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Intertidal Rocky Shore Communities of the Continental Portuguese Coast: Analysis of Distribution Patterns

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With 11 figures and 4 tables

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Abstract. A general description of rocky shore distribution patterns ("zonation") along the whole Portuguese coast is given to provide the context for comparisons of distribution patterns of mid-shore organisms. In order to test if there was any variation in species distribution and abundance in the upper and lower mid-shore zone (eulittoral) along the entire intertidal Portuguese coast, three main regions were studied (north, centre and south) and nine shores were visited in each region. At each one of the 27 locations, the shore was levelled and a general qualitative description was made, which also aided stratification of subsequent quantitative sampling. An upper zone (littoral fringe) characterised by the presence of encrusting lichens, small littorinid gastropods and cyanobacteria was found on most of the shores along the Portuguese coast. The mid-shore zone (eulittoral) is essentially dominated by barnacles and sometimes mussels. The distribution patterns observed on the lower shore (sub-littoral fringe) showed a distinction between northern shores, where large brown algae are present, and shores located in the central and southern regions, essentially dominated by red algal turf species. Multidimensional analysis and the ANOSIM test have revealed clear differences in the structure of the upper and lower mid-shore zone. Within each level, the northern region was considerably