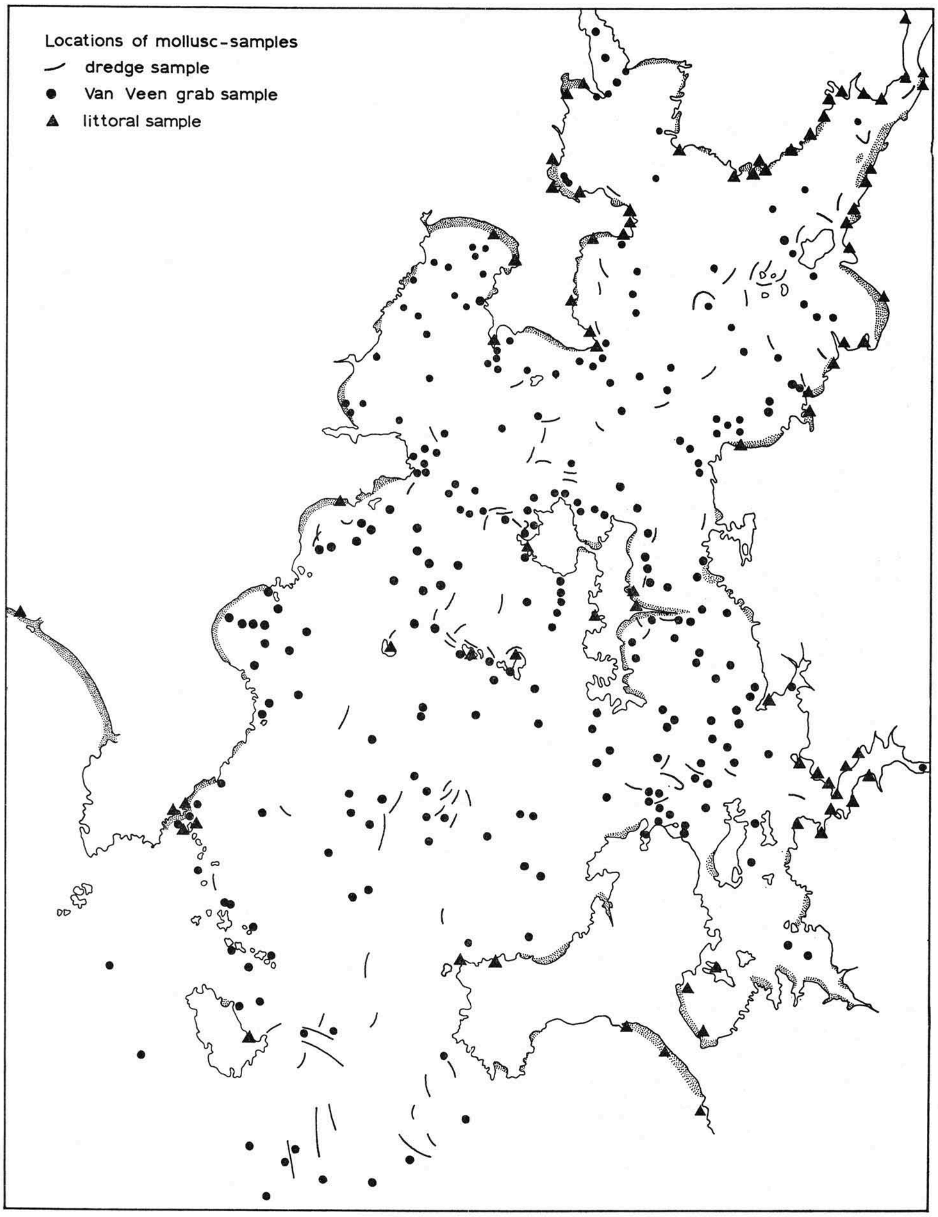


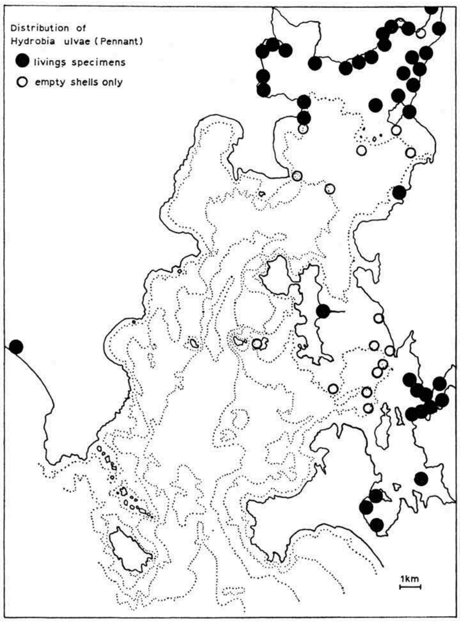
Fig. 19. Sample station map.

quantitative method because (1) it was thought to be less time consuming, (2) it gave a more complete picture of the fauna, and (3) the post mortem transport of small quantities could be better detected, as a larger number of shells per sample could be identified in a shorter time.

Living molluscs are best sampled with a dredge, using different types for different substrates. Special anchor dredges are also used to get a large quantitative sample (Holme, 1961; Picard, 1965). For this purpose, however, grabs are mostly used (Petersen, 1918; Thorson, 1957). The Van Veen grab (which we used) has a very good bite in different types of sediment (see also Gallardo, 1965). Thorson (1957:475) recommended a 0.1 m^2 grab as a standard for quantitative bottom surveys of waters less than 200 m deep. Therefore, the 0.05 m^2 grab we used in most cases in point of fact was too small. Picard (1965) found that a sample of 50 to 500 dm^3 sediment was large enough to contain the common animals. He plotted the number of species found against the amount of sediment sieved and found that the increase of species levelled off markedly after 50 to 500 dm^3, dependent on the type of habitat. This method to find what he calls a "minimum volume" is based on the "minimum area" of plant sociologists of the Braun-Blanquet school.

When comparing our sample size with those of Picard (1965) it may be concluded that even the sample (about 20 dm^3) collected by the Van Veen grab is too small to collect all the animals of common occurrence. As we did not use anchor-dredges our dredge samples also are not really quantitative. This should be kept in mind when these data are used for quantitative comparison of living and dead molluscan faunas. However, dense sampling (see map fig. 19) may partly compensate for this.

The staining method of Walton (1952, 1955) using Rose Bengal proved to be helpful, but the shells coloured red by this had to be opened to see if they really contained protoplasma, as a number of empty shells also took up the stain. Nevertheless a smaller number of shells had to be opened than without the use of Rose Bengal. In counting molluscs larger than 2 mm for quantitative data, the method of Van Straaten (1956 : 210) was used. In short this method is as follows: entire shells of gastropods and pelecypods are counted as one, valves of pelecypods as one half. Only characteristic fragments are counted, e.g. hinge fragments of pelecypods are counted as one half, axes, thickened mouth edges, etc. of gastropods (as one). To prevent the estimates from being too high, care was taken that different fragments of the same shell were not counted twice. This counting method may be a rather rough procedure, but a better method is not available.



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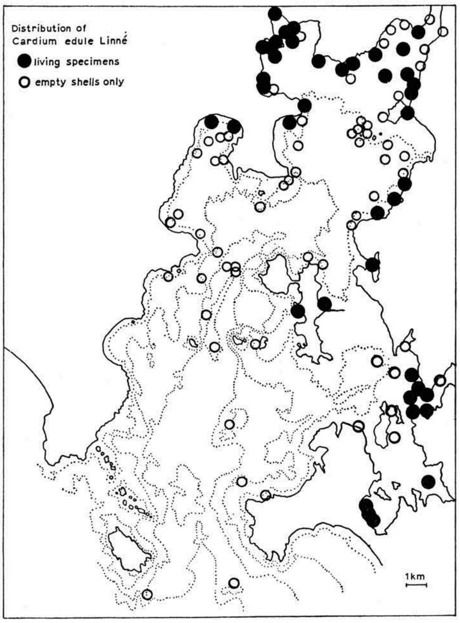

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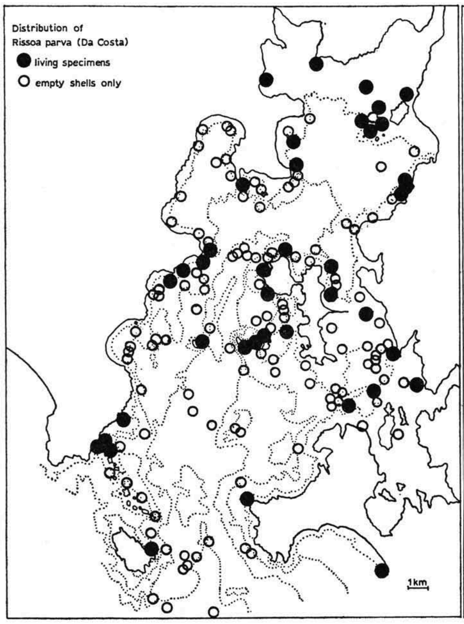

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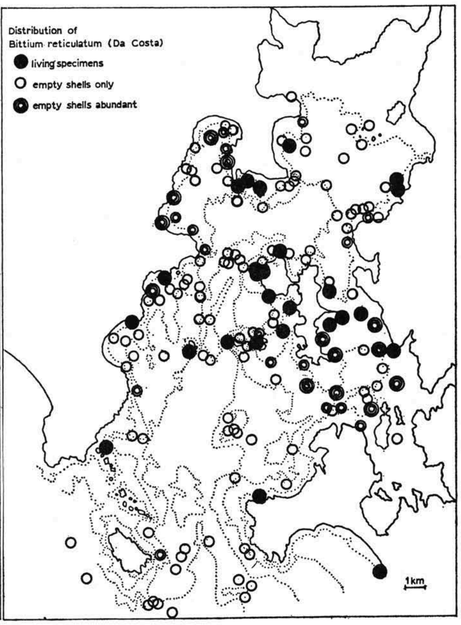

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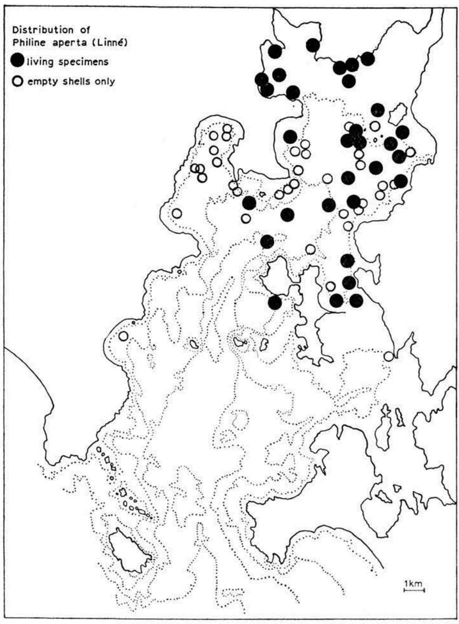

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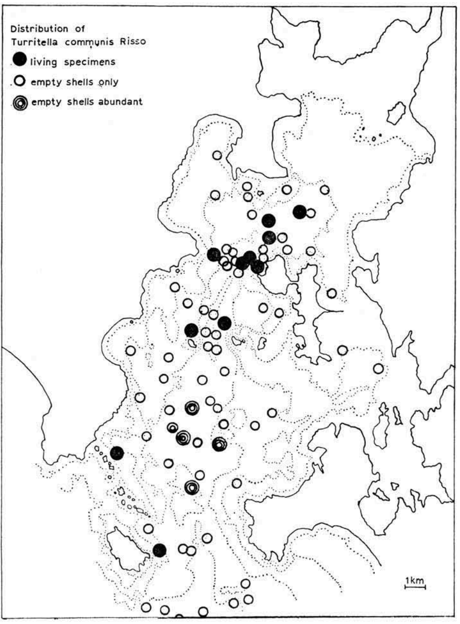

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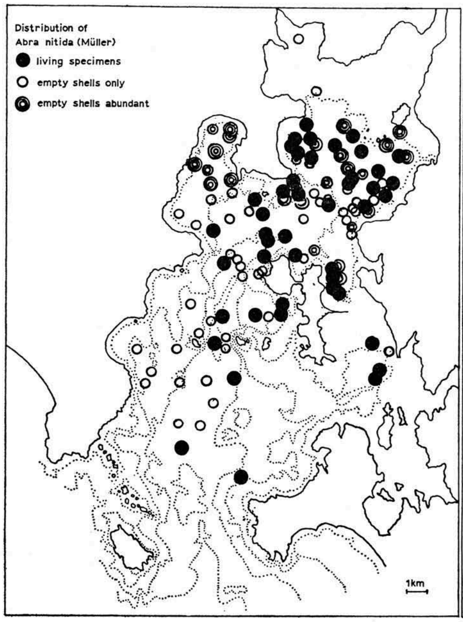


Fig. 26.

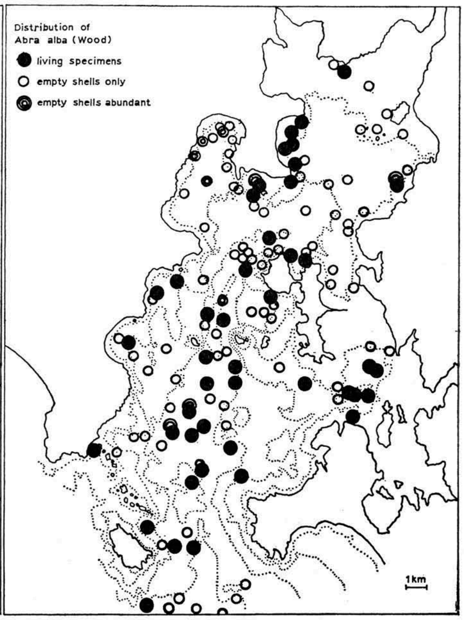


Fig. 27.

Mollusc-assemblages.

It soon became apparent from the distribution maps prepared of the more common molluscs (cf. figs. 20-31), that four types of distribution could be distinguished: (1) distribution confined to the estuarine part of the rivers (figs. 20, 21), (2) distribution confined to the marginal bay zone, (figs. 22, 23, 28, 30), (3) distribution confined to the central bay zone (figs. 24-27, 31), and (4) distribution confined to the oceanic zone outside the ria (figs. 28, 29). The estuarine part of Rio Ulla and Umia is inhabited by euryhaline species, which also occur in the marginal zone. The marginal zone, central bay and oceanic zone are in general characterized by different species. In the marginal zone and central bay subzones may be distinguished, they are frequently inhabited by the same species but in different frequencies.

In general differences between the distribution of living and dead shells were small, except for those living in the marginal zone, which were found usually in small quantities as empty shells in the deeper zones. Therefore the different zones can be recognized not only by using living molluscs, but also by using the total molluscan fauna (living and dead). When considering only the living molluscs it might be possible to make a finer subdivision of the marginal zone, due to the greater variety of microhabitats found in shallow water. As the shells of these microhabitats are intermingled with those from other microhabitats after death, these shells form only one thanatocoenosis. Valentine (1961:318) also remarked that a biologist could make finer sub-divisions of shallow water habitats than a paleontologist.

The distribution of all species found in the Ria de Arosa in the different zones is shown in table A (Appendix). The different zones are given in fig. 32.

III. THE RIO ULLA AND UMIA

Fauna and environment (figs, 33, 34).

The Rio Ulla and Rio Umia are the largest rivers which discharge in the Ria de Arosa, the Ulla being the most important. The Ulla was studied from where it enters the ria up to Padron, about 18 km upstream, of the Umia the last 9 km above its mouth were studied. The examined parts of both rivers can be divided into three parts: a zone with freshwater species, a zone without molluscan life and a zone with marine euryhaline species. The marine fauna in the last zone becomes gradually richer in species towards the mouth of the rivers. In the Rio Ulla the boundaries between these zones are found at 14 km and 5 km from its mouth, in the Umia at 4.5 and 1.5 km. The boundaries found in the molluscan fauna are rather sharp. At the mouth

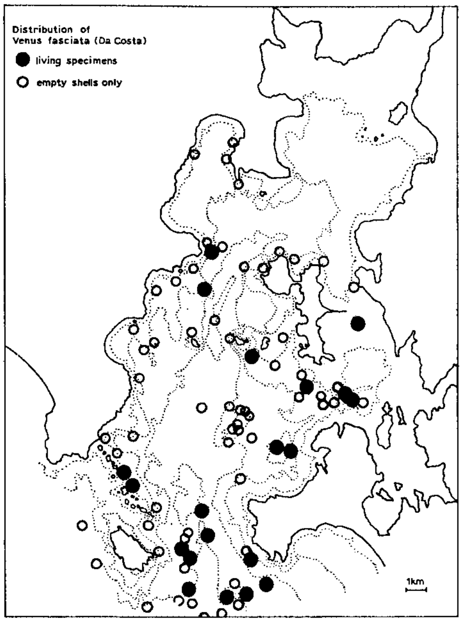


Fig. 28.

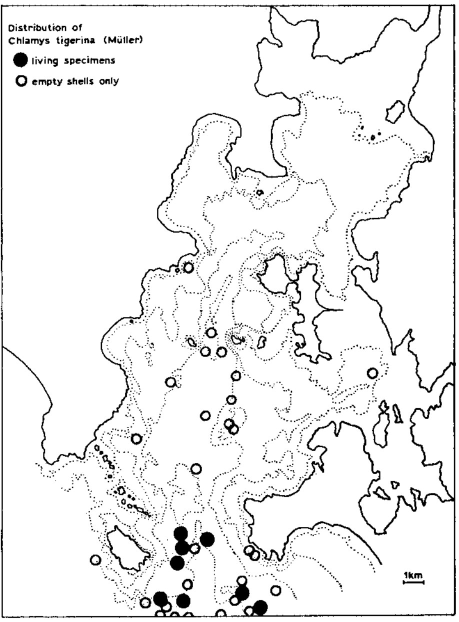


Fig. 29.

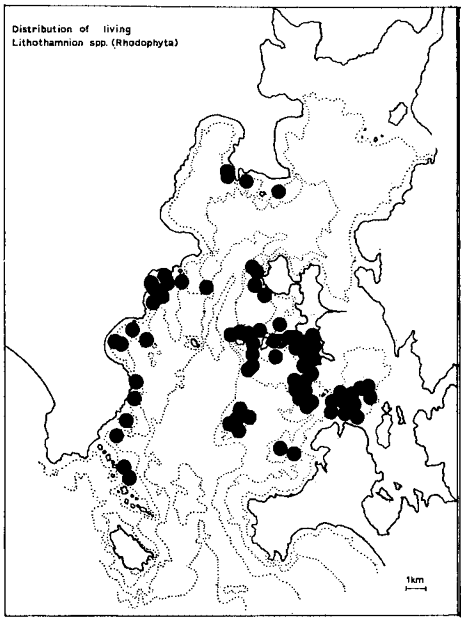


Fig. 30.

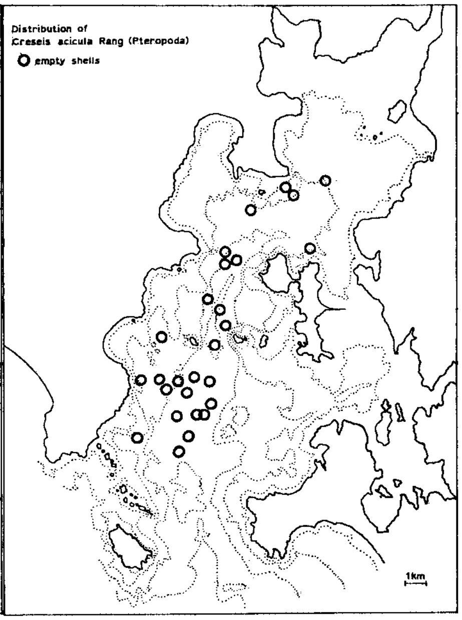


Fig. 31.

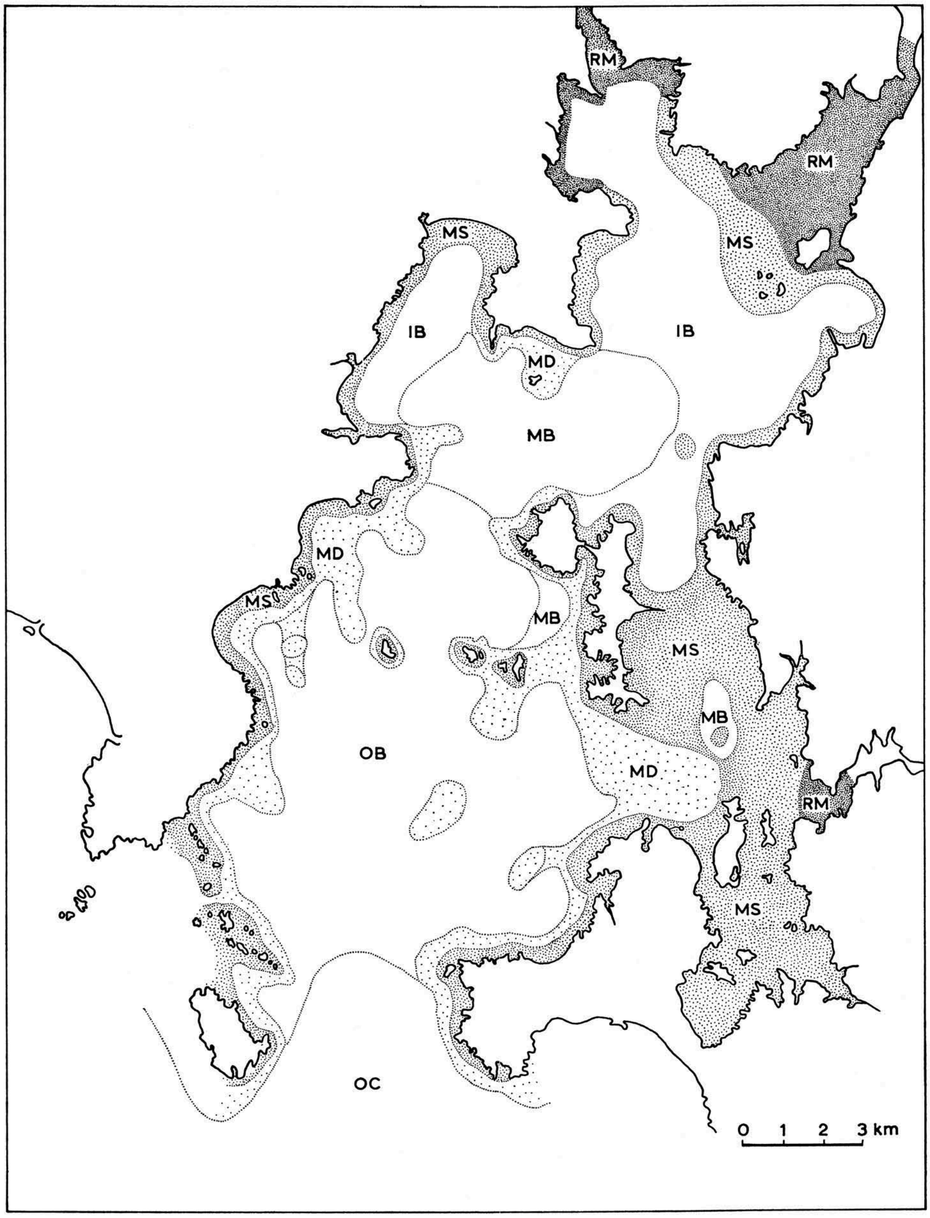


Fig. 32. Map showing the proposed zonation of the Ria de Arosa. IB, inner (central) bay; MB, middle (central) bay; MD, marginal deep zone; MS, marginal shallow zone; OB, outer (central) bay; OC, oceanic zone; RM, river mouth, polyhaline zone.

of the rivers another sharp boundary is found, which is formed by the appearance of many species which do not penetrate the rivers.

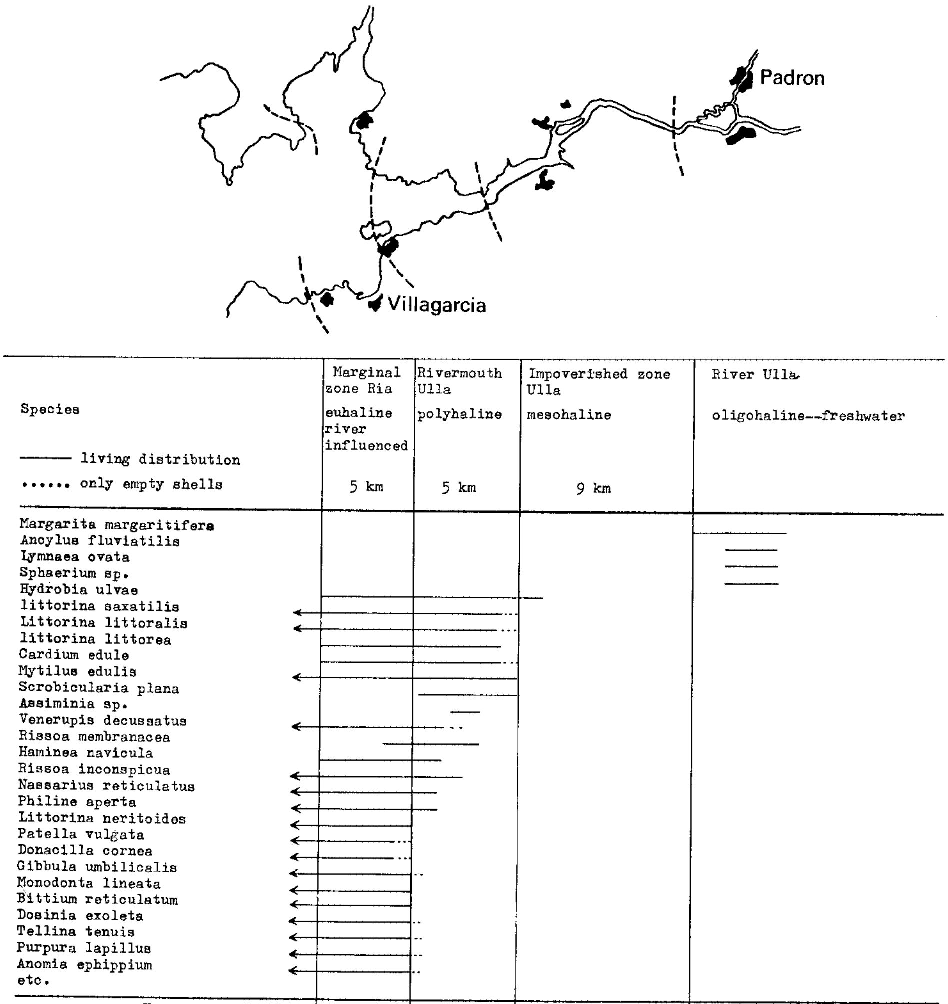
Hydrographical data are present for both rivers, the Ulla being the better known. The average values and range are given for salinity, temperature and suspended matter.

The salinity data from the Ulla show the largest differences in the different zones: not only in average value but also in range. The data of the Rio Umia are less complete. The high tidal salinity range seems to make the middle zone the most unsuitable for molluscan life, moreover the high turbidity of this zone (a phenomenon well known from other estuaries, see, e.g., Van Straaten, 1960b: 284) may influence life.

The classification of brackish waters has received much attention in literature. A recent approach to the problem is given by Den Hartog (1964). In the estuaries of the southwestern Netherlands he recognised three zones of brackish water (p. 378): oligo-, meso- and polyhaline. Although he gave an average salinity range (0.5-5S$^0/_{00}$, 5-18S$^0/_{00}$, and 18-30S$^0/_{00}$) for these zones, he also stressed the importance of fluctuations in salinity, which are the largest in the mesohaline zone. From earlier papers (Den Hartog, 1960, 1961; Redeke, 1932) concerning the same area, it becomes evident that their classification is based on the biological characteristics of the brackish water. Freshwater elements are dominant in the oligohaline zone, marine species dominate in the polyhaline zone, in the mesohaline zone typical brackish water species are dominant and the number of species is lower than in the other two zones.

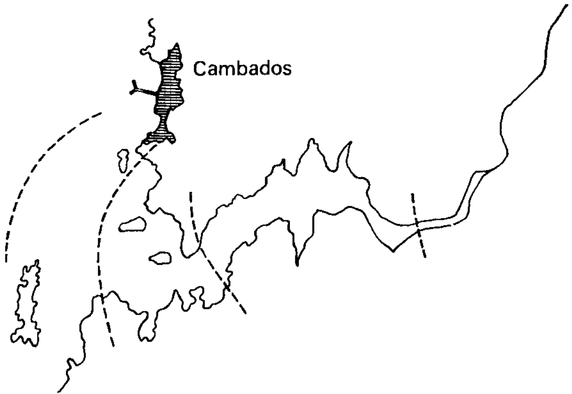
This classification resembles the division in three zones of the Ulla and Umia, which is also based in the first place on the (molluscan) fauna. The absence of molluscs in the mesohaline zone of the Ulla and the Umia seems to be due to the high fluctuations in salinity; in other estuaries where salinity fluctuations are less strong, freshwater species and marine species show an overlap in their distribution, but still there is a minimum of species in the mesohaline zone (Randersfjord, see Remane, 1940:7). Table 1 in Den Hartog (1964) clearly shows that freshwater species can endure higher average salinities and marine species lower average salinities if fluctuations in salinity are smaller.

Emery et al. (1957:700) state: "In general, penetration of estuaries (and also of the Baltic) by marine and, conversely, freshwater organisms is a function of the rate and magnitude of tidal change rather than of the actual salinity gradient. That is, marine organisms occur much farther upstream, and freshwater organisms much nearer the sea, in an estuary where the tides are small and the gradient relatively stable, than in an estuary with a large



	Marginal zone Ria	Rivermouth Ulla		Impoverished zone Ulla		River Ulla	
Salinity (S‰; ˣCl‰)		Surf.	Bott.	Surface	Bottom	Surface	Bottom
Average Summer	33.8	29.2	31.6	10.2	11.2	ˣ0.23	ˣ0.30
" Winter (dry period)	34.0	30.7		8.2		?	
Observed minimum (Summer)	29.8	18.0	28.5	ˣ 0.4	ˣ 0.5		ˣ0.05.
Observed maximum "	35.6	34.0	34.7	17.6	29.5		1.0
Tidal range	± 1.0	±6.0		±17.0			±1.0
Temperature (°C)							
Average Summer T.	17.7	19.0	17.1	22.2	22.1	21.9	
Average Winter T.	12.5	10.7		7.6			?
Observed minimum (Summer)	14.0	16.2	15.4	17.8	18.5	18.5	
Observed maximum "	21.6	20.5	18.7	24.7	24.2	25.3	
Tidal range	± 1	±2		±2		±1	
Suspended matter mg/l average	7.6	4.8		19.2		8.5	
observed range	5.8 – 18.6	3.1–6.0		5.1–76.4		7.7–10.1	

Fig. 33. Distribution of molluscs compared with the hydrographical data in the Rio Ulla.



Species ——— living distribution ...... only empty shells	Marginal zone Ria euhaline river influenced 1.5 km	Rivermouth Umia polyhaline 1.5 km	Impoverished zone Umia mesohaline 3 km	River Umia oligohaline-freshwater
Ancylus fluviatilis				———
Hydrobia ulvae	———	———	———	
Littorina saxatilis ←	———	———		
Littorina littoralis ←	———	———		
Littorina littorea ←	———	———		
Cardium edule	———	———	....	
Mytilus edulis ←	———	———		
Scrobicularia plana		———	....	
Venerupis decussatus ←	———	———		
Haminia navicula	———			
Rissoa incospicua ←	———			
Littorina neritoides ←	———			
Patella vulgata ←	———			
Gibula umbilicalis ←	———			
Monodonta lineata ←	———	———		
Dosinia exoleta ←	——— ...			
Purpura lapillus ←	———			
Venerupis aurea ←	———			
Cingula cingillus ←	———			
Summer data only				
Salinity (S‰; ^{x}Cl‰)				
Observed minimum	14.0	4.5	^{x}0.02	^{x}0.04
Observed maximum	35.5	34.0	35.2	^{x}0.05
Average	33.0	10.5	3.0	1.0
Temperature (°C)				
Average temperature	17.0	22.2	25.0	25.0
Suspended matter				
average (mg/l)	4.3	4.7	5.3	4.2
range	1.8-7.7	3.4-5.9	4.5-6.1	

Fig. 34. Distribution of molluscs compared with the hydrographical data of the Rio Umia.

tidal range and rapidly changing gradients. This means that the minimum number of species is to be expected in that part of the estuary where the salinity variation is greatest. A corollary to this is the greater penetration of marine species in estuaries of lower gradient although the salinity may also be lower, but more constant, as in Randers Fjord (Denmark) where tidal action is greatly reduced".

Important species (pl. 1).

The following species were found at more than 30% of the stations in the polyhaline zone (alive or as empty shells).

Gastropoda

Littorinidae: *Littorina littorea, L. saxatilis* and *L. littoralis.* Marine euryhaline, epifaunal littoral species feeding on diatoms, algal detritus, the latter also on fucoids, found also in the marginal zone.

Hydrobiidae: *Hydrobia ulvae* found alive in large quantities in this zone and only in some samples of the adjoining marginal zone (see fig. 20) A euryhaline brackish water species, feeding on diatoms, blue-green algae or fine detritus, which it collects by grazing the surface of mud-flats (Fretter & Graham, 1962:581). Newell (1965) stresses the importance of bacteria in the food of *H. ulvae,* which he demonstrated experimentally.

Rissoidae: *Rissoa inconspicua* found alive in more than 30% of the samples. In the ria this rissoid (together with *R. membranacea*) is more euryhaline than other *Rissoa* spp. The food consists of diatoms, algae and detritus (Fretter & Graham, 1962:261). It was found living on algae and *Zostera* sp. (on this latter plant in combination with *R. membranacea,* a species largely confined to this zone).

Lamellibranchia

Mytilidae: *Mytilus edulis,* euryhaline, suspension-feeder, lives attached by byssus threads to hard substrates (rocks). It is not confined to this zone but found in all littoral rocky habitats along the ria and outside.

Cardiidae: *Cardium edule,* a euryhaline suspension-feeder, lives buried in the sediment close to the surface. The highest densities are found in this zone, but this species is also found in the marginal zone (see fig. 21).

Veneridae: *Venerupis decussatus,* the most euryhaline species of the Venerids in the ria. A suspension-feeder which lives rather deep in the sediment (sand with some mud, sometimes smelling of H_2S). Also found in the marginal zone. This species is extensively fished for in the rias (Figueras, 1956:83).

Scrobiculariidae: *Scrobicularia plana,* an euryhaline brackish-water species, lives about 10 cm deep in the sediment. It feeds on detritus which it searches out with the long inhalent siphon from the sediment surface. Confined to this zone (habitat the same as that given by Yonge, 1949b : 38).

Comparison with other areas.

The fauna of the polyhaline zone just considered is comparable to the *Macoma* community of Petersen (Thorson, 1957: 505) with *Macoma balthica, Mya arenaria, Cardium edule, Scrobicularia plana, Hydrobia ulvae,* the polychaete worm *Arenicola marina* and a *Mytilus* epifauna. This community in its typical form is not found south of the English Channel. *Mya arenaria* and *Macoma balthica* have their southern limit in south-west France. A reduced "*Macoma*" community without these two species is found in the Rio Ulla and Umia which could be called a *Cardium edule-Scrobicularia plana* community. At somewhat higher salinities *Venerupis decussatus* is found with these species, and we get a community comparable with the *Cardium edule-Venerupis decussatus-Scrobicularia plana* community found in the Ria de Faro (Portugal) by Vilela (1947). For this community Vilela gave a temperature range of 12° to 23° C, the same as in the Ria de Arosa and a salinity range of 34.3 to 36.7 $^0/_{00}$, somewhat higher minimum and maximum values than in the Ria de Arosa.

Transport.

There is a distinct transport of shells in the polyhaline zone of the Rio Ulla and Rio Umia. The tidal flats which bear a rich molluscan fauna are usually devoid of empty shells. These are found on the shore and in the channels and gullies (see also Van Straaten, 1956: 224; Krause, 1950), but are not transported far away. Empty *Cardium* shells are frequent in samples taken just outside the rivermouth but absent from those taken a little farther away (fig. 21). Empty shells of *Hydrobia ulvae* are found in a zone about 4 km above the river-mouth of both the Ulla and the Umia (fig. 20). Empty freshwater shells were not found in our samples. These facts illustrate the minor importance of these rivers. If they brought large quantities of fresh water into the ria one would find freshwater shells in our ria samples and *Hydrobia* shells would be carried farther into the ria.

IV. THE MARGINAL ZONE

The environment (summarized from chapter I).

The marginal zone is characterized by a larger variation of the different ecological factors as compared with the central bay. The salinity is in general above 33 $^0/_{00}$, but in winter the surface water of the inner part of the ria may be diluted. The temperature ranges from 10 to 21.5° C. The sediment mostly consists of sand in the shallow subzone, shelly gravel with some mud in the deep subzone. Wave turbulence prevents the muds from settling. The lower boundary of the marginal zone is 3 to 5 m in the inner part of the ria and approximately 20 m in the outer part, due to the increase in exposure. The deep marginal subzone, which is largely confined to the outer part of the ria is characterized by the occurrence of large quantities of the calcareous alga *Lithothamnion*. The lower boundary of the marginal zone coincides with the thermocline which forms in the summer.

The marginal fauna.

In fig. 35 some general characteristics are given of the molluscan fauna of the entire marginal zone. Living and dead molluscs larger than 2 mm are compared. This zone is characterized by a high percentage of grazers among the gastropods, and of suspension-feeders among the pelecypods, and of epifauna among both groups. The greatest discrepancies between living and dead molluscs are found in the pelecypods, where deposit-feeders are more and suspension-feeders less numerous in the living fauna than in the dead. This is largely due to the presence in some samples of numerous living specimens of *Abra alba*, a species which we never found well represented in the dead fauna (see chapter VII).

In table A (Appendix) a list is given of all species found in the ria and their distribution over the different zones. From this table it becomes evident that most species living in the marginal zone are seldom found alive in the

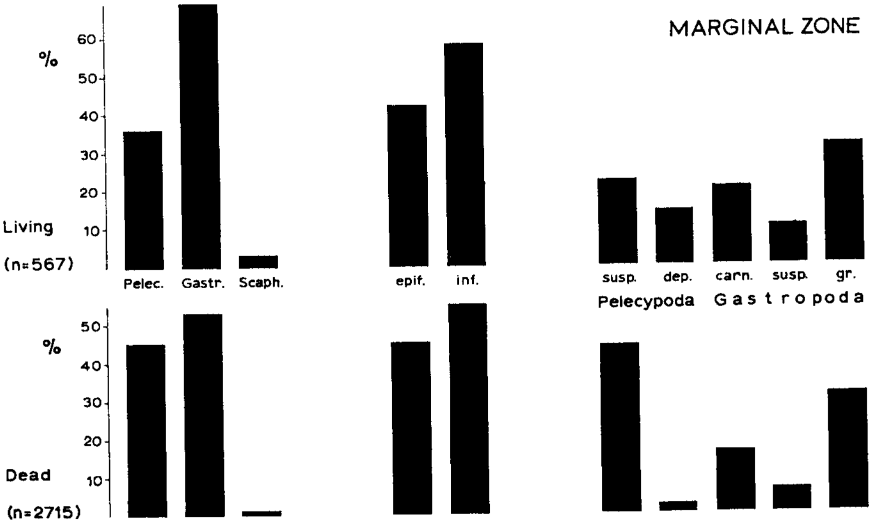


Fig. 35. Histograms showing the composition of the mollusc fauna in biocoenosis and thanatocoenosis.

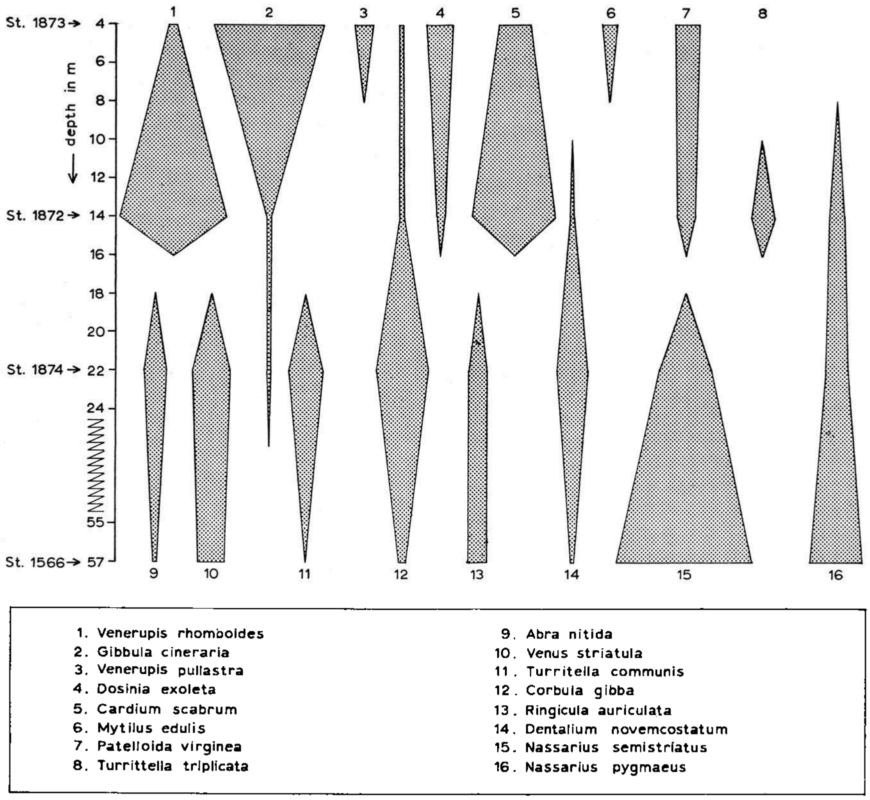


Fig. 36. Distribution of empty shells in 4 samples taken from a section normal to the shore in the middle part of the Ria de Arosa, showing the clear cut boundary between marginal zone and central bay also to be present in the thanatocoenosis.

central zone of the ria. The splitting up of the marginal zone into a shallow and a deep subzone can be seen to be largely based on the difference in relative frequencies of species found dead and alive in both subzones. Only a few species are restricted to one of these subzones. This is once more illustrated in fig. 36 which represents the quantitative distribution of the more important species of the dead fauna in four stations from a section normal to the north-west coast of the ria, opposite the Isla de Arosa. This figure clearly demonstrates that also in the dead fauna the different zones can be recognised.

Important species (pls. 1, 2).

The following is an annotated list of the species found at more than 30% of the stations in one or both of the subzones of the marginal zone. Species occurring in less than 30% of the stations are not considered. The species are arranged in systematic order. Except when stated otherwise, these species are found alive and as empty shell. Abbreviations: M. = marginal zone; M.S. = marginal shallow zone; M.D. = marginal deep zone; Fr.Gr. = Fretter & Graham, 1962.

Gastropoda, Prosobranchia

Fissurellidae: *Emarginula conica* and *Diodora apertura.* Rarely in M.S., common in M.D. They need a solid substrate and feed on sponges and detritus (Fr.Gr: 488). Food and substrate seem to be factors which restrict these species to the M.

Patellidae: *Patella* spp. Littoral species of rocky shores, feeding on diatoms, detritus and algae which they collect by grazing the rocks on which they live. Identification of the different species is largely based on the soft parts (Fr.Gr.: 493-502). Four species are reported from the Ria de Vigo (Ardré et al., 1958). As these four species all live in the littoral zone and as it is almost impossible to identify empty shells, for our purpose they have to be treated as one group. Because of their littoral habitat they exceed 30% only in the M.S.

Acmaeidae: *Patelloida virginea* exceeds 70% in M.D., only some 20% in M.S., alive in both. Lives on hard substrate and algae, feeds on red algae, *Lithothamnion* (Fr.Gr.: 261). As samples of the M.D. frequently contain large quantities of *Lithothamnion calcareum* (see below and fig. 30) the high frequencies of *Patelloida* are not astonishing. Food seems to be of major importance in its distribution.

Trochidae: *Gibbula magus, G. cineraria,* and *Cantharidus exasperatus* in M.S. and M.D.; *Gibbula umbilicalis* and *Cantharidus striatus* in M.S.; *Gibbula tumida* in M.D. These species feed on algae and algal detritus (Fr. Gr.: 261) and live on hard substrate (rock, stones, shells) or algae. *Cantharidus striatus* lives on *Zostera* (Fr. Gr.: 527-530, 654), but was not found alive on it in the ria. The depth distribution of the Trochidae in the ria is the same as reported from the British coast (Fr. Gr.: 527-530). *Gibbula tumida* was not found in the ria shallower than 7 m (we found that the less frequent trochid, *Cantharidus montagui* had the same distribution).

Littorinidae: *Littorina saxatilis* and *L. littoralis* were found in more than 30% of the M.S. samples. Littoral species, which feed on algal detritus and diatoms, the latter also on fucoids (Fr. Gr.: 261). They are well adapted for life in the littoral zone: *L. saxatilis,* e.g., can live a week in freshwater (rain!), a week in water of treble normal salinity, and can survive desiccation still longer. *L. littorea* is less resistant and lives consequently lower on the shore (Fr. Gr.: 533-543). We did not find them alive below the littoral zone but they may be found there accidentally (Fr. Gr., 533-543). This will occur more frequently in northern Europe where they are known to leave the littoral zone in winter.

Rissoidae: *Rissoa parva* was found in about 70% of the M.S. and M.D. samples, and *Rissoa lilacina* in approximately 50% of the M.S. and M.D. samples; although *Alvania punctura, A. cancellata, A. beanii, A. crassa, Cingula semistriata,* and *C. semicostata* were found in the M.S., they were only found in more than 30% of the samples of the M.D. *Cingula* spp. feed on detritus, other rissoids feed also on diatoms and algae (Fr. Gr: 261, 546). *Rissoa* spp. were found usually in large quantities associated with weeds. *Cingula* and *Alvania* species were not found alive in such large numbers probably as they live hidden under stones (Fr. Gr.: 647, 657, 658). They will find their food, as far as this consists of living algae and diatoms, in the M. Depth distribution of the rissoids reflects the varying amounts of detritus they can use as food. *Cingula* and *Alvania* occur deeper and more frequent in the M.D. than the *Rissoa* spp. The distribution of rissoids in the ria seems to be determined by their food and by their habitat requirements, i.e. the presence of seaweeds and stones.

Turritellidae: *Turritella triplicata* was found in 50% of the M.D. samples, but was practically absent (both living and dead) from the M.S. Presumably it lives buried in the sediment as a suspension-feeder (as does *T. communis,* see Fr. Gr.: 567). Although both species occur in the ria, they do not live together, *T. communis* is characteristic of the central bay zone. The factors influencing the distribution pattern of *T. triplicata* are uncertain.

Caecidae: *Caecum imperforatum* was found alive and as empty shell in the entire M., but was only found in more than 30% of the samples of the M.D. *Caecum imperforatum* and *C. glabrum* have the same distribution in the ria but the latter is less frequent. According to Götze (1938: 112) *C. glabrum* feeds on diatoms of the surface of sand-grains. Presumably *C. imperforatum* has the same feeding habits. It is only in the M. that sand-grains supporting a diatom flora are found.

Cerithiidae: *Bittium reticulatum* is abundant among weeds when alive. Empty shells are found in some 70% of the M. samples. The species feeds on diatoms, filamentous algae and detritus (Fr. Gr.: 553). It is restricted to the M. for the same reasons as the *Rissoa* spp. which live together with *B. reticulatum* on weeds.

Triphoridae: *Triphora perversa* was found in the M.D. and also in less than 10% of the M.S. samples. It feeds on sponges, diatoms and detritus

(Fr. Gr.: 554) as the *Cerithiopsis* spp. do, which were found less frequently in the same habitat. Sponges on which they feed need a hard substrate. Food seems to be an important factor in limiting these species to the M.

Calyptraeidae: *Calyptraea chinensis* was present in 50% of the M.S. and 70% of the M.D. samples. A suspension-feeder on phytoplankton and floating detritus, it lives on shells and stones which it grips with a broad sucker-like foot (Fr. Gr.: 262, 505). The substrate and perhaps the greater water movements in the M. supplying larger quantities of food may be factors which limit this species to the M.

Naticidae: *Natica alderi* was present in 50% of the M.D. samples but was also found alive in deeper water at the entrance of the ria, where empty shells were equally abundant. Naticids are carnivorous gastropods feeding on bivalves. Their mode of attack and boring of the well known circular hole in the bivalve shell was studied in detail by Ziegelmeier (1958). The exceptionally broad foot is used as a plough with which they can move with a remarkable rapidity just beneath the surface of the sand (Fr. Gr.: 572-574). As the food of *N. alderi* (bivalves) is found throughout the whole ria, this can not affect its restricted distribution. The construction of the foot seems to be better adapted for coarser, stiffer sediments than those found in the inner central bay zone. Therefore the type of sediment seems to be of major importance with regard to its distribution.

Muricidae: *Ocenebra erinacea* was found in 40% of the M.S., *Ocenebra aciculata* in 60% of the M.D. samples. Both are carnivorous gastropods. The food of the former consists of bivalves (*Venerupis, Cardium, Venus*) in subtidal habitats, and of barnacles, small tubicolous worms, mussels and anomiid bivalves in littoral habitats (Fr. Gr.: 516). The less well-known, smaller *O. aciculata* probably feeds in the same manner. They are epifaunal species which avoid the soft bottom of the central bay.

Nassariidae: *Nassarius reticulatus* and *N. incrassatus* were present in more than 30% of the M.S. and M.D., but were also found living in the entrance area. They are replaced in central bay by other *Nassarius* species: *N. pygmaeus* and *N. semistriatus*. Nassariids are scavengers living on dead or decaying animals (Fr. Gr.: 522), but Scheltema (1964) found that the American species *N. obsoletus* fed largely as a deposit-feeder on the microflora of the mud-flats on which it lives. Food other than decaying animals may be more important in the diet of nassariids than earlier thought. *N. pfeifferi,* found restricted to the mud-flat aera in the ria, may feed in the same manner as *N. obsoletus,* the other nassariids of the ria may feed partly on plant-material: the young of *N. pygmaeus* were found by us several times on the fronds of *Ulva* sp. *N. incrassatus* eats mainly decaying sponges according to Starmühlner (1956) (quoted in Fr. Gr.: 523). The nassariids of the ria inhabit different habitats which overlap. Substrate is one of the factors determining this distribution, food (sponges in the case of *N. incrassatus*) also plays a role. Nassariids are infaunal species which plough through the surface layers of the substrate or glide over the surface (Fr. Gr.: 522).

Turridae: *Mangelia coarctata* was present in more than 50% of M.D. samples. Carnivorous gastropod, prey-animals unknown (perhaps Polychaeta?, see Fr. Gr.: 525). It is also found alive in some other zones in the ria, which suggests that it preys on different species. Not characteristic of the M.

Opisthobranchia

Atyidae: *Haminea navicula* was present in 30% of the M.S. samples and largely confined to the inner part of the ria. Herbivore feeding on seaweeds found in association with *Zostera* (Guiart, 1901: 43, 78). We found it alive in association with *Zostera* sp. On some beaches large quantities of empty shells were found and dying animals were sometimes dredged near these beaches. As these dredge samples also contained egg-masses of the same species, it is suggested that the animals die after egg deposition; this has also been noted by Guiart, 1901: 60. Food and its association with *Zostera* probably limit this species to the M.S. of the inner part of the ria.

Lamellibranchia

The feeding methods of Lamellibranchia are described by Hunt (1925), and Yonge (1938).

Anomiidae: *Anomia ephippium* is found as empty shells in more than 30% of the M.S. and 50% of the M.D. samples. It lives frequently attached to living and dead shells of other bivalves (*Pecten*). It is an epifaunal suspension-feeding animal, its distribution is limited by availability of suitable substrate. *Heteranomia squamula* is an epifaunal species living attached to various objects. Empty shells were found in more than 40% of the M.D. samples. It was not found alive in other zones than M., although it can live in deeper water (e.g., in 1965 we found this species alive more than 50 m deep in the Trondheimfjord). The species is a suspension-feeder as the foregoing, its distribution seems restricted by availability of suitable substrate and water turbulence.

Mytilidae: *Mytilus edulis* lives in the littoral zone, it was found as empty shells in more than 50% of the M.S. samples. It is an epifaunal suspension-feeder. Its absence from deeper water seems to be due to predators (*Asterias rubens*, crabs). In the Baltic where its predators (echinoderms are absent due to low salinity, *Mytilus* lives down to greater depths (Petersen, 1918: 18). Ebling et al. (1965) found a negative correlation between the distribution of crabs and *Mytilus*. The same factors are probably at work in the ria, the empty shells found in 30% of the M.D. samples may have been transported from the M.S.

Pectinidae: *Chlamys varia* was found in 30% of the M.S., *C. opercularis* in more than 40% of the M.D. samples. The former species was found alive only in the M., the latter has a wide distribution and lives all over the ria. Pectinidae are epifaunal suspension-feeders, *C. varia* lives attached by byssus threads to stones and shells, *C. opercularis* lives free swimming but its young live attached. We found such juveniles e.g. in 1964 in abundance attached to Bryozoan colonies of the genus *Cellaria*. *Chlamys varia* is limited in its distribution by the availability of a suitable substrate, the wider distribution of *C. opercularis* can be explained by its free-swimming habit, although it is absent where turbulence is weak and renewal of suspended matter is low, as in the inner part of the central zone.

Astartidae: *Astarte triangularis* and *Digitaria digitaria* are found in the M.D., are almost absent from the M.S. and central bay zone. The absence of the former species from shallow water and from sediments finer than muddy sand is in accordance with its distribution in British waters (Tebble, 1966: 72; Jeffreys, 1868: 318). It is a small species (up to 3 mm) which feeds on suspended matter. Its small size will make life in more turbulent water impossible, Astartidae, namely, have short siphons and live near the sediment surface. Absence from finer deposists may be due to its suspension-feeding habit. *Digitaria digitaria* is a somewhat larger species and was found alive in the entrance area of the ria. Factors affecting its distribution may be the same as in the foregoing species.

Lucinidae: *Loripes lucinalis* in the M.S. on the less exposed beaches of the inner part of the ria (the same distribution was found by Figueras (1956) in the Ria de Vigo). The species is a suspension-feeder which lives buried in the sediment, which may be black and smelling of H_2S. An anterior inhalent tube, formed by the foot and through which the animal gets oxygen-rich water, enables the Lucinidae to live in habitats where there is usually a poor bottom fauna (Allen, 1958). According to Allen their absence from regions with a richer bottom fauna may be due to competition.

Montacutidae: *Mysella bidentata* is a species widely distributed dead and alive in the whole ria and therefore not characteristic for any zone. According to Boss (1965) this species is found in symbiosis with a wide variety of hosts, including annelids (*Nereis*), sipunculids (*Golfingia vulgaris* (Blainville)), ophiuroids (*Ophiocnida brachiata* (Mont.), *Amphiura filiformis* (O. F.

Müller)). Yonge (1949: 252) reported the holothurian *Labidoplax digitata* (Mont.) as a host. *M. bidentata* lives in the burrows made by these hosts and can use their respiratory or feeding currents to obtain its own food; it is a suspension-feeder. The fact that *M. bidentata* does not have a specific host may explain its wide distribution.

Cardiidae: *Cardium edule* and *C. exiguum* were found in the M.S.; *C. scabrum* in the M.D. and also alive in the oceanic zone. The species are suspension-feeding bivalves with short siphons living near the sediment surface. *C. exiguum* can live attached by long byssus threads and then becomes an epifaunal species (Høpner Petersen, 1958: 27). The restriction of *C. edule* to shallow water is thought to be due to light, as in less turbid waters in the Netherlands it is found deeper (Verwey, 1952: 175). Kristensen (1957: 42) noted that *C. edule* is extremely photosensitive. If a fish approaches a cockle, the siphons, on which the photokinetic sense-organs are located, are at once drawn in and the shell is closed. In deeper and darker water the cockle will be unable to discern its possible enemy (largely flatfish) and will be eliminated. *C. edule* and *C. exiguum* can withstand a lowering of salinity. *C. scabrum* is a marine species which, like in the ria, is absent from shallow water around the British coast (Tebble, 1966: 103-105).

Veneridae: *Dosinia exoleta,* and *Venus verrucosa* are found in the M.S. and M.D.; *Venerupis aurea,* and *V. pullastra* in the M.S.; *Gafrarium minimum, Venus ovata, V. fasciata,* and *Venerupis rhomboides* in the M.D. (and alive in the oceanic zone). Veneridae are suspension-feeders which live near the sediment surface, except *Dosinia* which lives deeper (Ansell, 1961). Different species are found in the different zones of the ria, but all are absent from the soft mud of the inner bay. According to Ansell (1961) the species mentioned above are all adapted to coarser sediments. As these coarser sediments are related to stronger turbulence of the water, which brings more food in a time unit to the animal than quiet water does, turbulence may be the primary factor in the distribution of these species.

Tellinacea: *Tellina donacina* and *Gari tellinella* were found in the M.D. but were more frequent in the oceanic zone, both alive and as empty shells and attained there a greater size and a higher age. This was also found in some other species, e.g., *Glycymeris glycymeris,* and *Arcopagia crassa.* The young of these species have a wider distribution than the adults, as a part settles in places where they can not maintain themselves. *Abra alba* was found in the M.S. and M.D. but was more frequent in the outer part of the central-bay zone. The Tellinacea are deposit-feeders (Yonge, 1949), the different species inhabit all types of sediment if these contain some organic debris. The habitats of the species mentioned here agree with those given for these species by Yonge (1949): coarse sand and gravel with some mud, while *Abra alba* lives also in finer sediments.

Mesodesmatidae: *Donacilla cornea,* although found in somewhat less than 30% of the M.S. samples, is a very characteristic species of the beaches of the ria, living in large quantities in the sand at the low water line. It does not occur alive in other zones, nor is it found on the more exposed ocean-beaches. Figueras (1956) reported the same distribution in the Ria de Vigo. *Donacilla cornea* is a suspension-feeder, which seems well adapted for life in the surf zone, because of its rather strong shell. Where the surf is too heavy for it, it is replaced by *Donax trunculus.*

Mactridae: *Spisula* sp., mostly *S. subtruncata* is found in the M.S., another species of *Spisula* is found in the oceanic zone. They are considered together here, as small specimens cannot be distinguished from each other (see also Eisma, 1966: 119). In other European waters *S. subtruncata* is also restricted to smaller depths. Tebble (1966: 133) gave its maximum depth in British waters as 36 m. *Spisula* is a suspension-feeder and this feeding method may be responsible for its restriction to shallow water.

Corbulidae: *Corbula gibba* was found in some 30% of the M.D. samples. This species is far more frequent in the central bay samples. It is a suspension-feeder which is very well adapted to life in silty habitats. Where such habitats occur in the marginal zone this species was found. Yonge (1946) clearly described how this species is adapted to life in muddy habitats. The inhalent siphon is short and draws in much bottom material. Therefore the animal produces great quantities of pseudo-faeces. The asymmetry of the shell valves enables *Corbula* to reduce the size of the inhalent chamber, in which these pseudo-faeces accumulate, more strongly than if the shells were symmetrical. Pseudo-faeces are expelled by periodical contractions of the "quick" portions of the adductor muscles which are very well developed. The foot assists in clearing of the inhalent chamber. The stomach, which inevitably has to deal with large quantities of inorganic matter, is large. *Corbula gibba* lives attached by only one byssus thread to pieces of stone or shell in the sediment (Yonge, 1946: 373). It seems that no large quantities of this substratum material are needed as I found this species in very soft mud with only a few shells (inner part of central bay).

Hiatellidae: *Hiatella arctica* s.l. (perhaps including more than one species) is an epifaunal species and suspension-feeder, found in more than 60% of the M.D. samples, but also found alive and as empty shells in other zones. It lives in holes or is attached by its byssus to *Laminaria* holdfasts and other dense bushes of algae. In deeper water where algae are absent it lives attached to colonies of the bryozoan *Cellaria.* In the ria *Hiatella* was not found boring in rocks, presumably because the soft rock it needs (limestone and soft sandstone according to Hunter, 1949: 283) does not occur in the ria. It is therefore restricted to those places in the ria where it can find suitable attachment. The absence of other boring species, e.g. *Gastrochaena dubia* (Pennant), *Pholas dactylus* L., *Petricola lithophaga* Retzius, *Barnea* spp., can be explained too by the absence of a suitable substrate such as soft rocks, limestone and peat.

Other skeletal remains.

The remains of barnacles, regular sea-urchins and encrusting Bryozoa make up only a small fraction of the samples. This was not the case with *Lithothamnion*. Fig. 30 represents the distribution of these calcareous algae in the ria. They are very characteristic for the marginal deep zone. 75% of the samples from this zone all contained living *Lithothamnion*. More than one species may be collected, but *L. calcareum* Aresch. is the most abundant. They were found alive outside this zone and may form as much as 90% of the coarse fraction (larger than 2 mm) of the samples. Dead fragments were encountered in small quantities down as far as 60 m in the central zone and were frequent in the beach samples from the outer part of the ria. *Lithothamnion* spp. live at a depth of 5 to 20 m in the outer part of the ria while they are absent in the inner part except on some exposed points. They are virtually absent from very exposed sites in the outer part of the ria and from the very exposed oceanic coast outside the ria, being only found on some spots behind the skerries N. of Isla de Arosa and not on the ocean side of the rocky reef of los Mezos. This typical distribution, namely on not too exposed and not too sheltered situations, I can explain only as follows: *Lithothamnion* spp. belong to the few algae that do not need a solid substrate, as they anchor themselves in the sediment. Like most red algae they are confined to the deeper part of the euphotic zone. In the inner part of the ria they are absent because where they find their light optimum the substrate is too soft. On the very exposed ocean coast they are absent because the sediment consists of shifting shelly sand, in which they cannot anchor themselves.

Transport.

Post-mortem transport of shells of molluscs living in the marginal zone may be in three directions, viz. (1) along the coast, (2) towards the coast and (3) towards deeper water.

(1) Transport along the coast tends to mix the shells from different biocoenoses in the marginal zone: epifaunal and infaunal shells are mixed and form one thanatocoenosis.

(2) Transport towards the coast can be studied by comparing depth distribution of living and dead specimens of a species. In general species living in the deep marginal zone are transported only rarely towards shallower water. Living specimens and empty shells of *Gibbula tumida* are not found above a depth of 7 m; living and dead *Turritella triplicata* and *Chlamys opercularis* are not found shallower than 5 m; *Gafrarium minimum, Venus ovata* and *Venus fasciata* occur alive in the ria below 7 m, empty shells occur regularly below 4 m depth, the last two species were found once as empty shells in a beach sample. These data, together with the absence of central-bay mollusc shells in beach samples of the ria, indicate that transport of shells towards the coast is confined to a belt from the tidal zone to about 5 m depth (i.e. the shallow-marginal zone).

A study of the transport of shells in other areas of Europe has been made by Johansen (1901, 1902), Wasmund (1926) and Antevs (1928). Johansen (1901: 21) studying the depth distribution in the Kattegat of those species of molluscs, of which empty shells were found on the beaches, arrived at the conclusion that only shells living inside the 12 m line are transported to the beach. Similar research on the west coast of Jylland, the Faeroe Islands and Iceland led Johansen to the conclusion that in a belt inside of the 15 m line along the coast, shells are transported upward or downward. The more sheltered the coast is the narrower this belt will be. In Bohuslän (S. Sweden) this belt, according to Antevs (1928: 523), is reduced to the 10 m line, due to the presence of skerries. The data from the sheltered Ria de Arosa fit in well with these records.

The mechanisms of transport are waves and currents. Wilderom (1966) gave an interesting example of shell transport by strong tidal currents: fossil shells from a shell bed 18 m deep and lying exposed on the bottom of the Wester Schelde, Netherlands, are transported towards the coast.

(3) Transport towards deeper water. Most mollusc species living in the marginal zone are found as empty shells in the samples from the deeper central bay, where they do not live. In fig. 37 the presence of a species in the marginal zone is plotted against its presence as empty shells in the central bay. This figure illustrates that the more common a species is found in the marginal zone, the more often it will be encountered in the central bay. The distribution map of *Bittium reticulatum* (fig. 23) moreover shows that most transported specimens are found in a belt along the coast: transport is related to distance from the coast. Transported marginal bay shells in the

central bay samples may be very well preserved, i.e. they do not show signs of transport. In my opinion this indicates that the shells are not transported along the bottom, as in that case they would show signs of wear, but by floating algae and small shells perhaps also drifting.

The transport of the gastropod epifauna by *Himanthalia*, a sublitoral brown alga, was studied by comparing the epifauna from plants in situ and from two samples of floating *Himanthalia*, one from the centre and the other from the entrance area of the ria. A decrease was found in the number of specimens and species on the floating algae compared with the algae in situ. The latter had 10 species of epifaunal gastropods, the floating *Himanthalia*

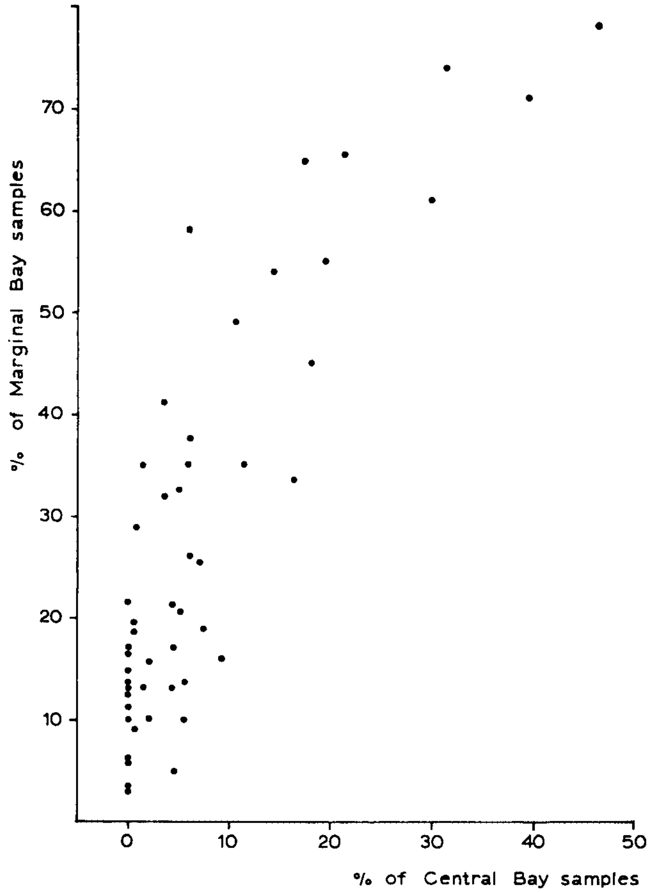


Fig. 37. Relationship between the presence of a species in the marginal zone and its presence as empty shell in the central bay.

5 and 1 respectively. The "lost" specimens perhaps left the algae in search of a better place, or may have dropped to the bottom of the ria where they died of starvation. A similar decrease in the epifauna of *Himanthalia* after long transport is well known to the shell collectors on the beaches of the Netherlands. Under favorable conditions *Himanthalia* from the English and French Channel coasts is transported towards the Dutch beaches. A small part of the epifauna may be found still alive on it (Van Regteren Altena, 1959). The rest will have left the drifting *Himanthalia* before this reached the beach, part of the shells will have contributed to the sediments of the sea bottom.

Quantitatively the transported marginal-bay shells form only a small part of the central-bay samples, usually less than 1%. Antevs (1928), studying shell beds in the Gullmarfjord and surroundings, also found a transport of shallow-water species towards deeper water, the importance of which decreased with distance from the coast.

Comparison with other areas.

The fauna of the shallow marginal subzone may be compared with the *Tellina* community (Thorson, 1957: 507) although the resemblance is not very exact, as of the characterizing genera *Tellina, Donax* and *Dosinia* only the last mentioned is frequently found.

The fauna of the deep marginal subzone may be compared with a *Venus* community (Thorson, 1957: 509) but here also only one of the characterizing genera, viz. *Spisula,* is present, further *Venus gallina* is found in greater quantities in deeper water on the mud bottom instead of on sand.

Forbes (1844) described a faunal zonation in the Aegean Sea and the British seas. Jeffreys (1862: ciii) somewhat extended the description of the zonation. The zonation found in the Ria de Arosa compares very well with their zonation; the littoral zone plus the laminarian zone of Jeffreys and Forbes may be compared with our shallow marginal zone. The coralline zone can be compared with our marginal deep zone, both are characterized by the calcareous alga *Lithothamnion.* Our findings agree very well with what Jeffreys (1862) recorded as being the molluscan species typical for these zones.

In the zonation given by Pérès & Picard (1964) our "shallow marginal zone" corresponds with their supra-, medio- and infra-littoral zones taken together, the lower boundary of which is formed by the lower limit of marine phanerogams and photophilous algae. Our deep marginal zone is their circalittoral zone, the lower limit of which is formed by the lower limit of (sciaphilous) algae. Parker (1959: 2125, 2156) describing some open Texas coastal bays of high salinity, also made a distinction between (1) a marginal zone with sandy sediments inhabited by filter-feeding lamellibranchs and (2) the bay centre with fine clayey sediments and deposit-feeders. He too thought that circulation was of major importance in this distribution pattern.

V. THE CENTRAL BAY

The environment (summarized from chapter I).

Compared with the marginal zone the central part of the bay is characterized by rather uniform conditions. The salinity ranges (near the bottom) from approximately 32.5 to 36.0°/₀₀. The temperature range is from approximately 11 to 17° C. The range of temperature and salinity is slightly larger in the inner part of the ria than in the outer part .

The sediment consists largely of silt and clay; in the inner part of the ria this forms up to 95% of the sediment, in the outer part lower percentages are found. Due to the more sheltered position of the inner bay, its nearness to the river Ulla, and perhaps the higher plankton production, the muds of this part of the ria are soft, black, smelling of H_2S and have a high organic carbon content (up to 7%). A thin layer of brown, oxydised mud on top of the sediment samples indicates that oxygen is still present in the bottom water. It seems reasonable to suggest that oxygen saturation near the bottom will be lower in the inner part of the ria, than in the outer part. Here the mud contains a smaller amount of organic carbon (2-4%) and is grey coloured. Currents near the bottom are supposed to be weak. The nearer to the ocean the richer the sediment becomes in coarse, shelly, material. In the inner bay this zone begins at a depth of 3 to 5 m, in the outer bay at approximately 20 m. It extends to the greatest depth encountered in the ria, 30 m in the inner, 60 m in the outer bay.

The central bay fauna.

Fig. 38 represents a section through the length of the ria from the Rio Ulla to the Atlantic Ocean. It shows the quantitative composition of the thanatocoenosis of shells larger than 2 mm. Gastropods are plotted cumulatively from below, pelecypods cumulatively from the upper side of the figure. The character of the central bay fauna differs markedly from that of the river mouth of the Ulla and that of the bottom of the inlet area and the shelf opposite the ria. Gastropods form 50% of the thanatocoenosis in the central bay and less than 10% in the other areas.

The two following graphs show the grain size and the organic carbon content of the sediment respectively. Graph D shows the abundance per

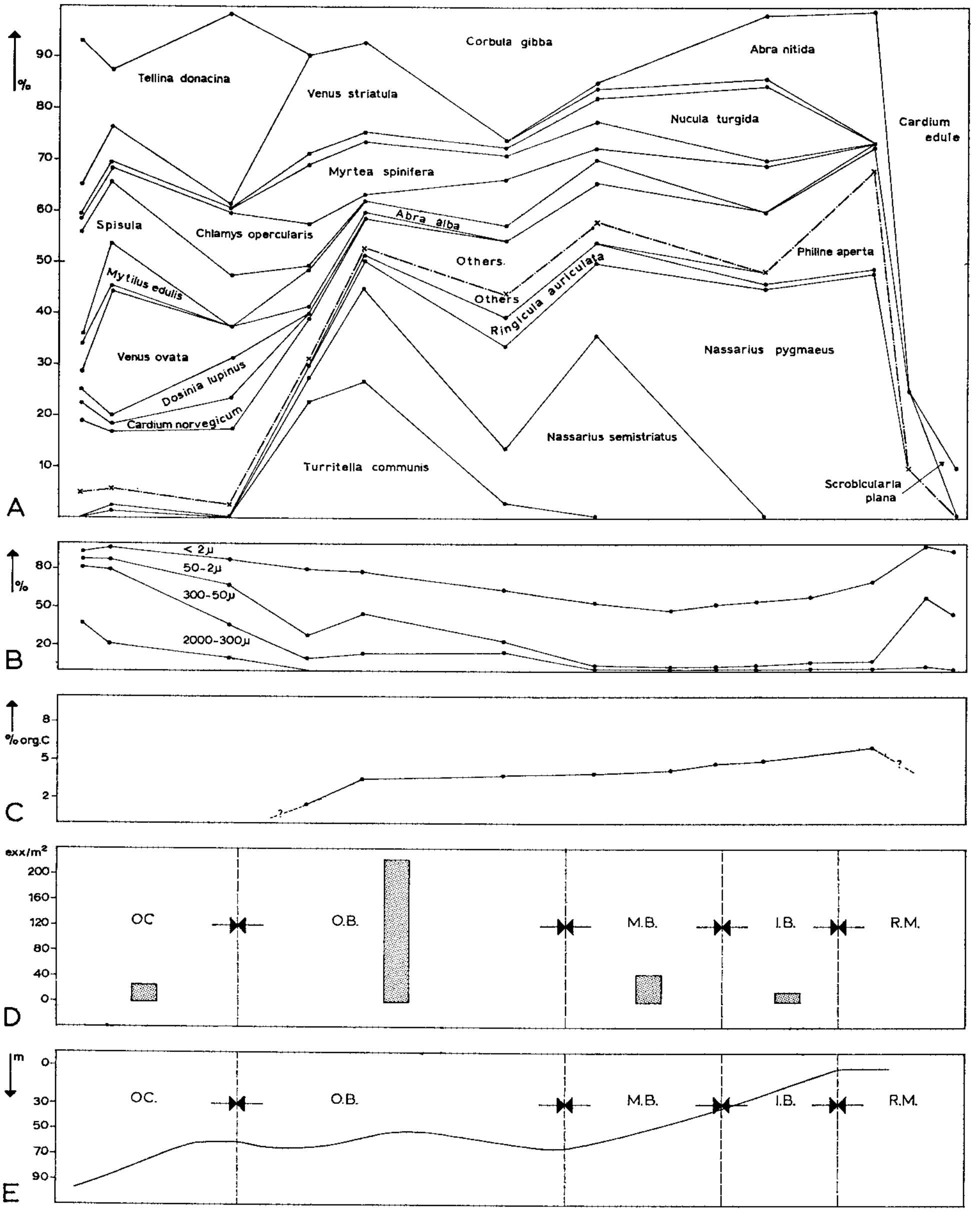


Fig. 38. Length section through the Ria de Arosa showing (A) the quantitative composition of the thanatocoenosis, (B) the grainsize composition of the sediments, (C) the organic carbon content of the sediment, (D) the number of living molluscs > 2 mm per m² in the different zones, (E) the depth and zone boundaries.

square metre of living molluscs larger than 2 mm. This clearly shows a deterioration of the environment in the inner bay (supposed to be due to lower oxygen saturation near the bottom). In the outer bay we found 14 times more molluscs per square metre than in the inner bay and 5 times more than in the middle bay (the data of three summers are taken together).

The first graph also shows the rather regular change in the composition of the thanatocoenosis of the central bay: the inner bay is characterized by *Philine aperta* and *Abra nitida,* the outer bay by *Turritella communis* and *Venus striatula,* there is a transitional zone — the middle bay — with no peculiar species of its own.

In fig. 39 some general characteristics are given of the molluscan fauna of the three subzones of the central bay, living and dead molluscs (larger than 2 mm) are compared.

Pelecypods and gastropods each make up almost 50% of the total molluscan fauna; they are largely infaunal species, epifauna is almost absent.

Deposit-feeders among the pelecypods are numerous, but do not always outnumber suspension-feeders, e.g., not in the middle bay. Carnivores are the most important group among the gastropods. Compared with the marginal zone, the central bay shows important differences: the epifauna and grazers are almost absent, and carnivorous gastropods are more important. Sediment-feeders among the pelecypods are in general more important than in the marginal zone. In the marginal zone they were less numerous in the thanatocoenosis than in the biocoenosis. The same is found in the outer bay, where many specimens of *Abra alba* are found alive but only very few dead (see chapter VII). *Abra nitida* in the inner bay and middle bay does not show this discrepancy.

Important species (pls. 3, 4).

The following is an annotated list of the species present in 30% or more of the samples from one or more of the subzones of the central bay. Abbreviations: C.B. = central bay; I.B. = inner bay; M.B. = middle bay; O.B. = outer bay; Fr. Gr. = Fretter & Graham, 1962.

Gastropoda, Prosobranchia

Trochidae: *Gibbula cineraria* is represented almost exclusively by empty shells. The deepest occurrence of living specimens in the ria was 23 m, empty shells were found down to the greatest depth in the ria. Only post-mortem transport can explain this. The distribution map shows a relation between transport and distance to the coast in the ria: large areas in the centre of the

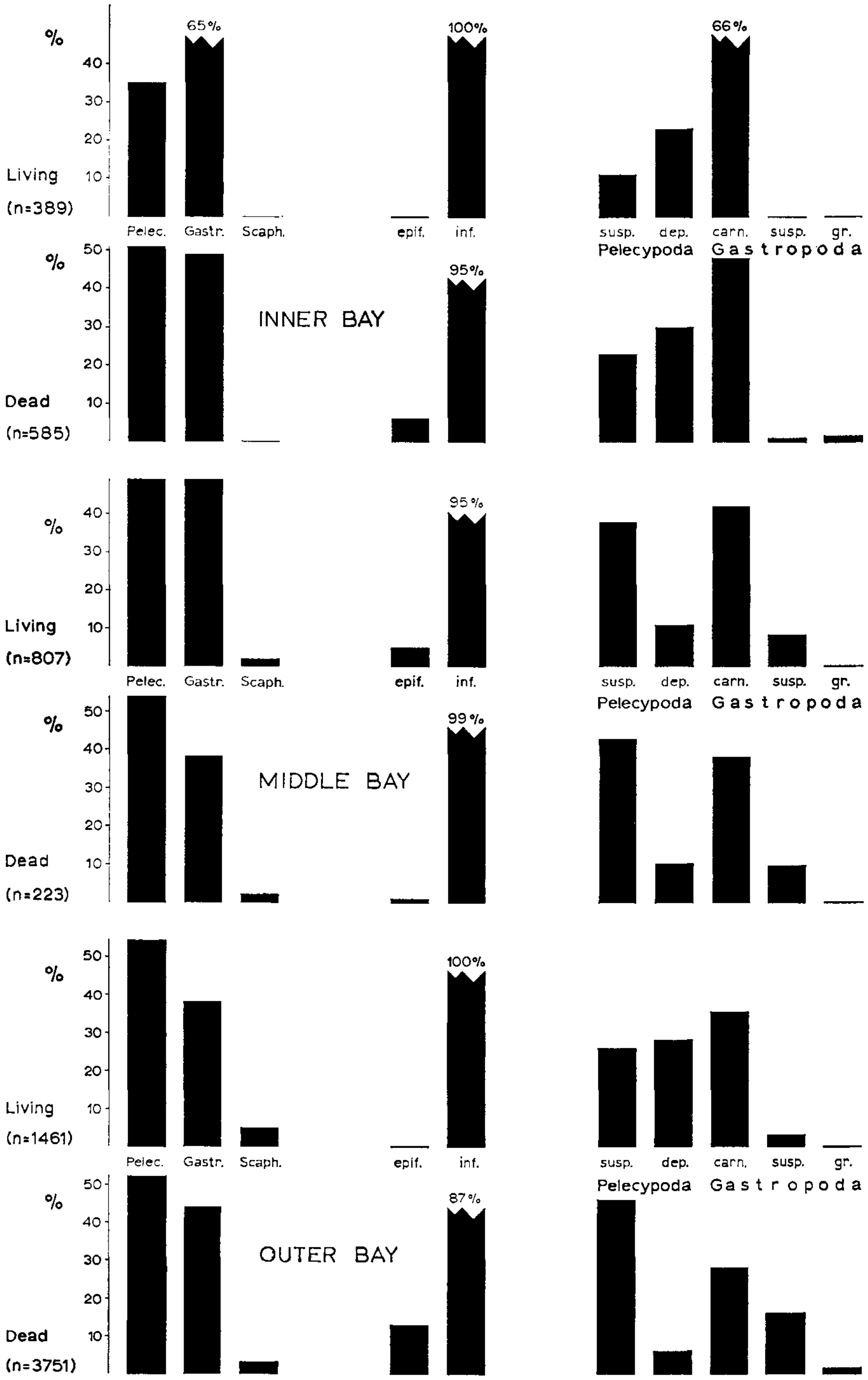


Fig. 39. Histograms showing the composition of the mollusc fauna in biocoenosis and thanatocoenosis.

ria are devoid of empty shells of *G. cineraria.* Of *Cantharidus exasperatus* only empty shells were found, transported from the marginal zone where this species is frequent.

Rissoidae: *Cingula vitrea* was found dead and alive in M.B. and O.B. Its food consists of detritus (Fr. Gr.: 261). No other rissoids were found alive at the depth where this species is found (down to 57 m) in the ria. Perhaps this is related to the type of food, as other rissoids require more living plant material. *Rissoa parva* and *R. lilacina* are for the greater part transported to C.B., the deepest occurrences of living specimens in the ria are respectively 15 m and 7 m.

Turritellidae: *Turritella communis* was found dead in great numbers and sometimes alive in the M.B. and O.B., it was practically absent from I.B. *T. communis* is a suspension-feeder (Fr. Gr.: 570, 571) which lives buried in stiff mud with some admixture of gravel (shells) (Yonge, 1946). Its absence from the inner part of the ria with its soft sediment therefore is in accordance with Yonge's findings. Suspension-feeding may be difficult in soft substrates.

Cerithiidae: The deepest occurrence of living specimens of *Bittium reticulatum* was 8 m, all empty shells found were probably transported from the marginal zone, where the species is found in considerable numbers. As in some other marginal species, empty shells are more frequently found in C.B. stations close to the marginal zone than in those farther away (fig. 23).

Naticidae: *Natica alderi,* a carnivorous species feeding on bivalves, lives in not too soft sediments in the marginal zone, the mouth of the ria and in the O.B. In softer sediments it is replaced by *Philine aperta.* A similar distribution of these two species was found by Clark & Milne (1955) in two bays along the coast of the Isle of Cumbrae, Firth of Clyde, Scotland: in the exposed White Bay with a sandy bottom, they found *Natica alderi* and in the sheltered Kames Bay with fine mud they found *Philine aperta.*

Nassariidae: *Nassarius pygmaeus* occurred in the whole C.B. with a high frequency (present in 90% of the samples) but quantitatively it was most important in the I.B. There was a regular increase in the presence of *N. semistriatus* from the I.B. to the O.B. (25% of I.B., 60% of M.B. and 95% of O.B. samples). This species is also quantitatively important in M.B. and O.B. (see fig. 38). *N. reticulatus* is a marginal species, the deepest occurrence of living specimens in the ria was 18 m, outside the ria 45 m. The presence of this species in C.B. samples is probably due to transport. Nassariids are infauna species and mainly scavengers. As they plough through the sediment (Fr. Gr.: 522), the coarseness and consistency of the sediment may influence their distribution. The distribution in the ria of the three species mentioned seems to indicate that *N. reticulatus* prefers sandy sediments, *N. semistriatus* not too soft mud, whilst *N. pygmaeus* prefers mud which may be very soft.

Turridae: *Mangelia coarctata* is a carnivorous gastropod present in 50% of the M.B. and 40% of the O.B. samples. This species lives in both zones and also in the marginal zone. It seems to have no preference for a special habitat but was absent from the soft I.B. mud. *Mangelia brachystoma* was present in some 50% of the M.B. and O.B. samples, only a few specimens were found alive (M.B.); it is a little known carnivorous species.

Opisthobranchia

Ringiculidae: *Ringicula auriculata* was present as empty shells in a little more than 80% of the C.B. samples. Living specimens were found in small numbers only in our third year of collecting (1964) which suggests a marked fluctuation in the population. Its importance in the thanatocoenosis suggests that this species may in some years also be an important member of the biocoenosis. Nothing is known of the biology of this species, it seems to live buried in the sediment using its large foot as a plough, it may be a carnivore like most of the other tectibranch opisthobranchs.

Pyramidellidae: *Turbonilla cf. elegantissima*, represented by specimens varying strongly in coarseness of sculpture and in length-width ratio, was present in 40-50% of the M.B. and of O.B. samples; *Odostomia* cf. *turrita* in some 50% of the I.B. and 30% of M.B. samples. The identification of *Odostomia* species is difficult, especially because the species are based on shell characteristics only, a new approach from a more ecological and anatomical view point is badly needed. Pyramidellids are ectoparasitic bloodsuckers and tissue-suckers as shown by Ankel (1948) and Fretter & Graham (1949), summarized in Fretter & Graham (1962: 251-254). The animals have a long proboscis, the apex of which is converted into a sucker. In *Odostomia* and *Chrysallida* a stylet has been found at the end of the proboscis. With this stylet species of *Odostomia* have been seen to penetrate the body of their host and then, with pumping movements, suck blood of their host into their gut. Some species of the pyramidellids seem to be predominantly associated with one particular host. The distribution of this host therefore will limit the distribution of the ectoparasite. Only the hosts of a small fraction of the pyramidellids are known: *Turbonilla elegantissima* is found as an ectoparasite on the polychaetes: *Audouinia tentaculata* (Mont.), *Amphitrite gracilis* (Grube) and *Cirratulus cirratus* O. F. Müller (see Fr. Gr.: 251-254), the host of *Odostomia turrita* is unknown. Living specimens of *T. elegantissima* were found only once (depth 30-40 m, M.B.); *O. turrita* was never found alive in the ria, perhaps due to its smallness. Our collecting gear was not very well adapted for collecting small animals. Working in 1965 in the Gullmarfjord (Sweden) I found the Ockelmann dredge to be far better at collecting small molluscs than normal dredges and grabs (cf. Ockelmann, 1964).

Retusidae: *Retusa truncatula* was found in about 40% of M.B. samples. This species has probably been transported to deeper water, living specimens were found only in shallow water (maximum depth 5 m).

Triclidae: *Cylichna cylindracea*, a species with a wide distribution in the ria wherever muddy sediments occur, was present only in the M.B. in more than 30% of the samples. This species lives 1 to 3 cm deep in the sediment. The food is not exactly known, as the stomach contents could not be identified (Lemche, 1956: 15-20). Hurst (1965) reported the same disappointing results, only once did she find a foraminiferan. Lemche suggested that the species feeds on rhizopods.

Philinidae: *Philine aperta*, an important species in the I.B. and M.B. samples, was practically absent in the O.B. Fig. 38 shows clearly a quantitative decrease from the inner to the outer bay in the thanatocoenosis, a similar decrease was found in the biocoenosis. *Philine aperta* lives beneath the surface of the sediment, its body-form is well adapted for ploughing through the sediment. Its food consists of diatoms, benthic Foraminifera and small molluscs (Fretter, 1939: 628). Hurst (1965) adds the polychaete *Pectinaria* to this list. The radula teeth are used as a grab. Calcareous plates in the gizzard wall masticate the food. Shells of molluscs and Foraminifera are crushed by these plates. In coarser sediments of the O.B. this species is replaced by the triclid, *Scaphander lignarius*, and in still coarser sediments by *Natica alderi*.

Living specimens of *Philine* were also encountered at low water on some muddy beaches close to the river Ulla; they are therefore able to endure somewhat lowered salinities (in the Baltic the species is found at a lowest mean salinity of 18 to $20^0/_{00}$ according to Sorgenfrei, 1958:398). Its competitors can not tolerate these low salinities: *Natica alderi* is found at a lowest mean salinity of $30^0/_{00}$, *Scaphander lignarius* at $33^0/_{00}$ (Sorgenfrei, 1958).

Pteropoda

Cavoliniidae: *Creseis acicula* (fig. 29) is an oceanic plankton species with empty shells in 40% of the O.B. samples. The presence of this species in the sediments indicates the great oceanic influence in the ria.

Scaphopoda

Dentaliidae: *Dentalium novemcostatum* was frequent in M.B. and O.B. samples, empty shells were found in about 80% and living specimens in some 25% of the samples; in the I.B. only empty shells were found and in the very inner part of the I.B. close to the Rio Ulla it was completely absent. Depth distribution: from 4 m down to the greatest depth in the ria. *Dentalium* lives buried in the sediment with the posterior part of the shell just above the sediment surface for water exchange. Its food probably consists of Foraminifera (cf. *D. entalis* studied by Morton, 1959), which are captured by captacula. The burrowing capacity of the different species seems to be adapted to different sediment types. Morton (1959) described the method of burrowing. Special lobes of the foot are used to anchor the animal in the sediment. The very soft sediments of the inner part of the ria may be unsuitable for anchoring the foot. *D. vulgare* is found in the coarser sediments of the entrance area of the ria. *D. novemcostatum* seems to be adapted to not too soft muddy sediments. *D. entalis* is adapted to medium and coarse sands (Morton, 1959).

Lamellibranchia

Nuculidae: Identification of European nuculids with crenulate margin (*N. hanleyi, N. nucleus, N. turgida* (syn. *N. nitida*) and *N. sulcata*) can best be based on the structure of the periostracum (see also Tebble, 1966: 24). stracum still present gave the following results. I.B. and M.B.: *N. turgida*; moreover shell measurements may vary with sediment type as shown in *N. sulcata* (see Allen, 1954: 465). Therefore empty shells of which the periostracum rapidly disintegrates cannot be identified. Van Regteren Altena et al. (1926: 7) came to the same conclusion with regards to empty *Nucula* shells from the beaches of the Netherlands.

Distribution of living *Nucula* specimens and empty shells with the periostracum still present gave the following results. I.B. and M.B.: *N. turgida;* O.B.: *N. turgida* and less frequent *N. nucleus*; in the oceanic zone *N. hanleyi,* less frequent *N. nucleus* and one specimen of *N. turgida.*

If the empty shells of *Nucula* in the I.B. and M.B. samples are therefore considered to be of *N. turgida* (those from the other zones cannot be taken into account as they may be one of three species), this species was present in 75% of I.B., 95% of M.B. and 35% of O.B. samples. It lives in muddy sediments which may be very soft and contain particles up to 90% finer than 50μ and up to 5% organic carbon. *N. nucleus* lives in mud with shell gravel. *N. hanleyi* lives in shelly gravel. There is some overlap;

N. turgida and *N. nucleus* are sometimes found in the same grab sample, *N. nucleus* and *N. hanleyi* in the same dredge sample.

The Nuculidae feed, by means of labial palps, on organic matter in the sediments (Yonge, 1939: 132), they live below the sediment surface and also collect their food from below the surface. The inhalent current plays a minor role in food collecting, which is shown by Stasek (1965) to be more important than Yonge (1939) believed. The difference between suspension-feeders and deposit-feeders seems to be less sharp than formerly supposed.

Both Yonge (1939: 81) and Allen (1954: 458-459) found the different *Nucula* species in different sediment types in the Plymouth area and Clyde Sea area respectively. However, they reported *N. turgida* from fine muddy sand and silt (Plymouth), and sands, sandy silts with particles up to 50% finer than 62.5 μ (Clyde Sea). In the Ria de Arosa this species lives also in such substrates and in much finer sediments which in the Clyde Sea are occupied by other species (*N. tenuis* and *N. sulcata*). Sediment type seems to be a very important factor in the distribution of the different *Nucula* species, each species being adapted to a certain type.

Nuculanidae: *Nuculana fragilis* is restricted to the O.B. Living habits and feeding methods of the Nuculanidae are almost the same as in the Nuculidae. One difference is the presence of inhalant and exhalant siphons in the Nuculanidae, which do not occur in the Nuculidae. Some Nuculanidae collect their food from the sediment surface, others from below the surface (Yonge, 1939: 85-90). Nothing is known of the biology of *N. fragilis*, but from Yonge's paper we may conclude that it is a sediment-feeder, which lives buried in the sediment but near the surface in order to remain in contact with the overlying water. The sediment of the inner part of the ria may be too soft for it.

Anomiidae: *Anomia ephippium* is present, as mentioned, in the marginal zone, but also in some 40% of M.B. samples. It lives attached to shells, frequently of living pectinids. *Chlamys opercularis* was present in 70% of the M.B. samples and was found sometimes with *Anomia* attached to it.

Mytilidae: *Mytilus edulis* was present as empty shells in some 40% of I.B. samples. These shells probably have been contributed to the sediment from the rafts on which *Mytilus* is cultured in the inner part of the ria. *Musculus marmoratus* occurred is about 35% of M.B. samples. It lives embedded in the skin of tunicates or attached by its byssus to old shells (Jeffreys, 1863: 123). In the ria we found them in the same habitats.

Pectinidae: In the M.B. *Chlamys varia* was found only as empty shells. These occurred in 40% of the samples and will probably have been transported from the marginal zone where this species lives. *Chlamys opercularis* was present in some 70% of the C.B. samples. Juvenile specimens live attached but the adult are free and are able to swim. According to Yonge (1936: 78) they are very active swimmers, living in shoals and making extensive migrations. These habits make it difficult to get a good idea of their density on the bottom by means of grab and dredge samples. They are suspension-feeders. They occur in large quantities in the central channel in the ria near the Isla de Arosa, where bottom currents are stronger and therefore food supply is better than in other parts of the C.B. Therefore empty shells are most abundant in the central channel. *C. opercularis* has a wide distribution in the ria. We also found it alive in the oceanic zone outside the ria.

Lucinacea: *Thyasira flexuosa* was present in about 80% of the C.B. samples, *Myrtea spinifera* in 90% of the M.B. and O.B. samples and less frequent (40%) in I.B. The Lucinacea were studied in detail by Allen (1958). They are suspension-feeders which live buried in the sediment. With their foot they form a tube of mucus-coated sand grains, which is used as an inhalant tube. They are frequently found in areas with a poor bottom fauna. This paucity is sometimes due to the presence of hydrogen sulphide in the sediment. The inhalant tube of the Lucinacea seems to enable them to live in such unfavourable regions. In more favourable environments Allen suggests that competition with other suspension-feeders is the reason for their absence. The fragile shell of *Thyasira* moreover makes life in rough habitats with shifting sands impossible. *Thyasira* is always found in muddy sediments in quiet habitats. *Thyasira flexuosa* seems somewhat better adapted to live in the soft, black sediments of the I.B. smelling of H_2S, than *Myrtea spinifera.*

Montacutidae: *Mysella bidentata* was present in some 60% of the C.B. samples. It is a species with a wide distribution in the ria, and not characteristic of one zone.

Cardiidae: *Cardium edule* was present in 30% of I.B. samples but only as empty shells. In chapter 3 the presence of these shells was stated to be probably due to transport from the sand-flats in the mouth of the river Ulla, where *Cardium edule* lives in large numbers. *Cardium paucicostatum* was present in almost 90% of I.B., 100% of M.B. samples, and was less frequent in O.B. (70%). Nothing is known of the special adaptations of this suspension-feeder to the muddy habitats in which it lives. In the ria it is the only *Cardium* species which can live in soft sediments. Large quantities of inorganic sediment must enter the mantle cavity through the inhalant siphon when this opens close to the sediment-water interface (cf. *Corbula gibba,* as discussed by Yonge, 1946). A large production of pseudo-faeces will probably be the result. For a „normal" suspension-feeder this would require too much energy, and the animal would not be able to grow in such an environment as was experimentally demonstrated by Pratt & Campbell (1956) for *Venus mercenaria.* However, it is uncertain whether *C. paucicostatum* has a special adaptation to overcome this disadvantage. It has also been found in muddy sediments of the Mediterranean near Marseilles (Van Straaten, 1960: 115, table 2; Picard, 1965: 49). *Cardium scabrum* was present in 40% of the M.B. and O.B. samples. This species was found alive on rare occasions at great depths (maximum 35 m, in mud with shelly gravel in the ria; 60 m outside the ria); the majority of the empty shells found in the C.B. samples, have probably been transported from the marginal zone where this species is abundant.

Veneridae: *Venus ovata* occurred in almost 40% of O.B. samples; *V. striatula* in 50% of the I.B., 95% of the M.B. and 80% of the O.B. samples; *Venerupis rhomboides* in a little more than 30% of the M.B. and O.B. samples. Veneridae are suspension-feeders which live near the sediment surface except *Dosinia* (cf. Ansell 1961). They live in general in sandy sediments. *V. striatula* forms an exception, it is found in the ria in finer sediments than it is found in other parts of Europe. Eisma (1966: 143) has compiled sediment data for this species from the literature: in northern Europe it is always found on sand which may be mixed with some mud. In the Mediterranean off Marseilles it is found on pure, fine sands (Picard, 1965: 49). Only Pérès (1959) reports this species from soft mud from dredgings off the south coast of Portugal, at a depth between 75 and 100 m.

Tellinacea: *Abra nitida* (distribution map fig. 26) occurred in 98% of the I.B. samples and decreased regularly towards the M.B. (85%) and O.B. (50%). *Abra alba* (distribution map fig. 27) had a somewhat reverse distribution (I.B. 40% of the samples and O.B. 75%). *Abra alba* lives in the O.B. and in a belt between the marginal zone and the soft sediments of the I.B. where *A. nitida* is found. In samples from a transitional area both species occurred together (alive). *A. nitida* is found in sediments of which 90% or more of the particles are finer than 50 μ and organic C content is 4 to 6%. *Abra alba* lives in sediments with less silt and clay and less organic carbon (1-4%). This distribution agrees well with that found by Glémarec (1964: 19) in Morbras and the Golfe du Morbihan (Brittany, France). *Abra nitida* seems to be better adapted to life in very soft sediments with H_2S just below the surface. Ekman (1947: 10) also reported that this species was very abundant in very soft sediments of the Gullmarfjord (Sweden). Moore (1931: 355) demonstrated that *A. alba* can live up to 3.5 days without oxygen, *A. nitida* according to its habitat may be able to live a longer time without oxygen (this remains to be shown by experiment). The Tellinacea are deposit-feeders. Yonge (1949: 35) described the method of feeding of *Abra*. *Abra* lives buried in the sediment; long siphons, of which the inhalant siphon is the longer, remain in contact with the sediment surface. The inhalant siphon searches over the surface of the mud from which it actively pulls in material. This process of continual rapid intake is interrupted about every 2½ minutes by a sudden extrusion of pseudo-faeces, which takes place in 3 seconds, with the siphon well clear of the bottom. Very large quantities of sediment are being reworked by the *Abra* species living in the ria. Rhoads (1963) studied the rate of sediment reworking by another deposit-feeder, *Yoldia limatula,* in Buzzards Bay and Long Island Sound (east coast of U.S.A.). He found that although they formed only some 10% of the macrobenthos, they were able to rework all the sediment deposited annually. The *Abra* species form about the same percentage of the bottom fauna in the ria, the rate of sediment reworking is high as sediment is almost constantly taken up. Therefore *Abra* species will be important homogenizers of the sediment in the ria (lamination and stratification of the sediments is almost absent). Summarizing we can state that *A. nitida* lives in that part of the C.B. where there is least oxygen. Competition with *A. alba* may play a role in this distribution, but *A. nitida* seems also to be better adapted to live in the very soft sediments which are found here. Neither salinity, nor temperature plays a role in this distribution: temperature differences between the I.B. and O.B. are very small. Salinity differences are also small. Exceptionally salinity may be somewhat lower near the bottom in the I.B. As *A. nitida* also was found in a sheltered bay near the Isla de Arosa where lower salinities are not to be expected and where the same fine sediments accumulate as in the I.B., the sediments and the oxygen content of the bottom water seem to be the chief factors in this distribution.

Mactridae: *Spisula* sp. occurred in about 40% of M.B. samples only and was always found in samples with the coarsest sediment in this zone. As a suspension-feeder *Spisula* sp. cannot live in the fine silt-clay sediments of the greater part of the C.B.

Corbulidae: *Corbula gibba* was present in 65% of I.B. and 90-100% of the other C.B. samples. It is an important member of the thanatocoenosis especially in M.B. and O.B. The adaptations of this suspension-feeder to muddy sediments as studied by Yonge (1964) are summarized on p. 41.

Hiatellidae: *Hiatella arctica* s.l. is an epifaunal suspension-feeder, already mentioned in the marginal zone. In the C.B. we found it attached to colonies of the bryozoan genus *Cellaria*. This species is able to live wherever it can find a suitable holdfast for its byssus and the currents are strong enough to bring a constant flow of suspended matter. *Saxicavella jeffreysi,* typical of M.B. (50%) and O.B. (60%), was only rarely found in other zones. The biology of this species is little known. Like other Hiatellidae it is a suspension-feeder, but unlike, e.g., *Hiatella arctica* it lives buried in the sediment. Tebble (1966: 175) reported this species from clean, sandy mud and gravel, i.e., from much coarser sediments than in the ria (silty clay with 50% or more of the particles finer than 50 μ).

Cuspidariidae: Of *Cuspidaria cuspidata* only empty shells were found in 40% to 50% of the M.B. and O.B. samples, with only very small percentages in other zones. Absence of living specimens in our collections is probably due to their rarity. It is also rare in other localities (Yonge, 1928: 222); as a result empty shells also are never abundant. Tebble (1966: 204) reported that in British water this species lives in muddy sand and gravel below 20 m depth. This is in accordance with its occurrence in the ria (and its absence from the soft muds of the I.B.). Yonge (1928: 248) studied the food of *C. cuspidata* which consists of small Crustacea and Annelida either dead or alive, which are pumped in through the inhalant siphon. *Cuspidaria* lives buried in the sediment and belongs to the few carnivorous lamellibranchs which exist. Fine particles and plankton, which form the food of other lamellibranchs and therefore constitute the stomach contents of them, were wholly absent from the stomach of *Cuspidaria,* which indicates that they do not feed on these.

Other skeletal remains.

The coarse fraction (components larger than 2 mm) and the fine fraction (1-2 mm) contain a small number of skeletal remains of fishes, coelenterates, echinoderms etc. We did not evaluate their percentages of the total fraction, but only compared where possible (echinoderms, coelenterates) the distribution of living specimens with skeletal fragments.

Ophiuroid remains: Vertebral plates and arm spines are present in the whole C.B. but only abundant in the O.B. They may originate from various species. *Amphiura chiajei* Forbes and *A. filiformis* (O. F. Müller) are found alive in the M.B. and O.B., *Ophiura texturata* Lam. was also found in the I.B. (identification by Mrs. A. A. M. C. Horixs and Mr. W. J. Wolff). Skeletal remains cannot be identified to the species (Mortensen, 1938).

Echinoid remains: Spines of irregular sea-urchins were found in the M.B. and O.B. samples. They belong to either *Echinocardium flavescens* (O. F. Müller) or *E. cordatum* (Pennant) which were found on a few occasions in the ria. Spines of regular sea-urchins were found only on a few occasions,

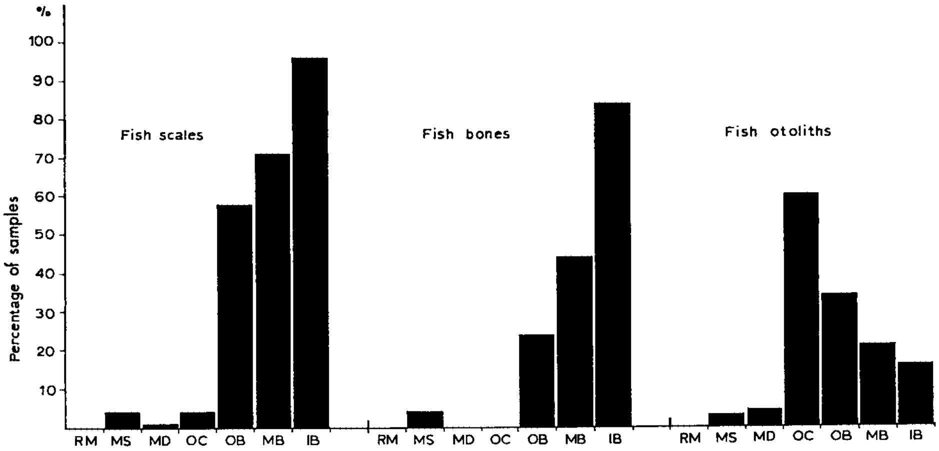


Fig. 40. Histograms showing the percentage of samples in which fish remains are found in the different zones.

living specimens occur only in the marginal zone. The spines therefore have probably been transported.

Octocorallia (Pennatulacea): Sclerites (small needles) of *Pteroides spinosum* (Ellis) were found in the M.B., O.B. and on the shelf outside the ria. Living specimens occur in the same zones. Pieces of the calcite axis of *Virgularia mirabilis* O. F. Müller were present in all samples of the C.B. Living specimens (identified by Dr. W. Vervoort) were found in the same area.

Bryozoa: Living specimens of a species of *Cellaria* were found in the M.B. and O.B., dead specimens in the same zones.

Fish remains (scales, bones, otoliths and teeth): Fig. 40 gives the percentage of samples in which these remains are found in the different zones. They were practically absent from the coarser sediments of the marginal zone, the mouth of the Rio Ulla and the oceanic zone. More scales and bones are found in the silt-clay sediments of the I.B. than in those of the O.B. Otoliths show a reverse distribution: most of them are found in the O.B., they are never abundant in the samples, but scales and bones may be quite abundant in the I.B. in the soft, black mud smelling of H_2S. The frequent occurrence of fish remains in the ria sediments seems, according to the literature, rather exceptional. Brongersma-Sanders (1949) reviewed most of the literature on this subject up to that date. From this review it becomes evident that fish remains on the sea bottom are rapidly and completely destroyed by carnivorous invertebrates. Accumulation of fish remains therefore will be found only in those places where these carnivorous invertebrates are absent (in anoxic or almost anoxic conditions). Schäfer (1962: 103, 104) pointed out the importance of mechanical wear: in coarser sediments only the strongest fish remains will not be destroyed by sediment movements. In finer sediments, which can only accumulate in a quieter environment, this mechanical destruction will not occur. According to that author fish remains are not infrequent in the finer sediments of the German Bight. Perhaps fish remains will eventually dissolve in seawater. In conclusion, we may state that the absence of fish remains in the coarser sediments of the ria are probably due to mechanical wear, and to carnivorous invertebrates (and the solvent action of seawater?). The abundance of fish remains especially in the silt-clay sediments of the inner part of the ria probably is due to the absence of carnivorous invertebrates, to the non-occurrence of mechnical wear and to the rather rapid sedimentation, which prevent the remains from being destroyed.

Transport.

Post-mortem transport of shells of molluscs living in the central bay zone is negligible: living and dead specimens of the same species show in general a good conformity in distribution. This indicates that currents along the bottom are of little importance as transport agents. There is only an admixture of shells from species living in the marginal zone.

This remarkable absence of post-mortem transport is in accordance with the findings of Habe (1956) for Japanese bays. Holme (1961: 443) also noted the absence of transport of shells (larger than 2.2 mm) in the English Channel, although the tidal currents are stronger there than in the ria.

This absence of transport along the bottom and the quantitatively not very important admixture of shells from the marginal zone are very promising for paleontologists working with fossil faunas.

Summary.

There is no sharp boundary between the mollusc faunae of the inner bay and the outer bay, in fact a transition zone (the middle bay) can be discerned in between. A sharp boundary was not to be expected, as there is no sharp boundary either in the measured ecological factors: temperature and salinity are almost the same in both, the sediment is somewhat coarser in the outer bay due to a larger admixture of shells. This can be related in part to a slower sedimentation in the outer bay, which is farther from the most important source of sediments, the Rio Ulla.

Important members of the outer bay fauna are *Turritella communis, Nassarius semistriatus, Venus striatula, Corbula gibba,* and *Abra alba.*

The fauna of the inner bay is largely made up of *Philine aperta, Abra nitida* and *Nassarius pygmaeus.*

The outer bay molluscs are found only in very small quantities in the inner bay, the inner bay molluscs in small quantities in the outer bay. The middle bay forms a transition area.

The mollusc fauna becomes poorer in species and in specimens per m^2 from the outer bay to the inner bay.

Salinity may also be a factor of importance, but for the faunal difference between the outer and inner bay (where river influence may be felt also on the bottom after a rainy period) this factor can be ruled out: in a small sheltered bay of the Isla de Arosa in the centre of the ria, the same soft muds smelling of H_2S and with an organic carbon content of 5% accumulate as in the inner bay and the fauna is the same, although the river influence in the former is negligeable.

Therefore I might suggest that the difference in fauna is due to the more sheltered position of the inner bay as compared with the outer bay. This sheltered position affects: (1) sedimentation, (2) renewal of bottom water, (3) phytoplankton production.

(1) Sedimentation. — Very soft muds with a high water content and more than 90% silt and clay particles are deposited in the most sheltered places of the ria.

2) Renewal of bottom water. — The vertical mixing of the water in summer does not reach the bottom. The oceanic water, which penetrates the ria along the bottom may have lost part of its oxygen, before it reaches the inner part of the ria. The oxygen of the bottom water in the inner part of the ria may be consumed more rapidly than it can be replenished.

(3) Phytoplankton production. — Vives & Fraga (1961) found phytoplankton production to be 3 to 4 times higher in the inner part of the Ria de Vigo than in the outer part. Presumably this is also the case in the Ria de Arosa. Ketchum (1954) noted the effect of the exchange ratio of an estuary on its plankton population: the larger the exchange with the sea, the more difficult it is for the plankton population to grow more rapidly than it is diluted by new seawater. The inner part of the rias is probably less affected by exchange with the ocean than the outer part as a consequence of its more sheltered position. Therefore phytoplankton production is higher in the inner part of the ria. The nutrient content of the water of the inner part and the outer part of the Ria de Arosa is almost the same according to the measurements made during the Ria de Arosa expedition. This indicates that nutrient content does not play a role in the higher phytoplankton production of the inner part.

The higher organic carbon content of the sediments in the most sheltered parts of the ria, will be the combined result of the above mentioned factors: sedimentation of organic matter absorbing clay particles, poor ventilation and higher phytoplankton production. Part of the organic matter is contributed by the rivers (plant-fragments are abundant in samples close to the mouths of the rivers Ulla and Umia), but Margalef (1958) demonstrated that in the Ria de Vigo organic matter was largely contributed to the sediment by the phytoplankton. It is very probable that this is also the case in the Ria de Arosa.

The very soft sediments of the inner part of the ria, the high organic content and perhaps the resulting lower oxygen saturation of the bottom water make apparently the inner part of the ria an unfavourable environment for molluscs. Even those species which can tolerate this hostile environment do not occur in great numbers.

Comparison with other areas.

The inner bay fauna is very similar to the *Abra alba* community described by Petersen (1918) from Danish waters. Thorson (1957: 510) gave the following characteristics: the *Abra alba* community is found in sheltered or estuarine areas, often with a somewhat reduced salinity and on mixed to muddy bottoms rich in organic matter, from 5 to about 30 m depth. It is characterized by the lamellibranchs *Abra alba, Cultellus pellucidus, Corbula gibba, Nucula turgida* and *N. nucleus,* by some polychaetes and some ophiuroids (*Ophiura texturata* Lam. and *O. albida* Forbes), while the echinoid *Echinocardium cordatum* (Pennant) may occur also in this community. The larger part of these species were found in the inner bay. Thorson (1957) reported this community from the Limfjord and other localities. Boysen Jensen (1919) described the *Abra alba* community from the Limfjord. He mentioned some other species which we also found in the inner bay of the Ria de Arose (*Philine aperta, Nassarius pygmaeus, Abra nitida*). Other species mentioned by Boysen Jensen do not occur so far to the south (*Mya truncata, Buccinum undatum*) and are therefore absent from the Ria de Arosa. *Abra nitida* outnumbers *Abra alba* in the inner bay of the ria. In the Limfjord *Abra alba* is more numerous than *A. nitida,* only in Nissum Bredning (part of the Limfjord) both are found in equal numbers. *Abra nitida* is most numerous in soft muds (Ekman, 1947:10). Difference in sediment type therefore will account for the difference in the ratio in which the *Abra* species are found both in the Limfjord and in the inner bay of the Ria de Arosa. In fact I found the same *Abra nitida*-rich fauna in the Ellösefjord (Bohuslän, southern Sweden) on a very soft mud. Glémarec

(1964b) found the same mollusc assemblage in the Golfe du Morbihan (Brittany, France) in his "Faciès à *Nucula turgida* type C", with *Nucula turgida* and *Abra nitida,* some other species being *Thyasira flexuosa* and *Philine aperta. Abra nitida* was found there and in the adjacent Mor Bras in the same soft muds with 90% or more particles smaller than 50 μ (Glémarec, 1964a; Vanney, 1965). According to Thorson (1957) and Mr. M. Horikoshi (1965, personal communication) the *Theora lubrica* community of the inner part of Japanese bays has to be seen as an iso-community of the *Abra alba* community of Europe.

In conclusion the inner bay molluscan assemblage can be regarded as being typical of muds in sheltered bays. Judging from other bays in which this assemblage is found, the salinity may be somewhat reduced; in the Ria de Arosa, however, the salinity near the bottom probably remains above 32‰.

The outer bay fauna shows great similarities with the boreo-mediterranean *Amphiura filiformis - A. chiaje* community (Thorson, 1957: 510). This community is characterized by the above mentioned ophiuroids and the molluscs *Turritella communis, Aporrhais pespelecani, Nucula* spp., *Thyasira flexuosa,* and in soft muds also by *Abra nitida.* Most of these species are found also in the outer bay.

Somewhat puzzling is the admixture of *Venus striatula* in the outer-bay fauna. According to Thorson (1957: 508) this species is characteristic of sandy intermediate-shelf sediments inhabitated by the *Venus* community. Pérès (1959), however, found this species also in muddy shelf sediments off Portugal.

Thorson (1957) gave a long list of localities where the boreo-mediterranean *Amphiura* community is found. From his list it is evident that this community is not only found in semi-enclosed bays (like the Ria de Arosa), but on all those places of the intermediate-shelf (ca. 15-100 m), where due to the sheltered position, muddy sediments can settle. Good examples of the occurrence of this community on the shelf are encountered along the English Channel coast(Ford, 1923; Holme, 1948, 1951). On muddy grounds, which are found in the sheltered Teignmouth Bay (10-22 m), Torbay (11-16 m), Start Bay (18 m) and off Berry Head (30-51 m) they found a fauna very similar to the outer bay fauna with the molluscs *Turritella communis, Nucula turgida, Thyasira flexuosa* and *Abra alba.*

In the terminology of Pérès & Picard (1964), the outer-bay fauna can be named a "Biocoenose des vases terrigènes côtières".

Picard (1965) describes this biocoenosis from the Rhone delta. It shows a great similarity to the outer bay fauna also in non-mollusca. The coelenterates *Veretillum cynomorium* (Pallas), *Virgularia mirabilis* O. F. Müller and *Pteroides spinosum* (Ellis) (identified by Dr. W. Vervoort), the polychaete *Sternaspis scutata* (Renier) (identified by Mr. J. van der Land) and the molluscs *Turritella communis*, *Cardium paucicostatum*, *Pteria hirundo* etc. occur in the ria and were reported from the Rhone delta by Picard (1965). Van Straaten (1960a) described the (dead) shell assemblages from the same Rhone delta. His assemblages 3, 5, 7, and 9 from slightly pelitic sand to pelite (Van Straaten, 1960a: 124, fig. 12), which are rather similar to each other, very much resemble the outer bay assemblage. *Turritella communis* makes up 50% of the samples in these Rhone delta assemblages; this is a higher percentage than in the ria. Vatova (1935) and Schmidt (1935) studied respectively the biocoenosis and the thanatocoenosis of the Canal di Leme, a long narrow bay in the north-western part of the Adriatic Sea close to Rovinj (= Rovigno), Yugoslavia. It is apparent that the biocoenosis and the thanatocoenosis from the Canal di Leme are very similar to the outer bay fauna of the Ria de Arosa. I made a similar comparison of the biocoenosis and the thanatocoenosis of the *Amphiura* community (Molander, 1928; renamed by Thorson, 1957: 512) in the Gullmarfjord in 1965 (unpublished). These too show great similarities with the outer bay fauna of the ria. In conclusion it can be stated that the outer bay assemblage is typical of intermediate muddy shelf deposits, not confined to enclosed bays but found on all sheltered parts on the shelf. The boreo-mediterranean *Amphiura* community which is found from Sweden to Israel (Thorson, 1957) seems to be accompanied by a very similar thanatocoenosis, as far as the more common species are concerned.

VI. THE OCEANIC ZONE

The environment (summarized from chapter I).

This zone comprises the entrance area of the ria and the shelf outside as far as sampled (max. depth 85 m).

Water movements are supposed to be stronger here than in the central bay zone: the large ocean waves and swell, and tidal currents, probably influence the bottom in this zone. Few measurements of such movements have been made but their influence is seen in the scarcity of silt and clay (less than 10%) in the sediment. This scarcity may also be partly a result of the small supply of this material, which may be trapped largely in the rias. As a result the sediment consists of large quantities of skeletal remains (molluscs, brachiopods, bryozoans, cirripedes, etc.). The slow rate of sedimentation is also demonstrated by the presence in one sample of beach-rounded pebbles, which date from a stage with lower sea level in the Pleistocene.

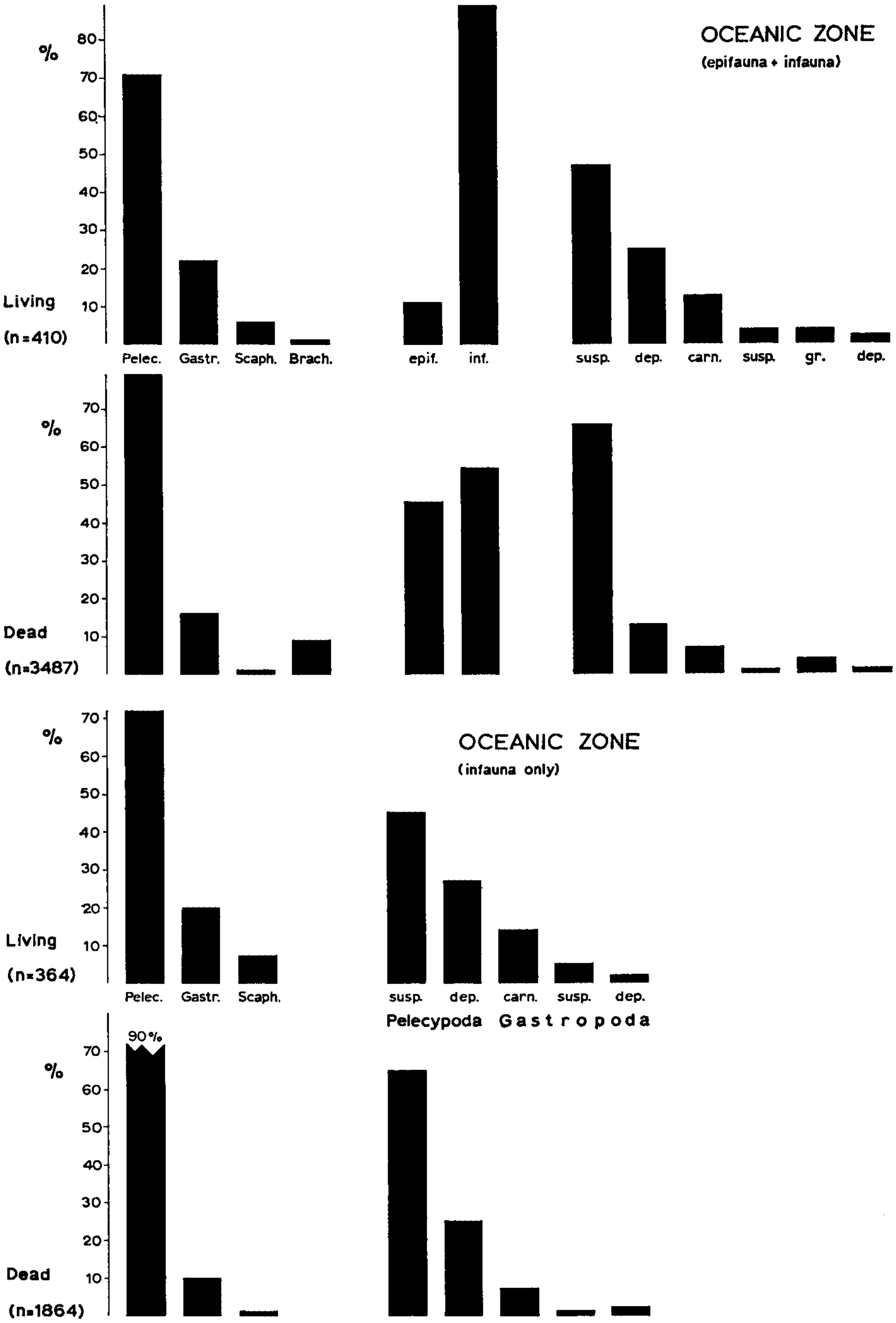


Fig. 41. Histograms showing the composition of the mollusc fauna in biocoenosis and thanatocoenosis.

The salinity range (near the bottom) is from approximately 34.9 to 36.0‰. The temperature range is from approximately 10 to 16° C. This means that the water of this zone is somewhat colder and has a slightly higher salinity than in the central bay zone. Oxygen saturation near the bottom is in general higher than in the central bay (80% against 60-70%).

Samples from this zone were taken at depths ranging from 40 to 85 m. Whether these depths (40 and 85 m) also indicate the boundaries of this zone is not exactly known. Samples from deeper water were not taken. The few samples which are present from shallow water outside the ria indicate a boundary between 30 and 40 m.

The oceanic fauna.

In fig. 41 some general characteristics are given of the shell-bearing fauna of the oceanic zone (brachiopods and molluscs). Pelecypods form a high percentage (70%) of the living fauna, a similar high percentage of pelecypods is found in the ria only in the estuarine zone of the Ulla. Infauna elements comprise almost 90% of the living fauna. Suspension-feeders among the pelecypods are twice as numerous as deposit-feeders. Among the gastropods the carnivores are most frequent. Comparing the quantitative composition of the biocoenosis with that of the thanatocoenosis, some important differences become evident. Epifaunal elements are far more frequent in the thanatocoenosis than in the biocoenosis; epifauna species which are not found alive in the oceanic zone apparently come from the rocky coast and from some rocky reefs. *Mytilus edulis*, which forms 10% of the thanatocoenosis, lives only in shallow water. These *Mytilus* shells may be sub-fossil, i.e. dating from a time with a lower sea level, but there are indications that they are recent and were transported from shallow water: (1) C_{14}-dating of *Mytilus* fragments from 60 m depth gave an age of 680 ±50 B.P. (analysis by dr. J. C. Vogel, Groningen, GrN. 4604); (2) two fragments of *Mytilus* were found at 60 m depth with the ligament (which rapidly decomposes) still present; (3) *Mytilus* fragments were most abundant in samples taken close to the coast; Boilot (1965: 365) found a similar belt of *Mytilus* shells, some 4 km wide, along the French Channel coast.

Brachiopods make up 8.6% of the thanatocoenosis, but less than 1% of the biocoenosis. They live on the rocky reefs which are found at 30 to 40 m depth outside the ria.

The post-mortem transport of epifauna species into this zone is important. The transport of infauna species is less important, therefore a comparison of only the infauna biocoenosis and thanatocoenosis (fig. 41) gives somewhat better results than a comparison of the total fauna, but some differences still remain (see further chapter VII).

In fossil faunae, which come from a high energy environment, the infauna species are probably of more help in paleoecologic interpretation than the epifauna species, because the latter are more liable to be transported. An epifaunal gastropod, e.g. living on algae, will certainly be transported after its death, an infaunal bivalve may remain in the sediment after death. Craig & Jones (1966) came to the same conclusion.

Important species (pls. 4, 5).

The following list enumerates the species present alive or as empty shell in 30% or more of the samples of the oceanic zone (O.C.). Fr. Gr. = Fretter & Graham, 1962; M.D. = marginal deep zone; O.B. = outer bay.

Gastropoda, Prosobranchia

Fissurellidae: Of *Emarginula reticulata* only empty shells were found. The species probably lives on the rocky reefs in this zone. It needs a hard substrate and feeds on sponges (Fr.Gr.: 488).

Patellidae: Of *Patella* species only empty shells were found; living specimens are not to be expected in this zone, because they occur intertidally. Therefore the dead shells must have been transported to the deeper water (compare also *Mytilus*). Of *Patina pellucida* only empty shells were found. This species was found alive below L.W. on *Himanthalia*. According to Fretter & Graham (1962: 502) this species feeds on the brown algae particularly on *Laminaria*, on which it is found, and on epiphytic diatoms. Only transport can explain the presence of the shells in deeper water.

Trochidae: Of *Calliostoma zizyphinum* and *Cantharidus exasperatus* only empty shells were found. They live in shallower water and their shells evidently have been transported to deeper water. *Gibbula tumida* and *Cantharidus montagui* which are grazers are found also alive in this zone. They were likewise found in the marginal deep zone.

Rissoidae: Of *Alvania cancellata* and *Rissoa parva* only empty shells were found. These rissoids are characteristic of the marginal zone of the ria. The shells obviously have been transported.

.Acmaeidae: Of *Patelloida virginea* only empty shells were found. This species lives in the marginal zone associated with calcareous algae on which it feeds. As calcareous algae are absent from the O.C. the shells probably have been transported to deeper water.

Solariidae: *Torinia sicula* was also found alive in the present zone. The biology of this species is unknown, therefore its presence in this zone cannot be discussed.

Turritellidae: Of *Turritella communis* only empty shells were found. This species lives in the central bay, but living specimens were also found on the shelf, e.g. off S. Portugal (Pérès, 1959) in muddy sediments. Therefore it is possible that this species lives in the oceanic zone and that we failed to collect it alive.

Cerithiidae: Of *Bittium reticulatum* only empty shells were found in the O.C. It is found in large quantities living among the finer algae in the marginal zone, from where the shells probably have been transported to deeper water. The same transport towards deeper water is found in the ria itself.

Capulidae: Of *Capulus ungaricus* only empty shells were found. It is possible that this species lives here, because most of its shells were found in this zone. All specimens are small, so they may be the neotenous dwarf-form described by Thorson (1965), which lives commensally on *Turritella communis*.

Aporrhaidae: Living specimens and empty shells of *Aporrhais pespelecani* were found in this zone. It is a deposit-feeder, which lives buried a little below the sediment surface (Yonge, 1937). Yonge also showed in experiments that *A. pespelecani* does not burrow in soft sediments. This may explain its almost complete absence from the central bay.

Naticidae: Of *Natica alderi* living specimens and empty shells were found. This infaunal, carnivorous gastropod was also found in the marginal zone and in the outer bay.

Cypraeidae: *Trivia monacha* was mostly represented by empty shells, but it was found alive once in a dredge sample from about 40 m. This species feeds on compound ascidians (Fr. Gr.: 26, 556). Living specimens were also found in the ria in small quantities in the marginal zone below L.W. Their distribution will be dependent on their food: compound ascidians (Fr. Gr.: 262, 556). These ascidians need a solid substrate (rock or shell). Therefore *Trivia monacha* may be restricted to the marginal and the oceanic zones.

Muricidae: Of *Nucella lapillus* and *Ocenebra erinacea* only empty shells were found. Both species occur in the tidal zone and below (*N. lapillus* to several meters, *O. erinacea* to 80 m; Fr. Gr.: 676). In the ria *O. erinacea* was found below L.W. (20 m depth). *Nucella lapillus* probably has been transported to this zone, *O. erinacea* may live here. Both species are carnivorous and feed largely on bivalves. The hole that they bore in bivalve shells is somewhat different from that made by *Natica* (Fr. Gr.: 243).

Nassariidae: Of *Nassarius reticulatus* and *N. incrassatus* living specimens and empty shells were found, of *N. semistriatus* only empty shells. According to Fretter & Graham (1962: 673, 674), *N. reticulatus* is found in British waters down to ca. 40 m, *N. incrassatus* down to 80 m. *N. semistriatus* is reported from muddy sediments of the shelf off southern Portugal (Pérès, 1958). These data explain the occurrence of all three species in the oceanic zone. *N. semistriatus* probably also lives on the shelf outside the ria, but we failed to collect this species. These nassariids are scavengers. They are infauna species which either plough through the sediment (Fr. Gr.: 552) or glide over the surface. The substrate will influence their distribution. Of the three species *N. incrassatus* prefers the coarsest and *N. semistriatus* the finest sediments.

Turridae: Of *Philbertia linearis* only empty shells were found, but as the largest numbers of this species were found in this zone, transport from elsewhere does not play an important role. *Philbertia* spp. are carnivorous gastropods, which live burrowing in the surface layers of the sediment. Although their exact food is unknown, it is presumed to consist of errant annelids (Fr. Gr.: 525-6). The type of substrate will be important for the burrowing life of *Philbertia,* therefore *P. linearis* may be restricted to sandy sediments as found in the O.C. zone. This species was also found in the M.D. and once alive there.

Opisthobranchia

These constitute an important part of the fauna of the silt-clay sediments of the central bay, but are unimportant in the O.C.

Scaphopoda

Dentaliidae: *Dentalium novemcostatum* and *D. vulgare* both occurred in about 40% of the O.C. samples. Both species were found alive but *D. vulgare* was the more frequent and is characteristic of this zone. *D. novemcostatum* occurs also in the central bay and seems to be restricted to those places in the O.C. where the highest silt-clay percentage is found. Sediment type was found to be of importance in the distribution of *Dentalium* spp. in the central bay (see p. 53).

Lamellibranchia

Nuculidae: Living specimens and empty shells of *Nucula hanleyi* were found in this zone. The presence of this species in the shelly gravel of the O.C. is in accordance with its occurrence in British waters (Tebble, 1966:27), see also under central bay fauna (p. 53).

Nuculanidae: *Nuculana fragilis* was only found as empty shells in the O.C. This species was found alive in the outer central bay. Pérès (1959) reported it from different depths of the shelf off southern Portugal down to 600 m. Therefore it is probable that this species also lives on the shelf off the Ria de Arosa, but we failed to collect it alive.

Glycymeridae: *Glycymeris glycymeris* occurred in 80% of the O.C. samples and some living specimens were found. It lives also in the M.D. zone, There it occurred in less than 30% of the samples. *Glycymeris* is a suspension-feeder; according to Tebble (1966: 33) it is common around the British Isles wherever a suitable bottom of muddy, sandy or shelly gravel is found into which it can burrow with its muscular foot. It was found during our investigations in the same type of bottom.

Arcidae: Of *Arca tetragona* only empty shells were found but it occurred in 80% of the samples. As there is no other zone in which this species is found in large numbers it must live here. *Arca tetragona* is an epifaunal suspension-feeder, which lives attached by a massive byssus on dead shells, among stones and in rock crevices, from the littoral zone down to 90 m in British waters (Tebble, 1966:31). This species presumably lives on the rocky reefs found in the O.C., but we failed to collect it there probably because of the difficulty of operating with dredges in these areas. *Arca lactea* was also found in this zone, and although less frequent (35% of the samples) than *A. tetragona,* this species was found alive in two samples, attached with its byssus to the inner-side of empty bivalve shells.

Anomiidae: Of *Monia squama* living specimens and empty shells were found, while of *Heteranomia squamula* only empty shells were found. The latter species lives from the littoral zone down to 50 m and perhaps also deeper. Therefore this species has not necessarily been transported from shallow water down to this depth, but may live here. The Anomiidae are epifaunal suspension-feeders, and thus their distribution will be restricted by the availability of suitable solid substrate to attach themselves to and by water turbulence sufficient to bring them food.

Mytilidae: Of *Mytilus edulis* only empty shells were found; these evidently have been transported from the littoral zone as pointed out on p. 66. *Modiolus phaseolinus* was present mostly as empty shells, but was once found alive in this zone. It is an epifaual suspension-feeder, which lives attached by its byssus to a hard substratum; in British waters it is found from the middle of the tidal zone down to ca. 170 m (Jeffreys, 1863: 119; Tebble, 1966:45). The nature of the substrate will be an important factor in the distribution of this species. *M. phaseolinus* can withstand a low oxygen concentration. In the Black Sea it is characteristic of the deepest zone of animal life (the *Phaseolina* muds 60-180 m, Caspers, 1957:848), but we did not find this species in the central bay of the ria.

Pteriidae: Living specimens of *Pteria hirundo* and empty shells were found in this zone, but the species is also found in small quantities dead and alive in the central channel of the central bay where the strongest currents in this zone are to be expected. *Pteria* is an epifaunal suspension-feeder which was found attached by its byssus to polychaete tubes and to a gorgonacean. Water movement and the presence or absence of a suitable substrate will influence its distribution.

Pectinidae: Of *Clamys opercularis* and *C. tigerina* living specimens and empty shells were found, of *C. distorta* only empty shells. *C. opercularis* has also a wide distribution in the ria, it lives attached only in the juvenile state, and the adults are able to swim. *C. tigerina* lives attached by its byssus also in the adult state. This species occurs in British waters from the littoral zone down to 80 m (Tebble, 1966: 62). The shallowest occurrence in the ria of living specimens is 35 m, in the English Channel it is restricted to deeper water, viz. of more than 65 m (Holme, 1966:445). It it a typical boreal species (Sorgenfrei, 1958:389). The summer temperature of the shallow water in and outside the ria may be too high for this species, therefore it will be restricted to the oceanic zone. In its adult life *C. distorta* lives attached by one valve to a solid substrate; in British waters it is found from the littoral zone down to 80 m. Therefore it is possible that this species lives in the present zone although we did not collect it alive. All Pectinidae are epifaunal suspension-feeders, they need sufficient turbulence of the water to bring them new food. Those species which live attached in adult life will be restricted in their distribution by the presence or absence of a suitable substrate. The free-swimming species *C. opercularis,* is less dependent on the substrate which may explain its wider distribution.

Astartidae: Of *Astarte triangularis* only empty shells were found. Living specimens were found in the marginal deep zone, in shelly gravel. This species, a small infaunal suspension-feeder, is found alive in British waters down to 90 m (Tebble, 1966:72), the empty shells found in the oceanic zone may have been transported to this zone from somewhat shallower water (25-30 m) outside the ria where we found this species in great abundance. Living specimens and empty shells of *Digitaria digitaria* were found in this zone and in the marginal deep zone. Like the foregoing species, it is an infaunal suspension-feeder and is confined to not too muddy sediments. This may be related to its feeding method.

Lucinidae: Of *Myrtea spinifera* and *Phacoides borealis* only empty shells were found. *Myrtea* was frequently found alive in the central bay. It may live also in muddy sediments on the shelf as found by Pérès (1959) off S. Portugal. *Phacoides borealis* was found alive in the marginal deep zone. In British waters this species occurs down to 100 m. It is therefore possible that both species live in the oceanic zone, but that we failed to collect them alive.

Montacutidae: Living specimens of *Mysella bidentata* and empty shells were found in this zone, but also in all other zones of the ria. It is not characteristic of one zone.

Cardiidae: Only empty shells of *Cardium tuberculatum,* were found but as the species occurred in larger numbers than in the other zones, this suggests that it may also live here. Of *Cardium scabrum* living specimens and empty shells were found not only in this zone, but also in the marginal zone. *Laevicardium crassum* is a very characteristic species of this zone, occurring in 96% of the samples. Living specimens occurred in this zone and in the outer bay, where they were far less frequent. Sediment type seems to be very important in the distribution of these infaunal suspension-feeders. Around the British Isles they are found in the same sediment types as in the oceanic zone of the ria: muddy sand, and shelly gravel (Tebble, 1966: 100, 103, 108).

Veneridae: *Dosinia lupinus, Gafrarium minimum, Venus casina, V. ovata, V. fasciata, V. striatula* were found alive, together with empty shells. Of *Venerupis rhomboides* only empty shells were found. The Veneridae are infaunal suspension-feeders and form an important part of the fauna of the oceanic zone. *Dosinia lupinus,* which is characteristic for the O.C. (only a very few living specimens occurred in the O.B.), here clearly replaces *D. exoleta* which lives in the marginal zone. *Gafrarium minimum* was also encountered in the marginal deep zone in shelly gravel, as well as *Venus fasciata. Venus ovata* is frequently cited as a species from mixed sediments (cf., Picard, 1965:49). It has a wide distribution in the ria where these sediments occur (M.D., O.B. and O.C.). *Venus casina* is cited as an indicator of relatively strong deep bottom currents (Picard, 1965:49). This seems in accordance with its presence in the O.C. and in the marginal deep zone outside the ria, where bottom currents are probably stronger than in the ria. *Venus striatula* and *Venerupis rhomboides* both have a wide distribution in the ria. Both species were found in a greater percentage of samples in zones other than the O.C.

Tellinacea: *Tellina donacina, Gari tellinella, Arcopagia crassa,* are three species which occurred here in a larger percentage of samples than in the other zones. They were also found (empty shells and alive) in the marginal deep zone. There they were never abundant nor did they attain such a great age or large size as in the O.C. This means that spat settles in both environments but that they can not maintain themselves in the M.D. zone, whereas some may reach the normal age of the species in the O.C. Of *Gari fervensis* only empty shells were found, but the species occurred in greatest numbers in this zone. The sediment type in this zone is the same as that which it prefers in British waters: coarse sand and (shelly) gravel (Tebble, 1966: 157). This suggests that it may live here. Of *Abra alba* living specimens and empty shells were found. This species was encountered everywhere in the ria where the sediment contained a smaller or larger fraction of mud. The same was stated by Picard (1965: 50) for the Mediterranean Sea off Marseilles. The Tellinacea are deposit-feeders (Yonge, 1949). Different species inhabit all those types of sediment that contain some organic debris. The species found in the O.C. are adapted to coarse sand and gravel with some mud, *Abra alba* may live also in finer sediments. The sediment type is an important factor in their distribution. In British and Mediterranean waters the above mentioned species are found in the same type of sediment (Yonge, 1949; Tebble, 1966; Picard, 1965).

Mactridae: *Spisula* sp. 1) is an important member of the living and dead fauna of the O.C. *Spisula* is a suspension-feeder. The different species of *Spisula* in British waters have a different depth distribution. *Spisula subtruncata* lives down to 36 m, *S. elliptica* is found down to 90 m. *S. solida* is a shallow-water species. *Spisula solida* does not enter the ria but seems to live below L.W. in sandy sediments off the ocean beaches, as indicated by the empty shells on these beaches. *S. subtruncata* enters the ria and is found in sandy sediments with some mud in the marginal zone. *Spisula* sp. was found in the shelly gravel of the O.C., living specimens down to about 60 m, i.e. in places where in British waters *S. elliptica* occurs.

Corbulidae: Of *Corbula gibba* living specimens and empty shells were found in this zone. The greatest numbers of this species were found in the central bay, but this species also had a wide distribution in other zones. It is a suspension-feeder adapted to live in muddy sediments (Yonge, 1946); however, it can thrive as well in sediments with high and with low mud contents.

Hiatellidae: *Hiatella arctica* s.l. is an important member of the fauna of the marginal zone but it was also found dead and alive in the O.C. zone. Some specimens may have been transported from the shallow water.

Other skeletal remains.

In the coarse fraction (>2 mm) of the samples from the O.C. skeletal

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1) Material of this species was submitted to Mr. R. van Urk, Leiden, who, however, could not assign it with certainty to one of the known species.

remains of brachiopods, bryozoans, solitary corals and barnacles form a minor constituent, only brachiopods may be relatively important.

Brachiopoda

Inarticulata: *Crania anomala* (O. F. Müller) (only as upper valves) was present in 42% of the samples of the O.C. Neither living specimens nor the lower cemented valve were collected. One living specimen was collected in 1849 at a depth of 50 m near the entrance of the Ria de Vigo (MacAndrew, 1850: 265). In the waters of northwestern Europe the species lives in depths from 30-180 m (Jeffreys, 1863:25) on rocky current-swept bottoms, attached to boulders or to the concave side of scallop valves (Rowell, 1960). It is a suspension-feeder (Atkins, 1962) which needs rather strong currents and a solid substrate. It was found in the ria in one locality only: Los Mezos, a rocky reef in the outer part of the ria, where presumably the currents are strong enough.

Articulata: *Macandrevia cranium* (O. F. Müller) was present in 50% of the O.C. samples but was only found alive here once (two specimens attached with their pedicle to an empty shell). In British waters this species occurs from 80 to 180 m deep on rocky and stony sediments (Jeffreys, 1863:12). We found living specimens in shallow water in a dredge sample 60 to 35 m deep in the O.C. and on the rocky reef Los Mezos in the ria at 23 m depth. They are suspension-feeders which seem to need rather strong currents. Other species were: *Terebratulina retusa* (L.) present in 23% of the O.C. samples, *Muehlfeldtia truncata* (L.) in 23% of the O.C. samples and once alive, *Megathyris detruncata* (Gmelin) present in 8% of the O.C. samples. The last three species are not found in the ria. The presence of brachiopods in samples is largely restricted to the O.C. where currents are strong enough and a suitable substrate is present at a depth of 20 to 40 m consisting of rocks without algae and large shells. The fauna of the rocky reefs, where the brachiopods presumably live, can be compared with the *Crania* epibiosis of Gislén (1930), which he found at a depth of some 30 m in the entrance area of the Gullmarfjord (southern Sweden).

Bryozoa

Bryozoan fragments found in the coarse fraction belonged to strongly calcified arborescent Cheilostomata: *Porella compressa* (Sow.), *Sertella beaniana* (King), *Palmicellaria skenei* (Ellis & Solander), *Hippodiplosia foliacea* (Ellis & Solander). Living specimens were sometimes found in dredge samples from the rocky reef outside the ria. This suggests that this is the source of the fragments in the sediments. This epifauna of strong eschariform and reteporiform Bryozoa is particulary adapted to a high energy environment (Stach, 1936). According to Pérès (1961:500, 501) this epifauna is characteristic of rocks in the "étage circalittoral" (below 15 to 20 m) of the northwestern Atlantic.

Transport.

The thanatocoenosis of the oceanic zone appears to be composed of the biocoenosis which lives there in shelly gravel and of elements of the biocoenosis of the rocky reefs in about the same depth (brachiopods, Bryozoa, and some molluscs like *Arca tetragona*) and of molluscs from shallow water and the intertidal zone (e.g. *Mytilus edulis*). Transport into this zone plays an important role. It results in an admixture of shells from other biocoenoses. This post-mortem transport affects epifauna species more than infauna species (cf. p. 66). This is once more illustrated by the fact that 18 of the 26 species which are present in more than 30% of the samples but which were not found alive, are epifauna species, all of which could be demonstrated to live in shallower water or presumably on the rocky reef. The others were infauna species, which live presumably in this environment but which we had failed to collect alive.

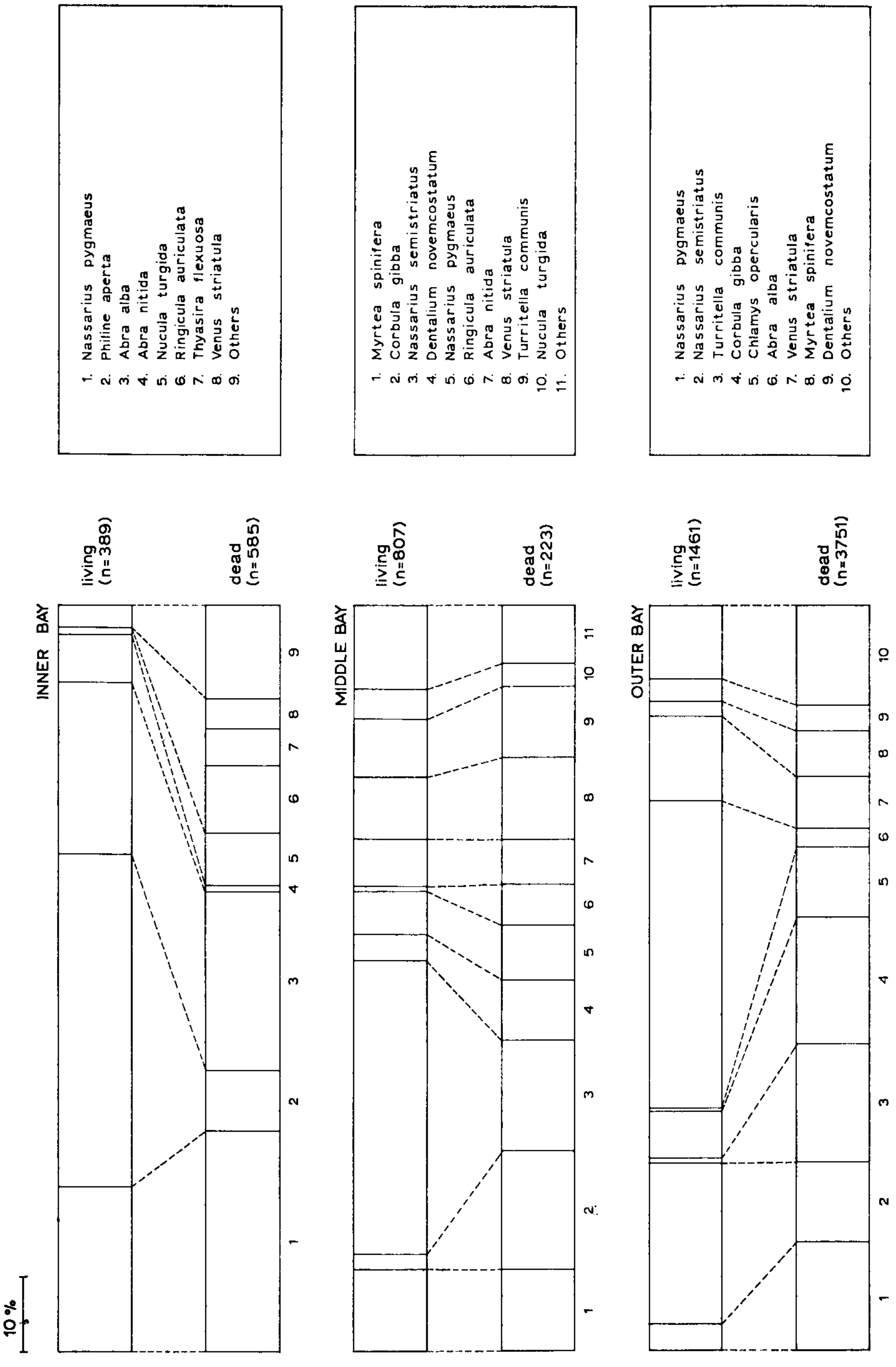
Comparison with other areas.

The fauna of the level bottom of the oceanic zone shows great similarities with the *Venus fasciata-Spisula elliptica-Branchiostoma* community (Thorson, 1957:509), first described by Ford (1923) from the Plymouth area of the English Channel as "the deep *Venus* community". *Venus fasciata* and *Branchiostoma* (lancelet) are found in both areas, *Spisula elliptica* can be compared with our *Spisula* sp. Other species which occur in both areas are: *Echinocyamus pusillus* (O. F. Müller) (a small sea-urchin) and the molluscs: *Abra prismatica, Dosinia lincta, Arcopagia crassa, Solecurtus scopula.*

The fauna of the oceanic zone also shows similarities with the "biocoenose des fonds détritiques côtiers" of Pérès & Picard (1964), described from the Mediterranean off Marseilles by Picard (1965:32). Picard mentioned a number of species which we found in our samples.

VII. QUANTITATIVE COMPARISON OF MOLLUSCAN BIOCOENOSES AND THANATOCOENOSES IN THE RIA DE AROSA.

In fig. 42 a comparison is given of the quantitative composition of the living and dead molluscan fauna (larger than 2 mm) of five zones in the ria. Species found in the biocoenosis occur also in the thanatocoenosis, but they


10 %
INNER BAY
living (n=389)
dead (n=585)
1 2 3 4 5 6 7 8 9
1. Nassarius pygmaeus
2. Philine aperta
3. Abra alba
4. Abra nitida
5. Nucula turgida
6. Ringicula auriculata
7. Thyasira flexuosa
8. Venus striatula
9. Others
MIDDLE BAY
living (n=807)
dead (n=223)
1 2 3 4 5 6 7 8 9 10 11
1. Myrtea spinifera
2. Corbula gibba
3. Nassarius semistriatus
4. Dentalium novemcostatum
5. Nassarius pygmaeus
6. Ringicula auriculata
7. Abra nitida
8. Venus striatula
9. Turritella communis
10. Nucula turgida
11. Others
OUTER BAY
living (n=1461)
dead (n=3751)
1 2 3 4 5 6 7 8 9 10
1. Nassarius pygmaeus
2. Nassarius semistriatus
3. Turritella communis
4. Corbula gibba
5. Chlamys opercularis
6. Abra alba
7. Venus striatula
8. Myrtea spinifera
9. Dentalium novemcostatum
10. Others

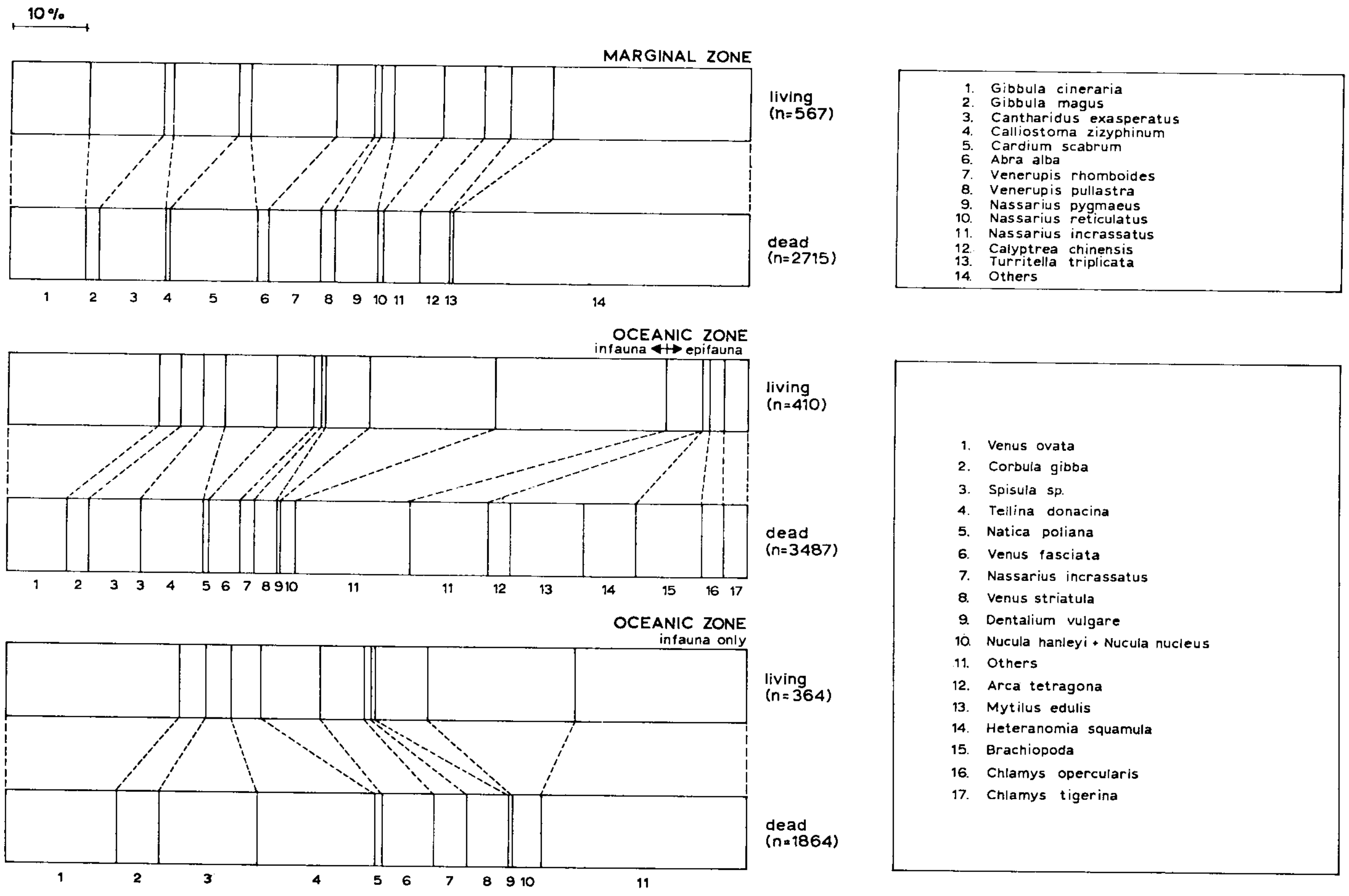


Fig. 42. Quantitative comparison of the species composition of biocoenosis and thanatocoenosis in 5 zones.

are not found in the same relative numbers. The differences found may be due to sampling errors, but we suppose them to be real: the thanatocoenosis data are likely to be reliable, the differences in the composition of samples taken in the same general locality throughout the period of investigation are small.

The biocoenosis data, however, can show large differences in two samples taken close together. Moreover, the composition of the biocoenosis was not the same in the three summers. In the central bay e.g. *Abra nitida* was not found alive in the first year (1962); we collected the first living specimen of *Ringicula auriculata* in 1963. In 1964 this species was found in somewhat greater numbers but these were not great enough to account for the 5% found in the thanatocoenosis of the inner and middle bay. In the former we found no living specimens, it seems reasonable therefore to suggest that in some years this species may live here in relatively large numbers.

Data in the literature show that the composition of the bottom fauna may show seasonal, annual and long term fluctuations. Examples are given in Pérès (1961: 382-389) and Johnson (1964: 124-128). Fluctuations seem to be the largest in shallow water. Zenkevitch (1963: 384-401) gave some data from the Sea of Azov: there the dominant species in spring was *Mytilaster lineatus*, in the autumn it was replaced by *Cardium edule*. Annual fluctuations were studied e.g. in the Limfjord, Denmark (1909-1950) by Boysen-Jensen (1919), and Blegvad (1928, 1951). Large fluctuations were found in the first period (1909-1927), they were smaller in the second (1927-1950). Thorson (1946) showed that these fluctuations were larger in species with a long pelagic larval life. Recruitment may vary considerably from year to year in such species, whereas fluctuations in species without pelagic larvae are much smaller. Long term fluctuations were studied by Ziegelmeier (1953, 1961, 1963, 1964) in the Heligoland Bight. He found an important decrease in southern species after two severe winters (1946/47 and 1962/63), after the first these species had recovered in 1950/51. Zenkevitch (1963) noted a replacement of a *Mytilaster* community by a *Cardium* community in ten years (1937-1947) in the Sea of Azov, due to the increased area of soft muds as a consequence of floodwaters of the Don in 1937-39. Pérès (1961: 386) mentioned some long term fluctuations which are not due to physical alterations in the environment, but which are thought to be due to biological factors, competition and predation.

Distribution of organisms in a biotope may be even (uniform, homogeneous), random or aggregated (clumped, patchy) (Odum, 1959:213). An even distribution has not yet been reported from the seabottom, more animals are found to have a random distribution than a patchy distribution.

However, of the level sea bottom few data are available: Jones, 1961, found that 15 species had a random distribution, and 4 a patchy distribution; Angel (1967) found that 3 out of 8 species had a random distribution. To eliminate the influence of fluctuations in the benthos in quantitative work, we have to collect data in different seasons and different years. To eliminate as far as possible the influence of the patchy distribution of some of the species, we have to take a large set of samples from one homogeneous biotope. Only then the quantitative data of the biocoenosis can be compared with the quantitative data of the thanatocoenosis. A comparison of the living and the dead fauna from one and the same sample will give in general no correlation, because a comparison is being made of a thanatocoenosis accumulated in several years with the biocoenosis of one moment, the latter will not be exactly the same as that which lived there several years, one year or even one month ago. Valentine (1961:324) and Johnson (1965) compared living and dead shells in one and the same sample. Valentine found that 14 to 19% of the dead shells were also represented by living specimens (St. Monica shelf, California). Johnson found in Tomales Bay (California) some 50% of the species not represented alive. In both cases correlation is poor as would be expected. Forbes in the Aegean sea, and Andrews & Barret in Norway (quoted in Woodward, 1910: 144-150) also found more species dead than alive in their dredge samples. Antevs (1928) compared living and dead shells in dredge samples from the Gullmarfjord to estimate the importance of transport of shells from shallow water. He found the admixture of shells to be small in deeper water at some distance from the shore. Caspers (1938) assumed the difference that he found between living and dead shells in his samples from the Heligoland deep to be due to recent changes in the fauna. Although there are objections against comparing the living and the dead fauna of a sample, this method has been used by others, and they have based their conclusions on these comparisons.

As to other groups, Shiflett (1961) and Murray (1965b) found little quantitative correlation between living and dead Foraminifera in their samples. Kornicker (1964) found a rather good correlation in an ostracod biocoenosis and thanatocoenosis.

The molluscs from the Ria de Arosa were collected at the same season in three successive years. All quantitative samples from one biotope have been put together. Fluctuation and patchy distribution will therefore influence our data only slightly. The biocoenosis data can be regarded as reliable. Moreover Picard (1965) found in similar biotopes in the Mediterranean only very small seasonal fluctuations. The quantitative biocoenosis data were obtained from samples taken with Van Veen grabs, and with a dredge, which in the soft central bay sediments worked like the anchor dredge used by other workers. Animals, e.g. *Lutraria* spp., which live too deep to be collected with this gear, were presumably few in the ria, they occurred in small quantities in the thanatocoenosis. Our collecting gear, however, almost failed to collect the free swimming *Chlamys opercularis,* which occurs in 10% of the outer bay thanatocoenosis. In this case our quantitative biocoenosis data were not reliable.

Reviewing once more the data (fig. 42), we see that there is a rather good correlation between the thanatocoenosis and the biocoenosis of the inner bay. The percentages are based, however, on only a few hundred specimens. The percentage of *Philine aperta* in the thanatocoenosis is lower than in the biocoenosis. *Thyasira flexuosa* and *Ringicula* were not found alive, as however, this species was found alive in 1964 in the middle bay, it can be supposed that in some years they live also in the inner bay.

The middle-bay data show a good correlation, all important species of the thanatocoenosis being also found alive. *Nassarius semistriatus* and *Corbula gibba* show significant differences in percentages in the thanatocoenosis and the biocoenosis.

In the outer bay data, based on a larger number of shells than the foregoing zones, all the important species of the thanatocoenosis are represented in the biocoenosis. However, there is a very marked difference in the percentages of *Abra alba* in the thanatocoenosis and the biocoenosis and also a somewhat less marked difference in those of *Turritella communis.*

The marginal bay data give the same picture: the same species are found dead and alive, *Abra alba* being under-represented in the thanatocoenosis, other species showing the reverse. The oceanic zone gives marked differences in *Nucula* spp., *Tellina donacina, Natica alderi* and *Spisula* spp. but all important infauna species were found dead and alive.

We can imagine that other factors affect the quantitative composition of the thanatocoenosis (of course it is impossible to explain each case individually). Such factors are: (1) transport, (2) mixing, (3) selective removal by predators, (4) differences in shell production, (5) differential mechanical destruction, (6) differential solubility.

(1) Transport. This is shown to be quantitatively of minor importance in the ria; in the oceanic zone it was largely confined to epifauna species, in that case therefore only infauna species were compared. It will be shown in chapter IX that small shells of *Tellina donacina* can be transported. In other species this transport played no role.

(2) Mixing of the present population (without transport) with shells which lived there some time ago or with fossil shells. This will be found if

there is no sedimentation, with or without submarine erosion. In the ria this will not play a role but may well do so on the shelf outside the ria. Here there are some indications (rounded quartz grains and sometimes beach pebbles, the latter with recent epifauna) that sediments, dating from a time when the sea level was lower, are still exposed. It seems impossible to indicate whether part of the shells also date from this time, as no species were found which are not found alive or could not live there. The shallow-water zone is so near that all shallow-water shells could be derived therefrom. A rather important fraction of unidentifiable shell fragments in the shelf samples may be old, but these will not affect our quantitative thanatocoenosis data, which are based on the identifiable fraction. Caspers (1938) supposed mixing with an older fauna to explain the difference that he found between the thanatocoenosis and the biocoenosis.

(3) Selective removal by predators. This factor has never been considered as being very important, but in my opinion it may explain in some cases the fact that fewer empty shells are found then would be expected from the biocoenosis. Only those predators which crush the shells of their prey to small partly unidentifiable fragments are important. These are found among the fish which feed on molluscs. The plaice (*Pleuronectes platessa*) is a well known example: Blegvad (1925), Ford (1925:532) and Ziegelmeier (1963) reported that this fish feeds on not too large, thin shelled bivalves, e.g. *Abra alba* and *Tellina fabula*. In fact the largest differences between the biocoenosis and thanatocoenosis observed in the ria are found in *Abra alba*. Therefore it seems reasonable to suggest that fish may play a role in the observed differences between living and dead molluscan fauna. The plaice prefers some species above others. Shell remains left behind are partly unidentifiable and too small to be represented in the coarse fraction studied.

(4) Differences in rate of shell production. A short-living species will contribute per unit of time more shells to the sediment than an equally abundant but long-living species. This factor is difficult to evaluate, but may perhaps account for the difference found in *Nucula* spp. in the oceanic zone. *Nucula* spp. are long-living. Allen (1954:466) supposed a maximum age of 13 years for *N. nucleus* and 14 years for *N. hanleyi*. They are found in greater number in the biocoenosis than in the thanatocoenosis. Other factors may, however, be at work.

(5) Differential mechanical destruction of shells. In high-energy environments destruction will eliminate the fragile shells in the thanatocoenosis first. In this case the thanatocoenosis in which only the strongest shells are represented may give a wrong idea of the quantitative composition of the

biocoenosis (Schäfer, 1962:184). In the ria this factor probably is unimportant.

(6) Differential solubility of shells. Skeletal carbonate composition differs from species to species. Chave et al. (1962) found a correlation between solubility in sea water of the shells and their chemical composition. If therefore dissolving of shells on the sea bottom takes place, differential solubility may cause differences in the biocoenosis and the thanatocoenosis. Lutze (1965:134) gave an example from the Arkona and Gotland deeps of the Baltic, where all calcareous foraminiferids are dissolved but the arenaceous foraminiferids are only partly affected. Chave (1964: 384) gave an example of differential solution by ground water in an Upper Cretaceous outcrop. In the ria we found only very slight dissolving phenomena (etching of shells) in the central bay. It is therefore not very probable that solubility will play a role here in the differences found between living and dead fauna.

In conclusion we may state that in general the quantitative correlation between a molluscan biocoenosis and thanatocoenosis will be poor. The most important species of the biocoenosis may be scantily represented in the thanatocoenosis.

The species compositions of the molluscan biocoenoses and thanatocoenoses were about the same in the Ria de Arosa. However, in other cases these too may differ. Not all species from the biocoenosis may be represented in the thanatocoenosis. Moreover mixing with shells from other biocoenoses or with fossil shells may give thanatocoenoses which when fossilized will be very difficult to interpret for a paleoecologist (see also chapter IX).

VIII. PRESERVATION OF SHELLS

A relatively large part of the coarse fraction (larger than 2 mm) of all the samples consists of fragmented shells, also in central-bay samples (see pl. 6). The central bay has to be seen as a low-energy environment, where transport plays a minor role. This indicates that still other factor(s) cause the fragmentation of shells in the sediment. A review of the literature on shell destruction can be found in Revelle & Fairbridge (1957: 278-282), Schäfer (1962: 176, 182-184, 459-462), Chave (1964) and Swinchatt (1965: 80-83).

The destruction of shells may be (1) mechanical, (2) chemical and (3) biological.

(1) Mechanical destruction was studied experimentally by Klähn (1932), Chave (1960, 1964) and Berthois (1965). They found that under marine conditions this destruction takes place by shifting sands in shallow water

and in the surf-zone. The resistance against mechanical breakdown differs strongly from species to species and is largely dependent on the microstructure of the shell. Schäfer (1962) gave some illustrations of recent shells collected on the beach which showed signs of mechanical destruction. The experiments mentioned indicate that mechanical destruction may lead to a selective removal of the fragile shells and finally also to a total disappearance of all shells.

(2) Chemical destruction was studied experimentally by Klähn (1932), Hecht (1933) and Chave et al. (1962). Solubility of the shells depends on the mineral composition of the shell and the chemistry of the water which surrounds it. Aragonite and calcite with more than 4% $MgCO_3$, which frequently occur in mollusc shells, are more easily dissolved in seawater than low Mg-calcite. Dissolving of shells in nature occurs particularly in the deeper parts of the oceans (below some 4700 m) and in the intertidal zone, where shells buried in muds with a high organic content may disappear (Revelle & Fairbridge, 1957: 244, 278-281). Chave et al. (1962) state that: "The chemical problem of the solubility of skeletal carbonates is not solved".

(3) Biological destruction of shells may be (a) praemortal, and/or (b) postmortal and/or (c) perimortal.

(a) Examples of praemortal destruction of the shell are found particularly in epifauna species. Destruction is brought about by the boring activity of organisms which use the shell as a habitat. A wide variety of boring organisms is found in shells. Quantitatively the most important are algae, the polychaete *Polydora* and the sponge *Cliona.* Boring algae are reported from the shells of living *Monodonta lineata* (cf. Jeffreys, 1863: 319), *Littorina littorea* (cf. Kessel, 1937), *Ostrea edulis* (cf. Korringa, 1951), *Trichotropis cancellata* (cf. Yonge, 1962), etc. *Polydora* spp. are reported from living *Crassostrea virginea* (cf. Owen, 1957), *Ostrea edulis* (cf. Korringa, 1951), *Littorina littorea, Gibbula cineraria, Crepidula fornicata, Patella vulgata* (cf. Schäfer, 1962: 175). *Cliona* spp. are known from living *Trichotropis cancellata* (cf. Yonge, 1962), *Ostrea edulis* (cf. Korringa, 1951). Pl. 5 fig. 6 shows a good example of a very damaged shell of *Charonia gyrinoides* collected alive in the Ria de Arosa. The damage was largely due to boring activity by *Cliona.* Yonge found similar heavy destruction of the shell during life in *Trichotropis cancellata.* He stated (Yonge, 1962: 162) "It seems doubtful whether the shell could provide adequate shelter for the animal for longer than the two years which for other reasons are postulated as the life span in this species". All the above-mentioned molluscs belong to the epifauna. Infauna species in general live in a position which makes them less attractive from the point of view of a boring-organism.

which has to remain in contact with the overlying water for food or light. If some part of the shell of an infauna species remains uncovered then this may also be attacked by boring-organisms. The posterior part of *Dentalium* is attacked by boring algae (G. J. Boekschoten, 1966: 334 and our own observations in the ria material). *Polydora* sp. was found in *Turritella communis* (cf. Schäfer, 1962: 175) and *Cliona* sp. was found in the posterior part of *Astarte sulcata* from the Trondheimfjord (own observation).

(b) Postmortal biological destruction of shells is accomplished by the same boring-organisms as mentioned above. In this event epifauna and infauna shells may be equally attacked, if they are exposed to the overlying water. Postmortal boring activity also differs from praemortal boring activity in that it affects both the inside and outside of the shell. In praemortal boring-activity only the outer side of the shell is attacked and frequently extra deposits of calcareous material are found on the inside of the shell opposite the boring sites. Very good pictures of the activity of boring algae in shell-fragments were given by Swinschatt (1965). They are very similar to the attacked fragments which I found frequently in the ria samples.

(c) Perimortal biological destruction of shells: this term is introduced to indicate the destruction of molluscan shells by predators. Important predators on molluscs which crush the shell are found among demersal fish, large crustaceans, gastropods and, in shallow water, birds. Schäfer (1962:182) mentioned ten species of fish from the North Sea which regularly feed on molluscs, the best known of which is the plaice (*Pleuronectes platessa*). They contribute only small fragments of the shell to the sediment: they crush the shells in their mouth or stomach. Large crustaceans which feed on molluscs crush the shell with their claws (chelae). They contribute large fragments to the sediment, the shells are crushed before being consumed, and the shell fragments do not enter the alimentary tract. Gastropods are opened by "Bandschnitte" (Schäfer, 1962: 459-462): the claws are used as a pair of scissors, they crush the mouth-edge of the shell and follow their way along the spiral towards the animal (see also fig. 43 which shows *Turritella* and *Nassarius* specimens opened by crustaceans). Fig. 43 also shows pelecypod shells presumably opened by crustaceans. Living gastropods sometimes escape total destruction of the shell as shown by subsequent repair of the shell (fig. 43 — 23, 24). Schäfer (1962:462) figured some gastropods shells broken by surf-action, which look very similar to those with "Bandschnitte" of crustaceans. All shells of fig. 43 were found in water deeper than 20 to 25 m, in silt-clay sediments where mechanical destruction does not occur. Besides this, some gastropods show repair of the shell and *Venus* shells are found sometimes with one valve broken but with

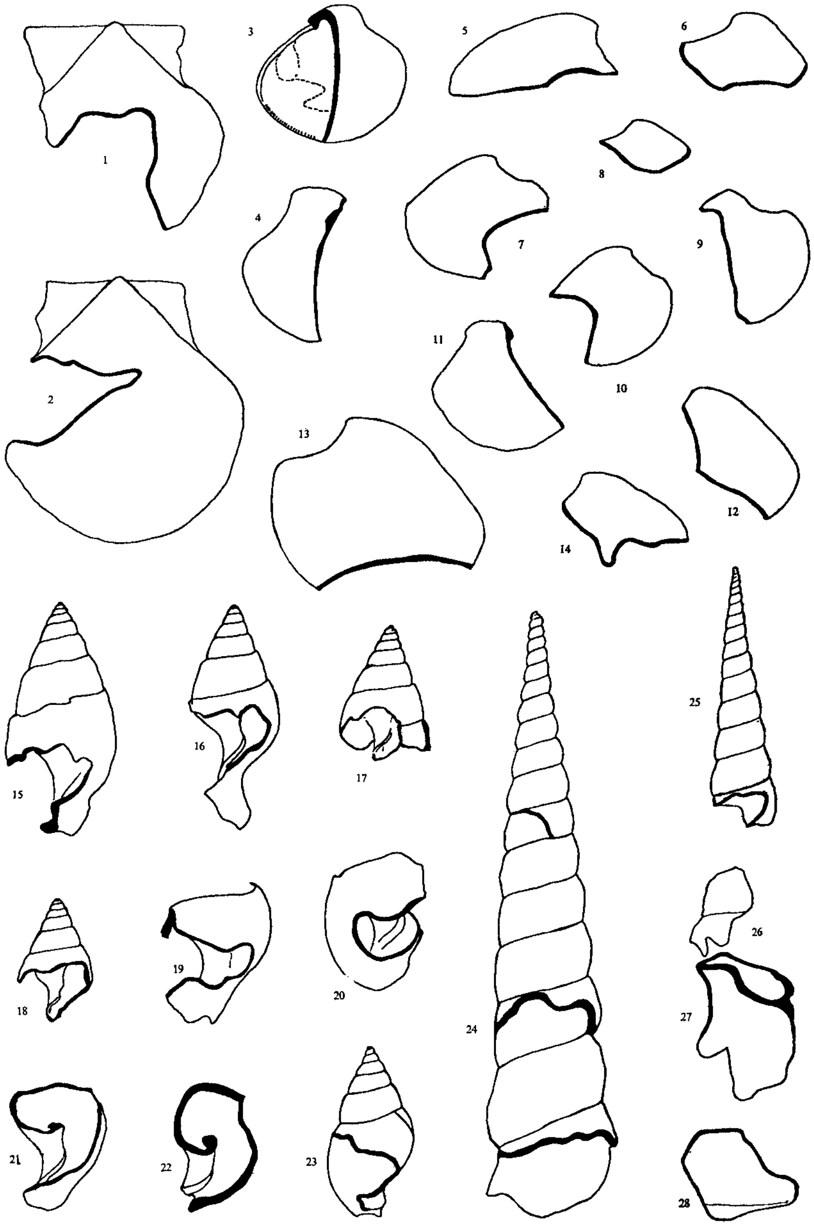


Fig. 43. Shell fracturing presumably due to Crustacea. The shells are from dredge samples from the middle central bay (bottom clay, depth about 25 m). 1, 2, *Chlamys opercularis* (L.); 3-14. *Venus striatula* (da C.); 15-23, *Nassarius semistriatus* (Brocchi); 24-28, *Turritella communis* Risso. 3, one valve crushed, the other still attached to it by the ligament; 23, shell repaired after fracturing as in 15 and 16; 24, shell three times repaired, fourth time succesfully broken and consumed by predator.

the ligament still present. All these things indicate that fragmentation is not due to mechanical factors but to predators, presumably crustaceans. Crab chelae found in the same samples belong to *Macropipus* sp., the most abundant *Macropipus* in the ria being *M. puber* (L.) (identifications by dr. L. B. Holthuis). *Macropipus puber* may be one of the crustaceans that have crushed large quantities of shells in the ria.

Gastropods feeding on molluscs crush the shell in their gizzard or bore a hole in the shell. Examples of the first group in the ria are *Philine aperta* and *Scaphander lignarius,* both tectibranchs provided with calcareous plates in their gizzard. The former feeds only on small molluscs (besides polychaetes and foraminiferans), the latter feeds also on larger bivalves of somewhat more than 1 cm length (Hurst, 1965; Massé, 1963). *Philine aperta* is an important member of the fauna of the inner part of the ria and probably crushes small molluscs and foraminiferans there. *Scaphander lignarius* is found rarely in the outer bay, consequently only a small part of the fragmentation will be due to this predator. Boring gastropods also occur in the ria. Fischer (1966:67) listed some 25 boring genera largely belonging to the Naticidae, Muricidae and Buccinidae. They make only one hole in the shell of their prey, which does not result in fragmentation of the shell, although it will diminish the strength against mechanical breakdown. Birds may be important predators on molluscs in shallow water and the intertidal zone (Schäfer, 1962: 465-466; Van der Baan et al., 1958). In the Ria de Arosa, however, birds play an unimportant part in shell fragmentation as they are not abundant. The Asteroidea, an important group of predators on molluscs leave the shell of the molluscs on which they feed intact, the valves of bivalves are frequently still held together by the ligament after consumption by starfish. Therefore we have to hold in mind that only part of the shells of molluscs which are consumed by predators are crushed.

An analysis of the coarse fraction of the Ria de Arosa samples arranged according to the zones which could be distinguished by their molluscan composition gives the results shown in table 2.

Table 2. The preservation of shells in the different zones

zone	fragmentation	boring organisms	epifauna on shells	abrasion	dissolving (etching)
Marginal shallow	+++	++	+	+	—
Marginal deep	+++	+++	++	—	—
Inner bay	+	—	—	—	+
Middle bay	++	+	—	—	—
Outer bay	++	++	+	—	—
Oceanic zone	+++	+++	+	+	—

(— absent, + present, ++ common, +++ abundant)

Dissolving was seen only in some shells from the inner bay. Boring activity (in particular by algae and *Cliona*) is high in all zones except in the inner bay. Here also epifauna on shells is absent. Both will be due to the unfavourable conditions in this zone, amongst which the high rate of sedimentation might play a major role.

Abrasion occurs in the shallow marginal zone, it becomes more frequent, resulting in more rounded shell fragments, nearer to the exposed ocean beaches. The rounded shell fragments, largely belonging to *Mytilus edulis,* found in the samples from the oceanic zone may have been transported from these beaches. They may also be remnants dating from the Pleistocene when due to the lowered sea level, these sampling localities were near the littoral zone (see also chapter 6).

Fragmentation is high in all zones, except in the inner bay, where predators are few because of unfavourable conditions. The higher fragmentation found in the oceanic zone (average 70% by weight) as compared with the outer bay (average 30%) is a result of the admixture of presumably subfossil fragments in the former. Comparing the fragmentation of the (recent) identifiable fraction of the samples of both zones, the outer bay gives somewhat higher figures than the oceanic zone (see table 3). Mechanical destruction does not take place in either zone, because the depth is too great (20-80 m). Fragmentation therefore is probably due entirely to predators.

Table 3. Percentage of fragments (hinge fragments in bivalves, top whorls in gastropods) in the total number of entire shells + fragments. This gives an indication of the fraction of shells destroyed by predators in this case.

Species	oceanic zone			outer bay		
	number of samples	total of shells and fragments	% fragments	number of samples	total of shells and fragments	% fragments
Spisula sp.	3	1053	28.9			
Venus ovata	4	883	24.5			
Venus fasciata	2	358	13.9			
Tellina donacina	4	1433	38.6			
Venus striatula	1	470	14.5	4	845	34.8
Chlamys opercularis				2	493	68.3
Myrtea spinifera				3	517	32.3
Nassarius pygmaeus				3	566	31.3
Nassarius semistriatus				3	526	46.4
Turritella communis				1	980	83.5

The data in table 3 show a difference from species to species in both zones which might be due to a difference in the percentage of consumed shells. Comparable shells in both zones, e.g. *Venus* spp., show a lower percentage of fragments in the oceanic zone.

Shells from the marginal zone transported to the central bay cannot be recognised as transported shells by their state of preservation. They do not show signs of transport, presumably because they are not transported along a sandy bottom, but by large algae. They may be recognised by a paleoecologist as transported shells only because they belong to a different assemblage.

In conclusion it can be stated that the preservation of the shells shows only slight differences from zone to zone (pl. 6). It is not possible to separate the mollusc samples from the ria in different groups on the state of preservation alone. Abrasion of shells indicates shallow water with shifting sands, but abraded fragments may be transported afterwards to environments where abrasion cannot take place. Epifauna on shells and boring-organisms in shells indicate an environment with a low rate of sedimentation. Fragmentation cannot be used as a measure of transport or of the energy of the environment: crushing of shells by predators may be important in low energy environments and may simulate the mechanical destruction of shells in a high-energy environment. Tauber (1942) distinguished "besiedelte Schalen" as indicators of quiet water, "ungeschliffene nicht besiedelte Schalen" as indicators of a rapid sedimentation and "geschliffene Schalen" as indicators of shifting sands in shallow water. This is in accordance with our findings, except for the fact that epifauna may occur also on shells in turbulent waters. Walther (1893: 890) had already indicated the important role played by predators in the formation of fragmented shells in the sediment, but this seems to have been overlooked by some geologists.

IX. SIZE-FREQUENCY DISTRIBUTION OF EMPTY SHELLS

Introduction.

The study of size-frequency distribution of fossils was introduced by Boucot (1953). An assemblage of fossils which has lived on the place of fossilisation (so-called life assemblage) would give a high number of small specimens and few large ones, because mortality is high in juveniles. An assemblage of transported fossils (death assemblage) would give a bell-shaped size-frequency distribution, the mean size being dependent on the transporting power of the medium. Boucot (1953:31), however, stated that a transported assemblage of largely juvenile shells may be very similar to the right-skewed size-frequency distribution of his life assemblage. Olson (1957) studied the problem from the theoretical point of view. Size-frequency distribution of the empty shells of a species (if transport plays no role) can be predicted if growth-rate and mortality-rate are known. She combined three types of growth-rates with four types of mortality-rates. For metazoan invertebrates her case 2c (slow growth and high early mortality) would be the most probable. This results in a size-frequency distribution as suggested by Boucot (1953) for a life assemblage. If growth and/or mortality deviate from this pattern, other size-frequency distributions may result, which may be bell-shaped or bimodal without any transport. She further compared the size-frequency distribution of 200 samples of extinct animals with her computed size-frequency distribution for each animal. Correlation between observed and computed curves was very poor. Her conclusion therefore sounds rather pessimistic (p. 330): "In short, the size-frequency distribution of the U.B. (the universe of the death assemblage) is not a factor of any importance in the determination of the form of the size-frequency distribution of the sample in the great majority of cases". Others have contributed to the problem of size-frequency in fossils and the paleoecological use of it (Boucot et al., 1958; Craig, 1953; Craig & Hallam, 1963; Fagerstrom, 1964; Hallam, 1962; Johnson, 1960, 1962; Kurtén 1954, 1964; Rigby, 1958; Rudwick, 1962, 1966). Fagerstrom (1964) stresses the importance of intermediate fossil assemblages. If part of the remains of organisms of a community is carried away, the remaining assemblage may be called a residual fossil assemblage. Further, in a fossil assemblage part of the fossils may have been imported to it from elsewhere, and have become mixed with remains of organisms which lived there, resulting in a mixed fossil assemblage.

In composing size-frequency curves for fossils, samples have to be very carefully collected. Normal collecting methods by hand picking are completely inadequate for this purpose, as beautifully illustrated by Sparks (in Ager, 1962:187). He compared two samples of the same Quaternary non-marine molluscs, one collected by hand and the other by bulk sampling and sieving. The difference in composition is enormous. In the hand-collected sample the species which are conspicuous by reason of size or colour are over-represented. This will result always in bell-shaped curves when using these samples for the construction of size-frequency curves. However, bulk sampling is often difficult for the paleontologist. In my opinion inadequate sampling is one of the reasons for the poor correlation that Olson (1957) found between the computed and observed size-frequency distribution in her samples. She stated (Olson, 1957:311) "The samples were of many sorts some collected carefully in the field to assure full representation, others taken casually from the surfaces of outcrops and many from museum collections, which, although the ways of collecting are unknown, undoubtedly represent a variety of techniques". Compare this for instance with the findings of Sparks (see above) and Kurtén (1964:91), who found museum collections of the cave bear (*Ursus spelaeus*) to consist for 90% of males. The males are larger than the females and as museums were only interested in the large specimens, the smaller were given to amateur collectors. This we hope is an exception.

Size-frequency distribution of empty shells in the ria samples.

Only part of the samples from the Ria de Arosa were large enough to contain a sufficient number of shells of different species to construct size-frequency curves. All these samples were collected by bulk sampling with subsequent sieving. Only the coarse fraction (larger than 2 mm) has been used. The samples are from the central bay and the oceanic zone. The central bay samples represent a regular accumulation of shells of species which live there, only a small percentage of the shells are imported from shallower water. Compared with the central bay the samples from the oceanic zone contain a larger part of imported shells. The size-frequency curves of some of the most abundant molluscs of the central bay samples will be discussed first (fig. 44). Only *Venus striatula* and *Myrtea spinifera* show the size-frequency curve which Boucot suggested for a non-transported assemblage. *Turritella communis* and *Nassarius semistriatus* show more or less a bimodal curve; *Chlamys opercularis* and *Nassarius pygmaeus* give different curves in different samples. How can we explain this if transport plays no role? A bimodal curve was calculated by Olson (1957) to occur in her case 2a (slow growth and low early mortality with high reproductive rate). Instead of predicting a size-frequency curve based on two variables: growth and mortality-rate as Olson did, a mortality curve can be constructed from the size-frequency distribution of the empty shells and the growth curve deduced from growth-markings on the shell (Kurtén, 1954, 1965; Craig & Hallam, 1963). We can compare in that case the mortality curve found with those known from studies on the population dynamics of recent species. If they differ we have to conclude that our mortality curve is not probable for a life assemblage and that some factor, e.g. transport, has affected the size-frequency distribution. The measurement of growth by means of growth rings is not always easy. A general treatment of growth in molluscs is given by Wilbur & Owen (1964). According to these authors (Willbur & Owen, 1964:223) rings on shells may be formed on three occasions: winter rings,

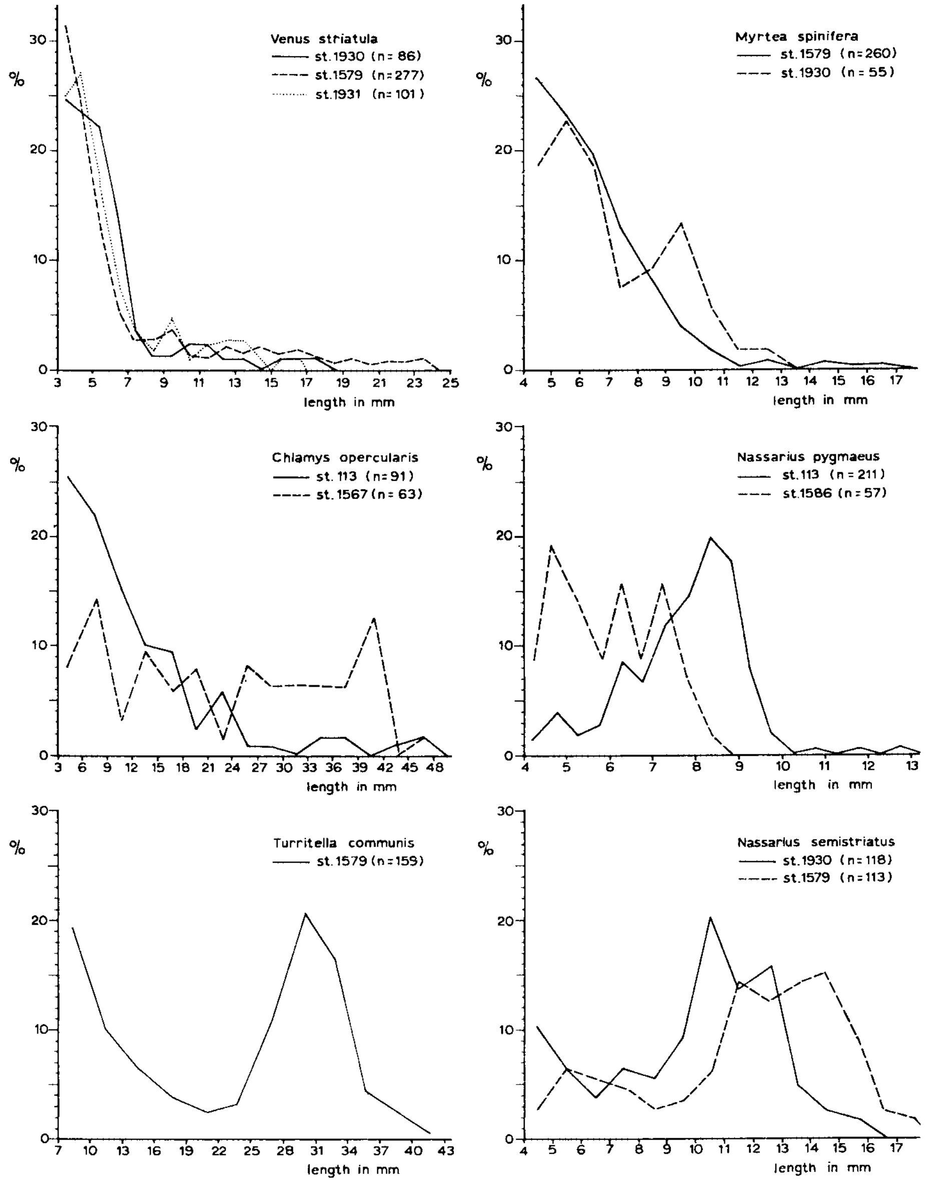


Fig. 44. Size-frequency distribution of empty shells in central bay samples (for location of samples see fig. 46).

formed during cessation of growth in winter, summer rings, formed if the temperature in summer becomes too high for growth (this seems to be rather rare) and disturbance rings, induced by (irregular) disturbances. In general winter rings are clearly visible on the shells from the ria. In some species disturbance rings are difficult to distinguish from winter rings, e.g. in *Spisula* sp. (as also reported by Ford, 1925). Our *Turritella communis* shells do not show winter rings. This might indicate that this species lives less than one year. Opinions in literature concerning the growth of this species are conflicting: Thorson (1957:510) thought the growth was slow, Sartenaer (1959) mentioned a rapid growth. Both authors gave no definite indication on the age attained by this species. In accordance with a faint indication of a bimodal size-frequency distribution in the living population in the ria I suppose that this species can become two years old.

The size-frequency data of the empty shells of a species in fact give the number of preserved deaths at each size. The construction of the mortality curve consists in altering a death/size curve in a death/age curve. Mortality curves in population dynamics most often are given as survivorship curves, in which the number of survivors is plotted on a logarithmic scale against relative age (see Odum, 1959). Fig. 45 illustrates how a survivorship curve can be constructed with the size-frequency data and the growth curve: suppose species A has the first winter ring at 5 mm length, the second at 7 mm, the third at 8 mm and the fourth and last at 9 mm. A growth curve can now be constructed if we suppose the first winter ring to be formed when the animal is half a year old. The shell-length is plotted on the y-axis right side, time on the x-axis. The samples used were sieved; this implies that the smallest shells are not present in the samples. The first fully represented size-class in the sample will depend on the type of sieve used and on the length-width ratio of the shell. Suppose the first complete represented size-class in species A is the 3-4 mm class. Suppose further that 35% of the shells fall within this class, 25% in the 4-5 mm class and 10% in the other classes. The size-class limits are now constructed on the time axis as indicated by arrows for the 6 mm line. If our population consisted at the start of 1000 specimens of 3 mm length, then 1000-35% = 650 have survived at the time the shells had attained a length of 4 mm. Following the same reasoning 650- (25% of 1000) = 400 survived at the time the shells had attained a length of 5 mm, there are 300 survivors of 6 mm, 200 of 7 mm, 100 of 8 mm and no specimen larger than 9 mm was found. These values, viz. 1000, 650, 400 etc. are plotted on the grid formed by the size-class boundaries constructed on the x-axis and the survivors on the y-axis. These constructed survivorship curves will be identical with the

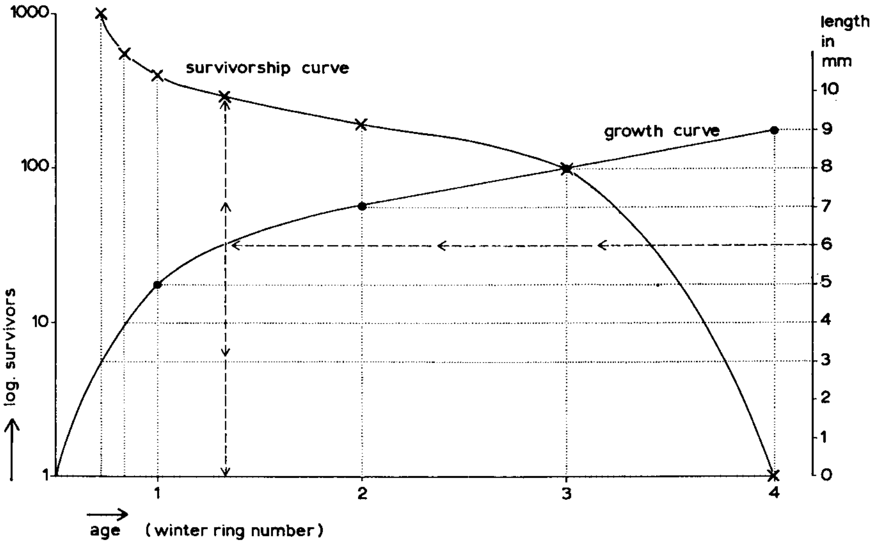


Fig. 45. The construction of a survivorship curve if size-frequency distribution of empty shells and growth-rate are known.

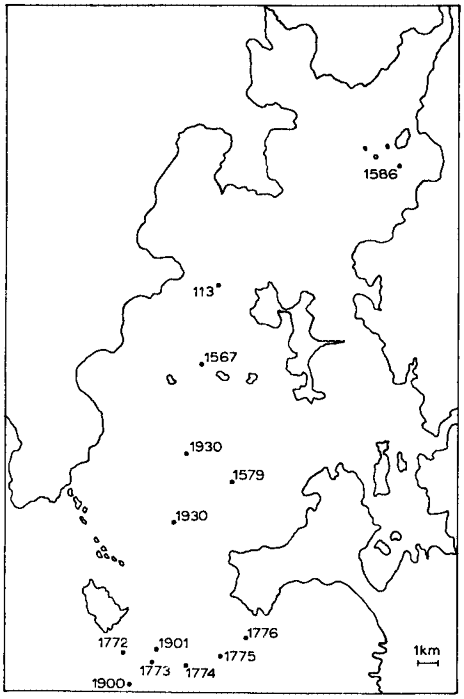


Fig. 46. Location of samples used for size-frequency data.

real survivorship curves (as found e.g. by following the mortality in one population throughout its life), if all empty shells remain entire and are not transported. In fact part of the molluscs die because of predation, which may result in the crushing of the shells. These shells are not represented in our size-frequency data. This will not affect the survivorship curves if equal percentages of all size-classes are crushed. This is rather unlikely; it is known, e.g., that fishes eat only small *Spisula* specimens (Ford, 1925: 532), and this will affect the size-frequency data, but fortunately less than if only large specimens were eaten. Fig. 47 gives the survivorship curves for the same species and based on the same data as fig. 44.

According to Kurtén (1954, 1964) a sigmoid survivorship curve will be the most probable for a life-assemblage: concave in early life, reflecting high but gradually diminishing juvenile mortality; approaching the straight diagonal in middle life; and convex when senescence sets in and mortality rates again increase.

The highly different size-frequency curves of *Venus striatula* and *Myrtea spinifera* compared with that of *Turritella communis* give very similar survivorship curves. This indicates that the differences were due to differences in growth.

Only one sample of *Nassarius pygmaeus* gives a probable survivorship curve, the same is found in *Chlamys opercularis.* Post-mortem transport does not occur in the central bay, therefore I would explain this as follows. The samples of *Nassarius pygmaeus* in which the juveniles are best represented comes from shallow water (4 m), the other sample is from 52 m depth. Now juvenile specimens were found alive in shallow water on the fronds of *Ulva* sp. and the adult specimens were found mostly in deeper water (they have probably migrated here and this is perhaps correlated with a change in feeding habits, i.e. from grazer to scavenger). A similar migration of older specimens is found sometimes in *Turritella communis,* e.g. at Plymouth and Millport (Fretter & Graham 1962: 571), and is also accompanied by a change in feeding habits, here from grazer to suspension-feeder.

Juvenile specimens of *Chlamys opercularis* live attached with their byssus; in the ria in 1964 they were found abundantly attached to *Cellaria* tufts. This "nursery" was not far from station 113, where the sample with most juveniles was taken. Adult specimens are able to swim. Perhaps the absence of juvenile specimens in sample 1567 is related to its greater distance from the "nursery", specimens reached this place only when they were able to swim.

The case of *Nassarius semistriatus* may be similar to that of *N. pygmaeus*; however, we have not found juvenile specimens which support this view.

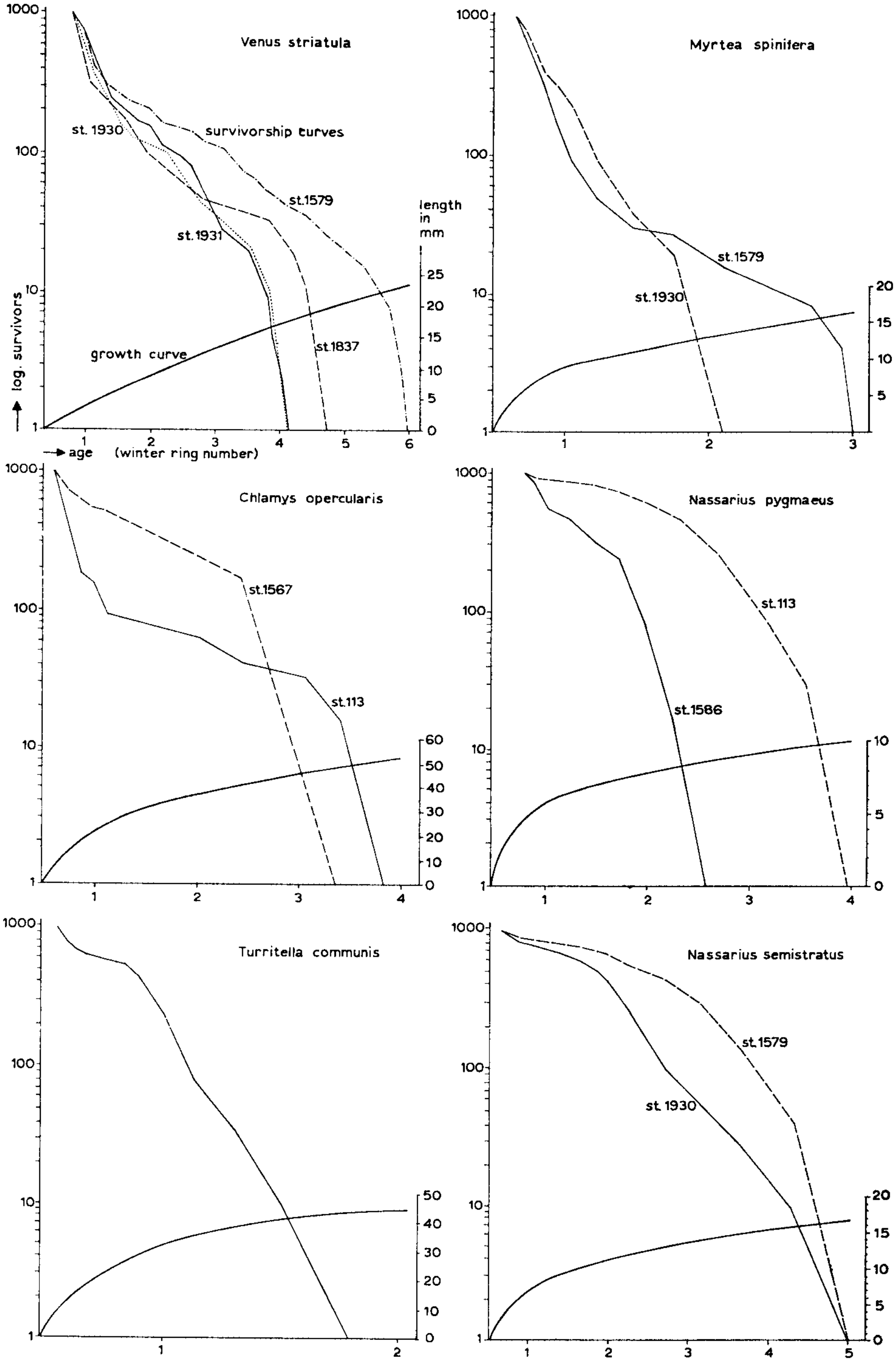


Fig. 47. Growth curves and survivorship curves for the same central bay species as in fig. 44, based on the same samples.

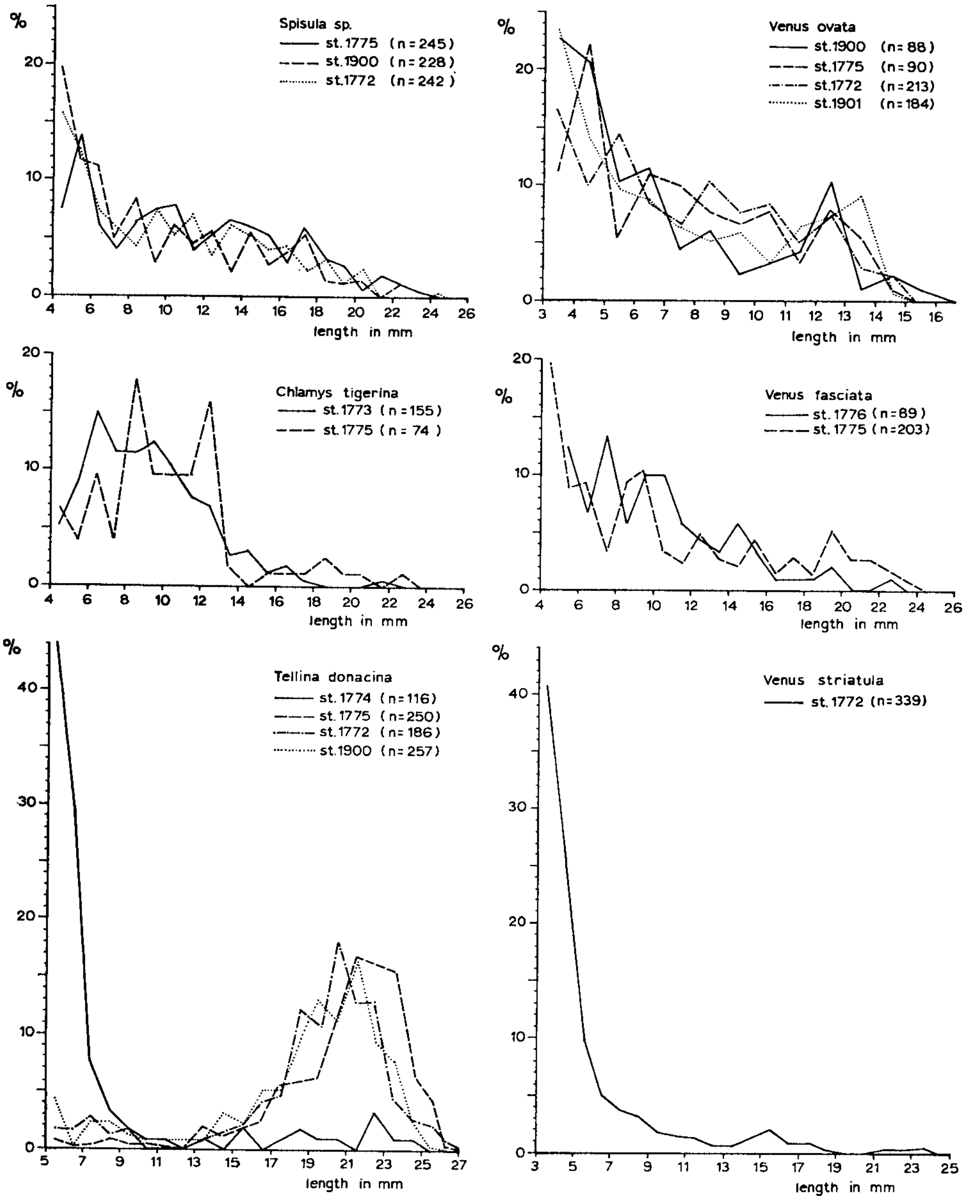
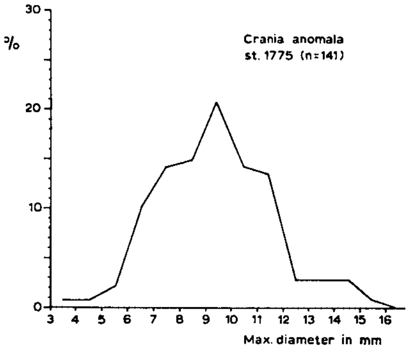


Fig. 48. Size-frequency distribution of empty shells in oceanic zone samples (for location of samples see fig. 46).



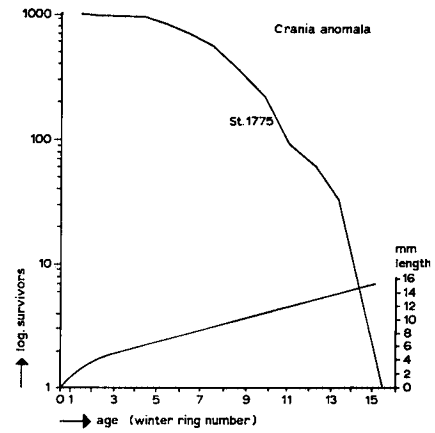


Fig. 49. Size-frequency distribution of empty upper valves of the brachiopod *Crania anomala* (O. F. Müller) in sample 1775 (Oceanic zone).

Fig. 50. Growth curve and survivorship curve for *Crania anomala* (O. F. Müller) (sample 1775).

Specimens of *N. semistriatus* kept alive in the laboratory were able to move very rapidly, this perhaps supports the hypothesis of migration. The size-frequency curves of some oceanic zone molluscs are given in fig. 48. All examples are of species which were found dead and alive in this zone, except the brachiopod *Crania anomala* (figs. 49, 50). The latter is supposed to live on the rocky reefs in this zone, but we could not prove this because of the reefs' inaccessibility. All examples are of species which live buried in the sediment or attached to the substrate and therefore were not so vagile as some of the central-bay examples.

In fact five out of seven species have a size-frequency distribution as predicted by Boucot when transport does not occur. *Crania* which is supposed to be transported shows a very good bell-shaped curve as predicted by Boucot. *Tellina donacina,* a species which lives here gives one "good" and three "wrong" curves. The survivorship curves constructed in fig. 51 give the same results: *Crania* and the three *Tellina donacina* samples give convex i.e. improbable survivorship curves. This means that other factors than growth are involved. In the case of *Crania* we suppose that the whole sample of shells has been transported (not in any sample did we find an empty attached lower-valve, which might have indicated that the animal lived here but was overlooked, the samples consisted only of the upper valves). In the case of *Tellina donacina* there are two possible explanations; either most

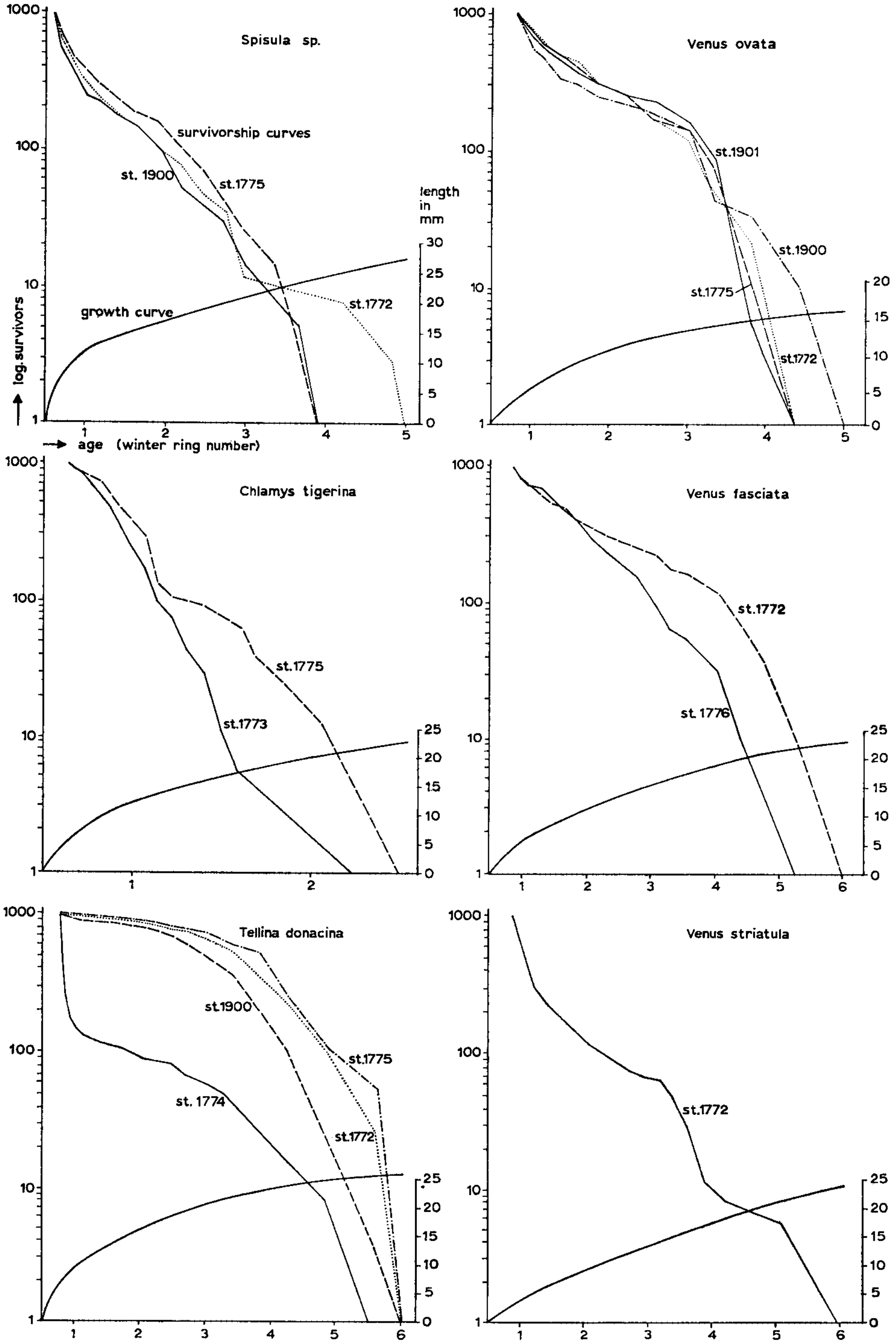


Fig. 51. Growth curves and survivorship curves for the same oceanic species as in fig. 48, based on the same samples.

of the juveniles are eaten by fish and crushed to small fragments, while the adults are too big for the same fish, or most of the juvenile shells are transported elsewhere. The first hypothesis based on Ford's observations (1925, see above) does not explain the presence of juvenile shells in sample 1774, nor the presence in all samples of small *Spisula* shells which also could have been crushed by predating fishes. The second hypothesis can explain the absence of small *Tellina* shells in all samples but one (sample 1774), as well as the presence of small shells of other species in all oceanic samples: the settling velocity of shells which can be used as an indication of their transportability, differs from species to species if we compare shells of equal length (Klähn, 1932: 319, 395; Tauber, 1942:472). Species with thin shells, i.e., a high surface/thickness ratio have lower settling velocities than thick shelled species. The lower the settling velocity the more easily are the shells transported by currents. Fig. 52 gives some settling velocity measurements of species found in the oceanic zone samples: *Tellina donacina, Spisula* sp., *Venus ovata* and *V. fasciata.* From these data it is evident that small *Tellina donacina* shells have a lower settling velocity than shells of equal length of the other oceanic zone species. This indicates that a current along the bottom which is able to remove sediment particles with a settling velocity of 6 cm/sec will transport small *Tellina donacina* shells, whereas small shells of the other species are not affected. According to Inman (in Shepard, 1963: 124, 128) the hydraulic equivalent of shells with a settling velocity of 6 cm/sec are sand grains of 0.4 mm diameter. If the current velocity, one metre above the bottom, exceeds approximately 20 cm/sec these particles begin to move (Hjulström, 1939), whereas a lower current velocity is able to keep them moving. Current velocities of this strength may occur on the part of the shelf where the oceanic zone samples come from (40-85 m depth). The presence of small *Tellina donacina* shells in sample 1774 may perhaps be explained by the irregularities in the bottom topography of the shelf outside the ria: sample 1774 comes perhaps from a pit. From these facts it is evident that the presence in a sample of juvenile shells of some species may coincide with the absence of juvenile shells of other species. Therefore Craig & Hallam (1963:737) may not be right in supposing their beach sample of *Mytilus edulis* to contain all shells produced by the biocoenosis. Small *Mytilus* shells are absent in their sample, but other small shells being present, this need not indicate that mortality in juvenile *Mytilus* is very low. Tauber (1942:472) had already noted the low settling velocity of *Mytilus* shells therefore particularly small *Mytilus* shells may very easily be transported. The survivorship curve, which they based on this beach sample, therefore seems improbable to me, because the first part is

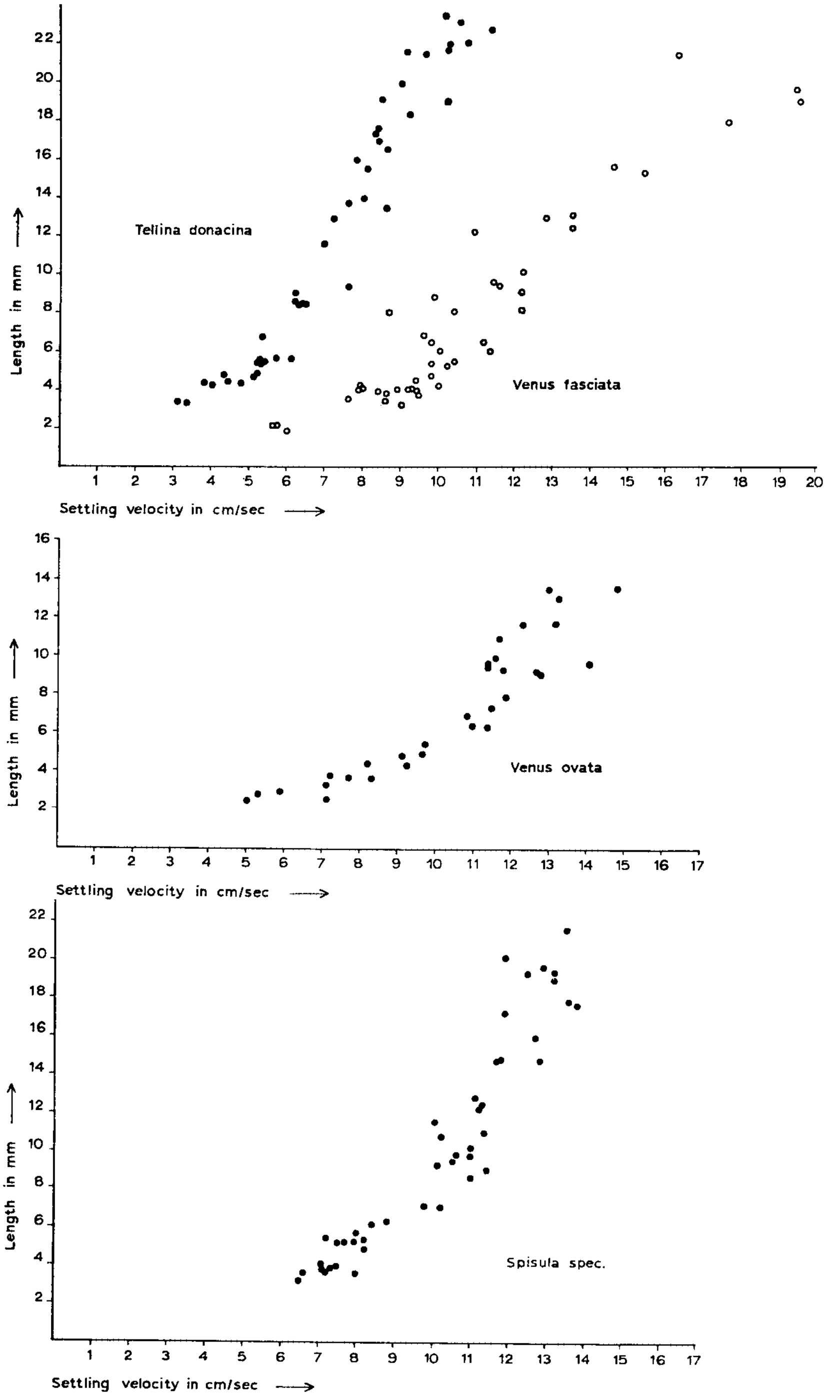


Fig. 52. Settling velocity of empty shells of different oceanic zone species.

horizontal instead of nearly vertical, and is in conflict with most data on juvenile mortality in literature. Thorson, e.g., estimated that only about 1.4% of the young, settling on a 18 m deep sandy bottom of the Øresund, grow up to the size retained by a 2 mm-mesh screen!

Summary.

The size-frequency distribution of empty shells in an autochthonous thanatocoenosis to which shells are regularly contributed by the biocoenosis may differ from species to species. Mortality rate and growth rate affect the size-frequency distribution of empty shells. Therefore the use of survivorship curves is suggested, if the growth can be deduced from growth markings on the shells. These survivorship curves show less variation from species to species, because they are based on mortality alone. A sigmoid survivorship curve is the most probable in an autochthonous thanatocoenosis. Deviation from this sigmoid curve indicates transport of the whole sample (*Crania*) or of the juvenile shells only (*Tellina donacina*).

A number of vagile species yielded a sigmoid curve in some samples and a convex one in other samples. This was thought to be due to the juveniles having a more restricted distribution than the adults. The sigmoid curves are found close to the "nursery", the convex curve where only adults live (*Chlamys opercularis, Nassarius* spp.). Therefore a paleoecologist can use the survivorship curve only for not too vagile species to decide whether or not transport occurred. The size-frequency data to be used should be obtained by bulk sampling; hand-collected samples are useless.

SUMMARY

The Ria de Arosa is a large inlet of the Atlantic Ocean in western Galicia, NW Spain, it covers an area of 230 km^2. It is little influenced by river discharge, the salinity therefore is the normal one for sea water, 33-36^{0}/oo. In the ria two very different molluscan faunas were found: a marginal bay fauna inhabiting sandy sediments and a central bay fauna inhabiting silt-clay sediments. An impoverished marginal fauna composed of euryhaline species lives in the estuarine part of the rivers emptying into the ria. The fauna of the shelly sands of the shelf outside the ria has some species in common with the ria, itself, but also contains some which are not found in the ria.

Circulation seems to be the most important factor in this distribution pattern, affecting on one side the sediments, on the other the fauna. Transport of shells is negligible in the central part of the ria: the distribution patterns of living specimens and empty shells are the same. A small quantity of shells from the marginal zone is transported to the deeper central bay. Transport of shallow water shells towards deeper water is more important on the (narrow) part of the shelf studied outside the ria, which receives shells from a very exposed ocean coast.

Species found in the biocoenosis are always represented in the thanatocoenosis, the proposed zonation therefore can be based also on empty shells only. There is however little quantitative correlation between thanatocoenosis and biocoenosis: the most important species in the living fauna may form only a small part of the dead fauna.

Destruction of shells by predators is important in the ria. This results in a high percentage of broken shells also in low energy environments, therefore fragmentation cannot be used as indicative of a high energy environment.

Size-frequency distribution of empty shells in the sediment shows a large variation from species to species, also in those places where transport of shells is negligible. Size-frequency distribution of fossils is therefore difficult to apply as an indicator of transport. If growth can be measured e.g. by the measuring of growth rings, these data together with the size-frequency distribution can be used to construct mortality curves. These will give better ideas about transport, but aberrant curves may still be found, due to migration of the species during its life.

Sumario

La Ria de Arosa es una bahia de 230 km^2 en la costa atlantica de Galicia occidental. Esta bahia es poco influenciada por desagüe de rios; por eso la salinidad es normal para agua del mar: 33-36^0/oo. En esta Ria se encontraron dos faunas de molluscos muy diferentes: una fauna de bahia marginal, viviendo en sedimentos arenosos y una fauna de bahia central viviendo en sedimentos limosos y arcillosos. En la parte estuarina de los rios que desembocan en la Ria, vive una fauna marginal empobrecida, compuesta de especies euryhalinas. La fauna de las arenas conchiferas en la plataforma fuera de la Ria tiene algunas especies en común con la Ria, y otras que no se encuentran en la misma. Parece que la circulación es el factor mas importante en este patrón de distribución pues tiene su influencia tanto en los sedimentos como en la fauna.

El transporte de conchas es casi nulo en la parte central de la Ria: patrones de distribución de especies vivas y de conchas vacias son iguales. Una cantidad pequeña de conchas de la zona marginal es transportada hasta la parte central de la bahia que es mas profunda. Transporte de conchas de agua poco profunda hacia agua mas profunda es mas importante en la parte (estrecha) de la plataforma fuera de la Ria, que fue investigada; pues esta recibe conchas desde una costa de oceano que es muy expuesta.

Las especies encontradas en la biocoenosis son todas representadas en la thanatocoenosis; la zonacion propuesta por la tanto puede sertambien basada solamente a base de conchas vacias. Hay sin embargo poco correlación cuantitativa entre thanatocoenosis y biocoenosis: especies que son las mas importantes en la fauna viviente, pueden formar solamente una pequeña parte de la fauna muerta.

Destrucción de conchas por predatores es importante en la Ria. Esto resulta en un percentaje alto de conchas rotas, tambien en ambientes de baja energia; por lo tanto fragmentación no puede ser usada como indicadora de un ambiente de alta energia.

La distribución de frequencia de medidas de conchas vacias en el sedimento demuestra gran variación de especie a especie, tambien en aquellos lugares donde transporte de conchas es casi nulo. La distribución de frequencia de medidas de fossiles por lo tanto es dificil de aplicarla como una indicadora de transporte. Si se puede medir el crecimiento, midiendo los anillos de invierno, esos datos juntos con la distribución de medidas de frequencia, pueden ser usadas para construir curvas de mortalidad. Esos daran una idea mejor acerca del transporte, pero curvas abnormales aún pueden ser encontradas, debido a migración de las especies durante su vida.

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Appendix

Systematic list of all Mollusc species found during the 1962-1964 investigations in the Ria de Arosa. The distribution of the species over the different zones is expressed as percentage of the samples from these zones in which they occurred. First column (L): only living specimens; second column (T): (living and) dead specimens.

RM = River mouth, MS = Marginal shallow zone, MD = Marginal deep zone, IB = Inner bay, MB = Middle bay, OB = Outer bay, OC = Oceanic zone.

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Gastropoda														
Archaeogastropoda														
Haliotis tuberculata L.	—	—	—	7	—	—	—	—	—	—	—	—	—	4
Emarginula reticulata Sow.	—	—	—	2	3	7	—	2	—	—	—	9	—	4
„ *conica* Lam.	—	—	2	2	17	49	—	—	—	—	—	2	4	15
„ *cancellata* Phil.	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Puncturella noachina (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Diodora apertura (Mont.)	—	—	7	2	7	39	—	8	—	17	—	9	—	50
Patella spp.	—	—	21	31	—	4	—	—	—	—	—	—	—	42
Patina pellucida (L.)	—	—	—	5	—	13	—	2	—	—	—	11	—	50
Patelloida virginea (Müller)	—	—	2	18	16	77	—	11	—	24	—	13	—	54
Calliostoma zizyphinum (L.)	—	—	8	21	11	25	—	9	—	7	—	7	—	30
„ *papillosum* (da C.)	—	—	—	—	—	—	—	—	—	—	—	—	4	8
Gibbula magus (L.)	—	—	7	54	24	65	2	23	—	17	—	13	—	19
„ *tumida* (Mont.)	—	—	—	—	15	59	—	—	—	3	4	15	19	42
„ *cineraria* (L.)	—	—	26	57	23	72	4	32	3	62	—	35	—	15
„ *umbilicalis* (da C.)	—	11	18	31	—	9	—	6	—	14	—	—	—	—
„ *pennanti* (Phil.)	—	—	33	3	—	—	—	—	—	—	—	—	—	—

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Cantharidus exasperatus (Penn.)	—	—	5	32	24	79	—	23	—	41	—	29	—	31
„ *montagui* (Wood)	—	—	—	—	1	14	—	—	—	—	—	2	15	54
„ *striatus* (L.)	—	—	—	33	—	—	—	11	—	21	—	2	—	—
Monodonta lineata (da C.)	7	11	20	25	—	—	—	—	—	—	—	—	—	—
Skenea serpuloides (Mont.)	—	—	—	2	1	16	—	—	—	—	—	—	—	12
„ *nitens* (Phil.)	—	—	—	2	6	24	—	—	—	—	—	—	—	—
„ *cutleriana* (Clark)	—	—	—	2	3	23	—	—	—	—	—	—	—	12
Circulus spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Tricolia pullus (L.)	—	—	7	16	1	16	—	—	—	7	—	7	—	12
Mesogastropoda														
Lacuna pallidula (da C.)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Littorina littorea (L.)	69	71	13	26	—	—	—	6	—	7	—	2	—	—
„ *saxatilis* (Olivi)	69	71	21	46	—	18	—	11	—	28	—	16	—	12
„ *neritoides* (L.)	—	—	16	23	—	13	—	—	—	—	—	2	—	15
„ *littoralis* (L.)	50	61	18	33	—	6	—	—	—	—	—	2	—	—
Hydrobia ulvae (Penn.)	86	86	13	24	—	3	—	13	—	14	—	—	—	—
„ spec.	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Cingulopsis fulgida (Adams)	—	—	15	18	1	7	—	—	—	—	—	—	—	—
Cingula pulcherrima (Jeffr.)	—	—	2	2	—	—	—	—	—	—	—	—	—	—
„ *alderi* (Jeffr.)	—	—	—	10	—	—	—	—	—	—	—	—	—	8
„ *vitrea* (Mont.)	—	—	2	2	1	8	—	19	17	52	9	42	—	4
„ *semicostata* (Mont.)	—	—	5	26	7	62	—	11	—	21	2	6	—	19
„ *semistriata* (Mont.)	—	—	2	5	5	32	—	6	—	7	—	2	—	12
„ *nitida* (Brusina)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Alvania crassa (Kanm.)	—	—	2	8	1	45	—	—	—	14	—	—	—	15
„ *beanii* (Thorpe)	—	—	—	2	7	55	—	—	—	3	—	11	—	—
„ *zetlandica* (Mont.)	—	—	—	—	—	3	—	—	—	—	—	4	—	4
„ *cancellata* (da C.)	—	—	—	2	3	34	—	2	—	7	—	18	—	31
„ *carinata* (da C.)	—	—	—	2	—	4	—	—	—	—	—	—	—	4
„ *lactea* (Michaud)	—	—	—	10	—	10	—	—	—	3	—	—	—	—

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L % T		L % T		L % T		L % T		L % T		L % T		L % T	
„ *abyssicola* (F. et H.)	—	—	—	—	—	—	—	—	—	—	—	15	—	12
„ *punctura* (Mont.)	—	—	—	2	1	39	—	6	—	7	—	16	—	27
Rissoa inconspicua Alder	32	32	10	26	6	28	—	21	3	24	—	4	—	8
„ *parva* (da C.)	7	7	33	67	8	70	6	32	—	52	—	27	—	31
„ *guerini* Récluz	—	—	9	18	—	10	—	—	—	7	—	2	—	—
„ *lilacina* Récluz	—	—	16	51	3	45	—	21	—	55	—	15	—	—
„ *membranacea* (Adams)	25	25	2	15	—	1	—	2	—	3	—	—	—	—
Barleeia unifasciata (Mont.)	—	—	10	16	—	15	—	—	—	7	—	7	—	4
Plagiostyla asturiana (Fischer)	—	—	—	2	—	4	—	—	—	—	—	—	—	—
Assiminea grayana Fleming	4	4	—	—	—	—	—	—	—	—	—	—	—	—
Tornus subcarinatus (Mont.)	—	—	—	2	—	11	—	4	—	—	—	2	—	—
Skeneopsis planorbis (Fabr.)	—	—	10	15	—	3	—	—	—	—	—	—	—	—
Omalogyra atomus (Phil.)	—	—	8	12	1	7	—	—	—	—	—	—	—	—
Rissoella diaphana (Alder)	—	—	5	7	6	14	—	—	—	—	—	—	—	—
„ *opalina* (Jeffr.)	—	—	5	8	4	16	—	—	—	—	—	—	—	—
Philippia hybrida (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	15
Torinia sicula (Cantr.)	—	—	—	—	—	4	—	2	3	3	4	9	23	31
Turritella communis Risso	—	—	—	2	—	4	—	4	7	52	7	87	—	39
„ *triplicata* (Brocchi)	—	—	2	7	23	49	—	—	—	14	2	4	8	19
Caecum imperforatum (Kanm.)	—	—	8	18	25	45	—	2	—	3	—	—	—	4
„ *glabrum* (Mont.)	—	—	—	5	4	18	—	—	—	—	—	—	—	15
Bittium reticulatum (da C.)	—	—	20	67	5	76	2	58	—	52	—	35	—	46
Cerithiopsis tubercularis (Mont.)	—	—	—	—	—	8	—	—	—	—	—	—	—	—
„ *barleei* Jeffr.	—	—	—	—	—	7	—	—	—	3	—	—	—	—
„ *metaxae* Chiaje	—	—	—	—	—	3	—	—	—	—	—	—	—	4
Triphora perversa (L.)	—	—	2	8	1	34	—	—	—	—	—	4	—	27
Clathrus clathrus (L.)	—	—	—	7	—	3	—	—	—	—	—	7	—	—
„ ***turtonis*** (Turton)	—	—	—	2	—	1	—	—	—	—	—	6	—	—
„ *clathratulus* (Kanm.)	—	—	—	2	—	3	—	—	—	—	—	16	—	12
Janthina janthina (L.)	—	—	—	3	—	—	—	—	—	—	—	—	—	—
„ *exigua* Lam.	—	—	—	2	—	—	—	—	—	—	—	—	—	—

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Aclis minor (Brown)	—	—	—	—	—	—	—	2	—	—	—	4	—	—
Eulima glabra (da C.)	—	—	—	—	—	—	—	—	—	—	—	6	—	4
Balcis alba (da C.)	—	—	—	2	1	6	—	—	—	—	2	13	4	27
„ *lubrica* (Monterosato)	—	—	—	2	—	5	—	—	—	4	—	4	—	—
„ *devians* (Monterosato)	—	—	—	—	—	7	—	—	—	—	—	—	—	—
„ *curva* (Monterosato)	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Fossarus costatus (Brocchi)	—	—	—	—	—	—	—	—	—	—	—	2	—	—
Capulus ungaricus (L.)	—	—	—	8	—	—	—	—	—	—	—	2	—	38
Calyptraea chinensis (L.)	—	—	13	49	17	70	—	23	—	31	—	15	—	27
Aporrhais pespelecani (L.)	—	—	—	2	—	1	2	2	—	10	2	13	23	58
Natica alderi Forbes	—	—	2	16	10	51	—	9	—	31	9	44	39	73
„ sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Lamellaria latens (Müller)	—	—	2	2	—	4	—	—	—	3	—	2	—	—
Erato voluta (Mont.)	—	—	—	—	1	3	—	—	—	—	—	2	4	15
Trivia monacha (da C.)	—	—	3	13	7	24	—	2	—	3	2	7	4	43
Simnia patula (Penn.)	—	—	—	—	—	1	—	—	—	—	—	—	—	4
Galeodea saburon (Brug.)	—	—	—	3	—	1	—	—	—	—	—	4	—	23
Cymatium cutaceum (L.)	—	—	—	3	—	—	—	—	—	—	—	—	—	—
Charonia corrugata (Lam.)	—	—	—	—	—	—	—	—	—	—	—	—	8	8
„ *gyrinoides* (Brocchi)	—	—	—	3	1	3	—	—	—	—	2	2	—	—
Trophon muricatus (Mont.)	—	—	—	—	3	23	—	—	—	7	4	24	8	23
Nucella lapillus (L.)	11	18	8	13	5	18	—	4	—	10	—	2	—	50
Ocenebra erinaceus (L.)	—	—	13	39	4	17	—	11	—	7	—	2	—	38
„ *aciculata* (Lam.)	—	—	9	23	30	61	—	—	—	17	—	4	—	19
Muricopsis blainvillei (Payr.)	—	—	—	—	—	—	—	—	—	—	—	2	—	8
Columbella (*Atilia*) *minor* Schacchi	—	—	—	—	6	30	—	2	7	17	2	15	—	—
Neptunea contraria L.	—	—	—	—	—	—	—	—	—	3	4	13	8	15
Chauvetia brunnea (Donovan)	—	—	—	3	18	27	—	—	—	7	—	—	—	—
„ spec.	—	—	—	3	—	—	—	—	—	—	—	—	—	—
Nassarius reticulatus (L.)	7	11	10	56	23	47	—	21	—	35	2	13	4	38

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
„ *incrassatus* (Ström)	—	—	12	31	20	44	—	9	—	10	10	22	8	54
„ *pygmaeus* (Lam.)	4	4	12	28	6	30	21	98	17	90	22	93	4	15
„ *semistriatus* (Brocchi)	—	—	—	—	—	6	9	26	14	59	47	96	—	31
„ *pfeifferi* (Phil.)	—	—	3	3	—	—	—	—	—	—	—	—	—	—
Haedropleura septangularis (Mont.)	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Mangelia attenuata (Mont.)	—	—	—	5	1	4	—	6	3	21	—	9	—	8
„ *coarctata* (Forb.)	—	—	3	15	10	54	—	21	11	52	2	40	—	15
„ *brachyostoma* (Phil.)	—	—	—	5	1	8	—	17	7	59	—	49	—	—
„ *nebula* (Mont.)	—	—	—	5	—	6	—	—	—	3	—	—	—	8
Philbertia gracilis (Mont.)	—	—	—	—	—	—	—	—	—	—	—	—	8	8
„ *leufroyi* (Michaud)	—	—	—	—	—	3	—	—	—	—	—	—	—	8
„ *purpurea* (Mont.)	—	—	—	2	6	11	—	—	—	—	—	—	4	15
„ *linearis* (Mont.)	—	—	—	2	1	17	—	—	—	—	—	11	—	46
„ *asperrima* (Brown)	—	—	—	—	—	—	—	—	—	—	—	2	—	—
„ *teres* (Reeve)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Drilla maravignae (Bivona)	—	—	—	—	—	1	—	—	—	—	—	—	4	19
Opisthobranchia														
Ringicula auriculata Brocchi	—	—	3	7	—	4	2	81	10	83	11	87	—	15
Actaeon tornatilis (L.)	—	—	—	—	—	—	—	—	—	3	—	—	—	8
Chrysallida obtusa (Brown)	—	—	—	7	—	20	—	9	—	3	—	—	—	8
„ *indistincta* (Mont.)	—	—	—	2	—	13	—	4	—	24	—	—	—	—
„ *clathrata* (Jeffr.)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
„ *decussata* (Mont.)	—	—	—	5	—	20	—	—	—	3	—	2	—	8
„ *excavata* (Phil.)	—	—	—	—	—	4	—	—	—	—	—	—	—	—
„ *spiralis* (Mont.)	—	—	—	—	—	4	—	—	—	—	—	2	—	19
Menestho obliqua (Alder)	—	—	—	—	—	13	—	—	—	—	—	7	—	—
Odostomia plicata (Mont.)	—	—	—	7	—	4	—	—	—	—	—	—	—	—
„ *turrita* Hanley	—	—	—	10	—	3	—	51	—	31	—	2	—	—
„ *unidentata* (Mont.)	—	—	—	—	—	—	—	—	—	—	—	—	—	8
„ *acuta* Jeffr.	—	—	—	—	—	3	—	4	—	14	—	6	—	8

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Odostomia conoidea (Brocchi)	—	—	—	—	—	1	—	—	—	—	—	—	4	8
„ *nivosa* (Mont.)	—	—	—	—	—	6	—	—	—	—	—	—	—	—
„ spec.	—	—	—	—	—	—	—	2	—	3	—	9	—	4
Brachystomia scalaris (Macgillivray)	—	—	—	—	—	1	—	—	—	—	—	—	—	—
„ *eulimoides* (Hanley)	—	—	—	13	—	34	—	11	—	7	—	18	—	—
„ *perezi* (Dautz. et Fischer)	—	—	—	—	—	3	—	—	—	3	—	9	—	4
Eulimella macandrei (Forbes)	—	—	—	—	—	—	—	—	—	—	—	2	—	4
„ *laevis* (Brown)	—	—	—	—	—	1	—	2	—	3	—	13	—	19
„ *nitidissima* (Mont.)	—	—	—	—	—	3	—	—	—	—	—	—	—	—
Turbonilla elegantissima (Mont.)	—	—	—	25	—	10	—	19	—	48	—	40	—	4
„ *rufa* (Phil.)	—	—	—	—	—	—	—	—	—	—	—	—	4	12
„ *jeffreysii* (F. et H.)	—	—	—	—	—	7	—	—	—	3	—	6	—	12
„ *fenestrata* (Jeffr.)	—	—	—	5	—	1	—	17	—	17	—	6	—	—
Diaphana minuta (Brown)	—	—	—	—	—	3	—	—	—	—	—	—	—	—
Haminea navicula (da C.)	11	25	10	30	—	—	4	17	—	3	—	—	—	—
Retusa truncata (Brug.)	4	4	2	26	1	28	2	15	—	38	—	—	—	8
„ *pellucida* (Brown)	—	—	—	—	—	10	—	—	—	3	—	—	—	4
„ *umbilicata* (Mont.)	—	—	—	2	—	4	—	—	—	17	—	4	—	19
Rhizorus acuminatus (Brug.)	—	—	—	2	—	—	—	2	—	14	—	2	—	—
Akera bullata Müller	7	11	5	5	—	—	9	28	—	3	—	—	—	—
Cylichna cylindracea (Penn.)	—	—	—	3	1	4	—	23	7	55	6	26	—	15
Scaphander lignarius (L.)	—	—	—	—	—	1	—	—	—	—	4	11	—	23
Philine aperta (L.)	14	14	5	7	—	1	21	55	17	48	2	4	—	—
„ *catena* (Mont.)	—	—	—	2	—	—	—	—	—	—	—	4	—	4
„ *scabra* (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	19
„ *punctata* (Adams)	—	—	—	—	—	4	—	—	—	—	—	—	—	—
Pteropoda														
Creseis acicula Rang	—	—	—	—	—	—	—	2	—	7	—	40	—	—

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Pulmonata														
Leucophytia bidentata (Mont.)	—	—	—	3	—	—	—	—	—	3	—	—	—	—
Ovatella myosotis (Draparnaud)	7	7	2	2	—	—	—	—	—	—	—	—	—	—
Otina ovata (Brown)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Scaphopoda														
Dentalium novemcostatum Lam.	—	—	2	3	4	14	—	30	28	81	26	76	8	35
„ *vulgare* (da C.)	—	—	—	—	—	—	—	—	—	—	—	—	23	42
Cadulus politus (Wood)	—	—	—	—	—	1	—	—	—	—	—	—	—	15
Lamellibranchia														
Taxodonta														
Nucula nucleus (L.)	—	—	—	—	—	—	—	—	—	—	7	9	15	15
„ *turgida* Leckenby et Marshall	—	—	—	—	—	1	9	74	17	97	31	36	4	4
„ *hanleyi* Winckworth	—	—	—	—	—	—	—	—	—	—	—	—	35	46
„ spec. indet.	—	—	—	—	—	—	—	—	—	—	—	36	—	15
Nuculana fragilis (Chemnitz)	—	—	—	—	—	4	—	—	—	—	4	43	—	35
Glycymeris glycymeris (L.)	—	—	—	2	1	28	—	2	—	—	—	6	8	81
Arca tetragona Poli	—	—	—	2	—	18	—	2	—	7	—	13	—	81
„ *lactea* L.	—	—	—	—	3	21	—	—	—	—	—	4	8	35
„ *polii* Mayer	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Anisomyaria														
Anomia ephippium L.	—	4	8	34	8	52	—	26	3	38	2	9	—	19
Monia cf. *squama* (Gmelin)	—	—	—	2	—	8	—	—	—	—	2	4	4	54
Heteranomia squamula (L.)	—	—	3	13	1	42	—	13	—	14	—	20	—	50
Mytilus edulis L.	72	72	21	53	—	30	—	38	—	21	—	20	—	69
Modiolus barbatus (L.)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
„ *adriaticus* (Lam.)	—	—	2	7	8	20	—	6	—	3	7	16	8	23

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Modiolus phaseolinus (Phil.)	—	—	—	10	—	24	—	2	—	14	—	22	4	42
Musculus marmoratus (Forb.)	—	—	2	12	—	23	—	28	10	35	—	9	—	—
„ *costulatus* (Risso)	4	4	8	12	—	6	—	—	—	3	—	—	—	4
„ *sulcatus* (Risso)	—	—	—	—	—	1	—	—	—	—	—	—	—	4
Pteria hirundo (L.)	—	—	—	—	—	1	—	—	7	10	2	27	4	31
Ostrea edulis L.	4	14	3	13	—	3	—	13	—	3	—	9	—	12
Pinna fragilis Penn.	—	—	—	—	—	—	—	—	—	—	—	7	4	15
Chlamys varia (L.)	—	—	7	30	6	23	—	23	—	41	—	4	—	4
„ *distorta* (da C.)	—	—	—	5	—	13	—	2	—	7	—	6	—	50
„ *opercularis* (L.)	—	—	2	15	11	46	2	75	10	69	11	66	23	81
„ *tigerina* (Müller)	—	—	—	—	—	11	—	—	—	—	—	15	35	89
„ *similis* (Laskey)	—	—	—	—	—	—	—	—	—	—	—	—	—	12
„ *striata* (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
„ *pesfelis* (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
„ *furtiva* (Lovén)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Pecten maximus (L.)	—	—	—	18	1	27	—	23	—	14	2	15	—	38
Lima hians (Gmelin)	—	—	—	—	—	1	—	—	—	—	—	—	—	—
„ *loscombi* Sow.	—	—	—	—	—	6	—	—	—	—	—	—	4	27
„ *subauriculata* Brown	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Eulamellibranchia														
Astarte triangularis (Mont.)	—	—	—	2	3	30	—	—	—	—	—	—	—	35
„ *montagui* (Dillwyn)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Digitaria digitaria (L.)	—	—	2	26	1	55	—	15	—	21	—	20	4	62
Thyasira flexuosa (Mont.)	—	—	—	7	1	20	6	75	14	86	26	76	—	12
Loripes lucinalis (Lam.)	—	—	5	46	—	6	—	9	—	14	—	—	—	—
Myrtea spinifera (Mont.)	—	—	—	5	1	11	—	43	35	93	16	89	—	46
Phacoides borealis (L.)	—	—	—	18	3	17	—	—	—	24	—	6	—	46
Divaricella divaricata (L.)	—	—	—	23	—	3	—	2	3	7	—	2	—	—
Diplodonta rotundata (Mont.)	—	—	—	7	1	18	—	—	—	3	—	—	12	54
Kellia suborbicularis (Mont.)	—	—	2	5	6	27	—	4	—	3	2	9	4	23

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Lasaca rubra (Mont.)	—	—	13	23	—	14	—	6	—	7	—	20	—	19
Lepton squamosum (Mont.)	—	—	—	—	—	1	—	—	—	3	—	—	—	8
„ *nitidum* Turton	—	4	—	—	—	3	—	—	—	—	—	6	—	2
Epilepton clarkiae (Clark)	—	—	—	3	3	20	—	—	—	3	—	—	—	4
Neolepton obliquatum (Chaster)	—	—	—	—	—	—	—	—	—	—	2	4	—	—
Pythina macandrewi (Fischer)	—	—	5	31	—	24	—	11	—	3	—	—	—	—
Galeomma turtoni Sow.	—	—	—	—	—	1	—	—	—	—	—	2	—	15
Scintilla rotunda Jeffr.	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Spaniorinus ambiguus (Nyst. et West)	—	—	—	—	—	—	—	—	—	—	—	7	—	4
Devonia perrieri (Malard)	—	—	—	—	—	—	—	—	—	—	—	4	—	—
Montacuta ferruginosa (Mont.)	—	—	—	—	—	—	—	4	—	—	—	4	—	12
„ *phascolionis* Dautz. et Fischer	—	—	—	—	—	—	—	—	—	—	2	4	—	8
Mysella bidentata (Mont.)	4	4	5	42	14	56	6	68	10	55	11	64	8	46
Cardium aculeatum L.	—	—	—	—	—	1	—	—	—	—	2	2	8	12
„ *tuberculatum* L.	—	—	—	8	—	—	—	—	—	—	—	—	—	35
„ *paucicostatum* Sow.	—	—	—	10	1	7	13	87	24	100	6	69	—	8
„ *papillosum* Poli	—	—	—	—	—	1	—	—	—	—	—	2	—	20
„ *ovale* Sow.	—	—	—	—	—	—	—	—	—	—	—	4	—	27
„ *scabrum* Phil.	—	—	—	8	9	66	—	13	—	38	6	46	8	69
„ *exiguum* Gmelin	4	4	13	43	1	3	2	17	—	10	—	—	—	—
„ *edule* L.	50	82	15	41	7	7	32	32	—	24	—	7	—	8
„ *minimum* Phil.	—	—	—	—	—	—	—	—	—	—	—	—	—	15
Laevicardium crassum (Gmelin)	—	—	—	5	—	13	—	2	—	14	4	20	19	96
Coralliophaga lithophagella (Lam.)	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Dosinia exoleta (L.)	—	4	5	49	13	58	—	6	3	21	2	2	—	—
„ *lupinus* (L.)	—	—	—	2	—	4	—	—	3	3	4	7	15	62
Gafrarium minimum (Mont.)	—	—	—	7	13	58	—	4	—	3	—	15	8	69
Pitar rudis (Poli)	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Callista chione (L.)	—	—	—	3	—	—	—	—	—	—	—	—	—	4

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Venus ***verrucosa*** **L.**	—	4	5	36	6	40	—	6	—	7	—	—	—	—
„ ***casina*** **L.**	—	—	—	—	1	3	—	—	—	—	—	—	4	35
„ *ovata* Penn.	—	—	—	7	10	45	—	4	—	17	9	38	50	92
„ *fasciata* (da C.)	—	—	—	7	14	55	—	—	—	—	—	15	42	96
„ *striatula* (da C.)	—	—	2	21	4	25	2	51	28	97	40	82	8	58
Venerupis aurea (Gmelin)	—	4	13	31	—	—	—	6	—	—	—	—	—	—
„ *rhomboides* (Penn.)	—	—	7	28	37	86	2	15	7	35	4	33	—	58
„ *pullastra* (Mont.)	—	14	20	57	—	16	2	17	—	3	—	—	—	4
„ *decussata* (L.)	32	43	18	23	—	—	—	—	—	—	—	—	—	—
Irus irus (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Petricola lithophaga (Retzius)	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Mysia undata (Penn.)	—	—	—	—	—	—	—	2	—	3	2	7	—	12
Donax trunculus L.	—	—	2	2	—	—	—	—	—	—	—	—	—	—
Ervilia castanea (Mont.)	—	—	2	5	—	13	—	—	—	—	—	—	—	15
Tellina squalida (Mont.)	—	—	—	3	—	3	—	—	—	—	—	—	—	—
„ *tenuis* (da C.)	—	7	7	23	—	4	—	2	—	10	—	—	—	—
„ *fabula* (Gmelin)	—	—	—	2	—	—	—	—	—	—	—	2	—	—
„ *donacina* (L.)	—	—	3	23	13	37	—	4	—	—	—	13	27	89
„ *pygmaea* (Lovén)	—	—	—	—	—	1	—	—	—	—	—	—	—	12
„ *compressa* Brocchi	—	—	—	—	—	—	—	—	—	—	4	11	4	15
„ *serrata* Renieri	—	—	—	3	—	4	—	2	—	17	4	27	4	15
Gastrana fragilis (L.)	—	—	3	15	—	1	—	2	—	—	—	—	—	—
Arcopagia crassa (Penn.)	—	—	—	2	—	16	—	2	—	—	—	4	4	38
Scrobicularia plana (da C.)	18	61	3	7	—	—	—	—	—	—	—	—	—	—
Abra tenuis (Mont.)	—	—	2	2	—	—	—	—	—	—	—	—	—	—
„ *alba* (Wood)	—	4	7	33	10	35	6	43	14	76	27	76	15	46
„ *nitida* (Müller)	—	—	—	5	1	3	43	98	38	86	15	49	—	—
„ *prismatica* (Mont.)	—	—	—	—	—	—	—	—	—	—	—	—	—	19
Gari fervensis (Gmelin)	—	—	—	5	—	1	—	2	—	10	2	2	—	54
„ *depressa* (Penn.)	—	—	—	12	—	1	—	—	—	—	—	—	—	—
„ *tellinella* (Lam.)	—	—	2	3	4	34	—	—	—	—	—	—	19	73

Zone	RM		MS		MD		IB		MB		OB		OC	
Number of samples	28		61		71		47		29		55		26	
	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T	L %	T
Solecurtus scopula (Turton)	—	—	—	—	—	1	—	—	—	—	—	—	—	31
Cultellus pellucidus (Penn.)	—	—	—	—	—	1	—	—	—	14	9	15	—	23
Ensis arcuatus (Jeffr.)	—	—	2	8	—	14	—	2	—	—	—	—	—	4
„ *minor* (Chenu)	—	—	—	3	—	—	—	—	—	—	—	—	—	—
„ *siliqua* (L.)	—	—	—	3	—	—	—	—	—	—	—	—	—	—
Solen marginatus Mont.	—	4	—	7	—	—	—	—	—	—	—	—	—	—
Donacilla cornea (Poli)	—	—	12	26	—	—	—	2	—	3	—	—	—	—
Mactra corallina (L.)	—	—	—	2	—	—	—	—	—	7	—	—	—	4
Spisula solida (L.)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
„ spec.	—	—	3	31	1	24	—	23	3	38	—	16	19	85
Lutraria lutraria (L.)	—	—	2	12	3	11	—	13	—	24	2	6	—	15
„ *magna* (da C.)	—	—	—	8	—	—	—	2	—	—	—	—	—	—
Sphenia binghami Turton	—	—	—	—	—	3	—	—	—	—	—	—	—	—
Corbula gibba (Olivi)	—	—	2	18	1	32	11	66	17	100	31	91	23	58
Hiatella arctica (L.)	—	—	2	21	13	65	—	23	3	28	4	33	4	66
Saxicavella jeffreysi Winckworth	—	—	—	—	—	1	—	11	—	48	4	60	—	12
Teredo spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	12
Cochlodesma praetenue (Mont.)	—	—	—	—	—	1	—	—	—	—	—	—	—	4
Thracia phaseolina (Lam.)	—	—	10	17	—	—	2	11	3	10	—	—	—	—
„ *villosiuscula* (Macgill.)	—	—	—	—	1	8	—	—	—	—	—	—	—	38
Lyonsia norwegica (Gmelin)	—	—	—	—	—	1	—	—	—	—	—	—	—	4
Calopodium albidum Röding	—	—	—	—	—	—	—	2	—	3	—	—	—	—
Cuspidaria cuspidata (Olivi)	—	—	—	—	—	4	—	15	—	41	—	49	—	4


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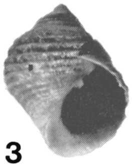
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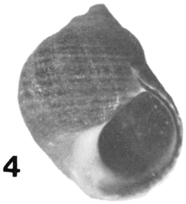
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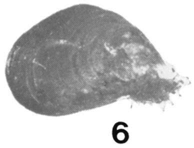
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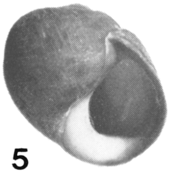
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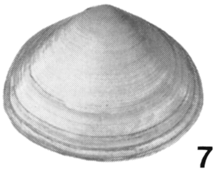
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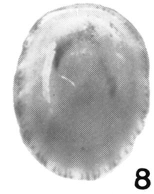
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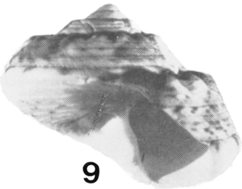
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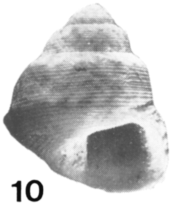
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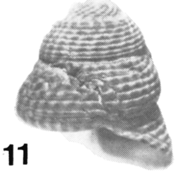
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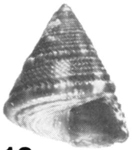
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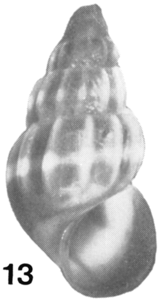
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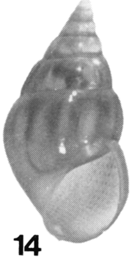
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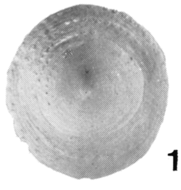
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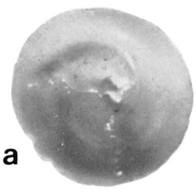
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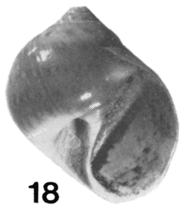
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PLATE I

Fig. 1-7, Mollusca found in more than 50% of the samples from the polyhaline rivermouth zone (RM); length given in mm, 1, *Hydrobia ulvae* Pennant, 6 mm; 2, *Cardium edule* Linné, 32 mm; 2a, the same, interior view; 3, *Littorina saxatilis* (Olivi), 12 mm; 4, *Littorina littorea* (Linné), 19 mm; 5, *Littorina littoralis* (Linné), 12 mm; 6, *Mytilus edulis* Linné, 32 mm (also in more than 50% of the MS samples); 7, *Scrobicularia plana* (da Costa), 44 mm; 7a, the same, interior view.

Fig. 8-18, Mollusca found in more than 50% of the samples from the marginal zone (MS, marginal shallow zone; MD, marginal deep zone); length given in mm. 8, *Patelloida virginea* (Müller), 7 mm (MD); 8a, the same, exterior view; 9, *Gibbula magus* (Linné), 16 mm (MS, MD); 10, *Gibbula tumida* (Montagu), 7 mm (MD); 11, *Gibbula cineraria* (Linné), 13 mm (MS, MD); 12, *Cantharidus exasperatus* (Pennant), 5 mm (MD); 13, *Rissoa parva* (da Costa), 3 mm (MS, MD); 14, *Rissoa lilacina* Récluz, 5 mm (MS); 15, *Turritella triplicata* (Brocchi), 43 mm (MD); 16, *Bittium reticulatum* (da Costa), 8 mm (MS, MD); 17, *Calyptraea chinensis* (Linné), 13 mm (MS, MD); 17a, the same, interior view; 18, *Natica alderi* Forbes, 10 mm (MD, also in more than 50% of the OC samples).

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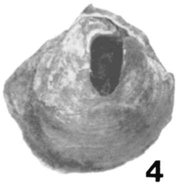

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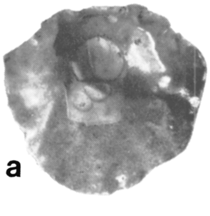

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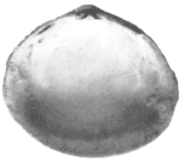

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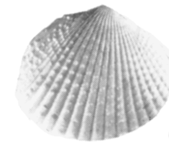

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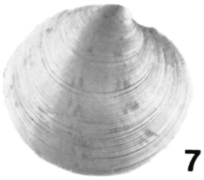

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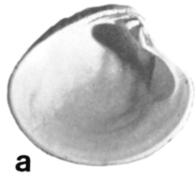

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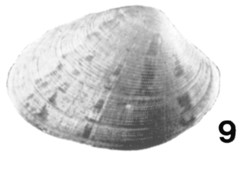

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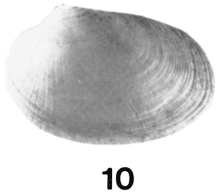

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PLATE II

Fig. 1-11. Mollusca found in more than 50% of the samples from the marginal zone (continued); length given in mm. 1, *Ocenebra aciculata* (Lamarck), 11 mm (MD); 2, *Nassarius reticulatus* (Linné), 32 mm (MS); 3, *Mangelia coarctata* (Forbes), 8 mm (MD); 4, *Anomia ephippium* Linné, lower valve, exterior, 40 mm (MD); 4a, *Anomia ephippium* Linné, upper valve, interior, 25 mm (MD); 5, *Digitaria digitaria* (Linné), 5 mm (MD, also in more than 50% of the OC samples); 5a, the same, interior view; 6, *Cardium scabrum* Philippi, 6 mm (MD, also in more than 50% of the OC samples); 6a, the same, interior view; 7, *Dosinia exoleta* (Linné), 51 mm (MS, MD); 7a, the same, interior view; 8, *Venus fasciata* (da Costa), 19 mm (MD, also in more than 50% of the OC samples); 8a, the same, interior view; 9, *Venerupis rhomboides* (Pennant), 51 mm (MD); 9a, the same, interior view; 10, *Venerupis pullastra* (Montagu), 31 mm (MS); 10a, the same, interior view; 11, *Hiatella arctica* (Linné), 13 mm (MD, also in more than 50% of the OC samples); 11a, the same, exterior view.


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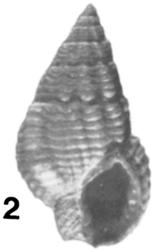
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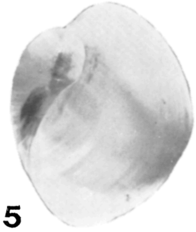
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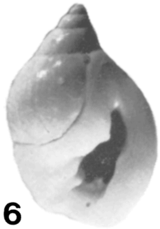
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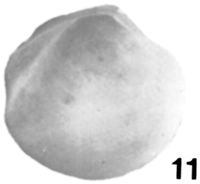
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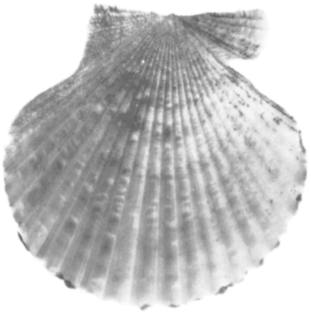
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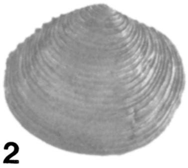
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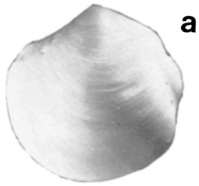
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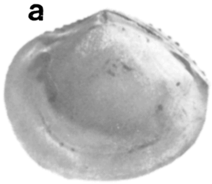
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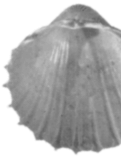
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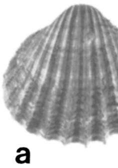
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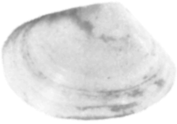
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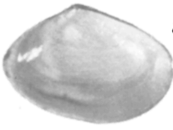
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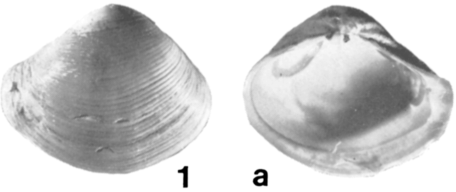
PLATE III

Fig. 1-16, Mollusca found in more than 50% of the samples from the central bay zone (IB = inner bay; MB = middle bay; OB = outer bay); length given in mm. 1, *Turritella communis* Risso, 39 mm (MB, OB); 2, *Nassarius pygmaeus* (Lamarck), 9 mm (IB, MB, OB); 3, *Nassarius semistriatus* (Brocchi), 15 mm (MB, OB); 4, *Mangelia brachystoma* (Philippi), 9 mm (MB); 5, *Philine aperta* (Linné), 16 mm (IB, MB); 6, *Ringicula auriculata* Brocchi, 5 mm (IB, MB, OB); 7, *Cylichna cylindracea* (Pennant), 7 mm (MB); 8, *Dentalium novemcostatum* Lamarck, 39 mm (MB, OB); 9, *Nucula turgida* Leckenby & Marshall, 10 mm (IB, MB); 9a, the same, interior view; 10, *Chlamys opercularis* (Linné), 38 mm (MB, OB, also in more than 50% of the OC samples); 11, *Thyasira flexuosa* (Montagu), 6 mm (IB, MB, OB); 11a, the same, exterior view; 12, *Myrtea spinifera* (Montagu), 15 mm (MB, OB); 12a, the same, interior view; 13, *Cardium paucicostatum* Sowerby, 41 mm (IB, MB, OB); 13a, the same, exterior view; 14, *Venus striatula* (da Costa), 23 mm (IB, MB, OB, also in more than 50% of the OC samples); 14a, the same, interior view; 15, *Abra alba* (Wood), 17 mm (MB, OB); 15a, the same, interior view; 16, *Abra nitida* (Müller), 16 mm (IB, MB); 16a, the same, interior view.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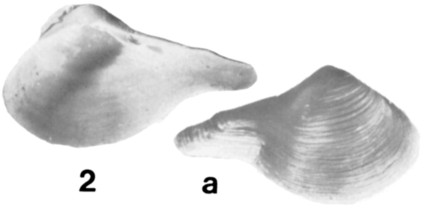
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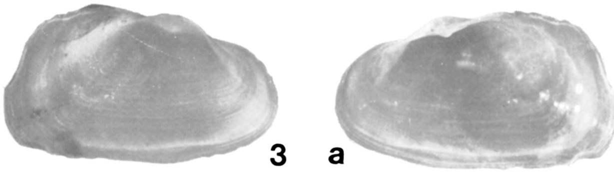
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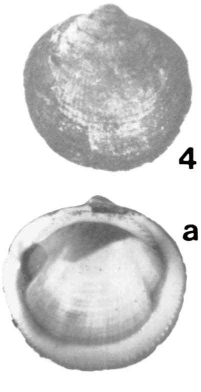
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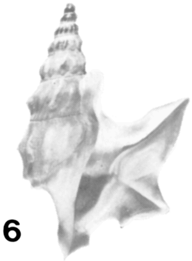
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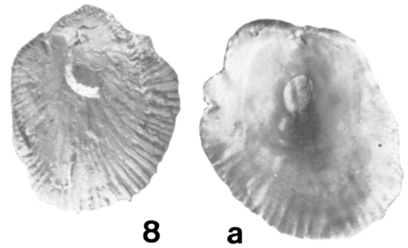
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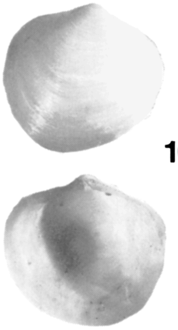
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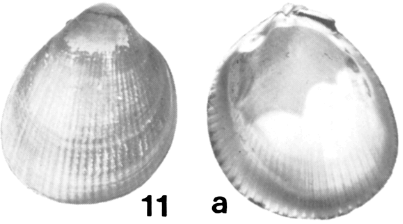
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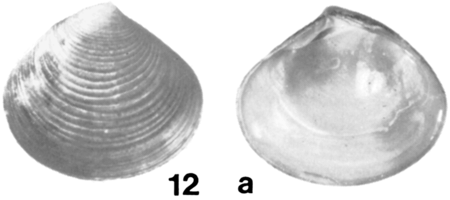
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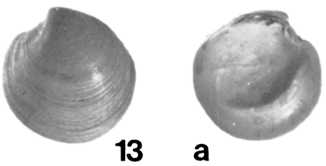
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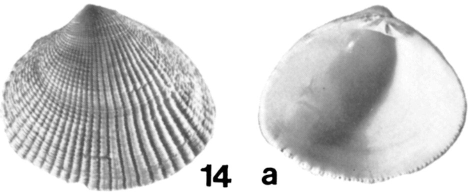
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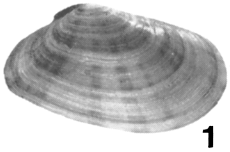
PLATE IV

Fig. 1-3, Mollusca found in more than 50% of the samples from the central bay zone (continued); length given in mm. 1, *Corbula gibba* (Olivi), 13 mm (IB, MB, OB, also in more than 50% of the OC samples); 1a, the same, interior view; 2, *Cuspidaria cuspidata* (Olivi), 16 mm (OB); 2a, the same, exterior view; 3, *Saxicavella jeffreysi* Winckworth, 9 mm (OB): 3a, the same, interior view.

Fig. 4-14, Mollusca found in more than 50% of the samples from the oceanic zone (= the shelf off the Ria de Arosa, 30-85 m depth (the deepest point sampled)); length given in mm. 4, *Glycymeris glycymeris* (Linné), 66 mm; 4a, the same, interior view; 5, *Cantharidus montagui* (Wood), 6 mm; 6, *Aporrhais pespelecani* (Linné), 36 mm; 7, *Nassarius incrassatus* (Ström), 10 mm; 8, *Monica* cf. *squama* (Gmelin), 34 mm; 8a, the same, interior view; 9, *Chlamys tigerina* (Müller), 24 mm; 10, *Diplodonta rotundata* (Montagu), 18 mm; 10a, the same, interior view; 11, *Laevicardium crassum* (Gmelin), 54 mm; 11a, the same, interior view; 12, *Gafrarium minimum* (Montagu), 15 mm; 12a, the same, interior view; 13, *Dosinia lupinus* (Linné), 29 mm; 13a, the same, interior view; 14, *Venus ovata* Pennant, 13 mm; 14a, the same, interior view.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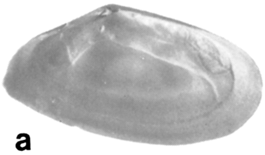
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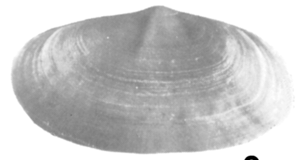
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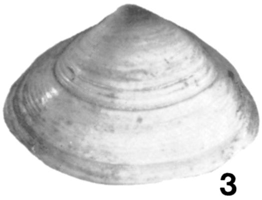
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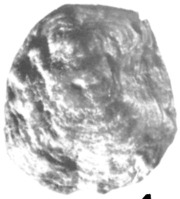
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PLATE V

Fig. 1-5, Mollusca and Brachiopoda found in more than 50% of the samples from the oceanic zone (continued); length given in mm. 1, *Tellina donacina* Linné, 21 mm; 1a, the same, interior view; 2, *Gari tellinella* (Lamarck), 20 mm; 2a, the same, interior view; 3, *Spisula* sp. cf. *elliptica* (Brown), 15 mm; 3a, the same, interior view; 4, *Crania anomala* (Müller), upper valve, exterior, 12 mm; 4a, *Crania anomala* (Müller), upper valve, interior, 11 mm; 5, *Macandrevia cranium* (Müller), 10 mm.

Fig. 6, Shells of *Charonia gyrinoides* (Brocchi), collected alive in the Ria de Arosa, damaged by the boring sponge *Cliona*.

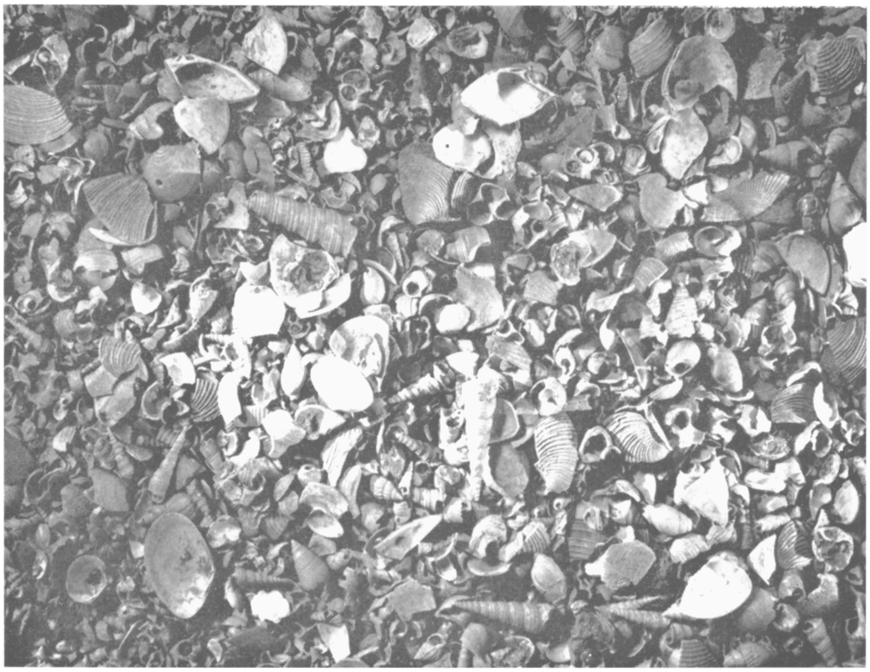

PLATE VI

The coarse fractions of a sample from the outer part of the central bay (sample 1930, upper figure) and of one from the oceanic zone (sample 1775, lower figure), showing the great similarity in the high rate of fragmentation, although sample 1930 comes from a much quieter habitat and shows a strongly different species composition. Fragmentation in both cases is presumably due to predators (Crustacea).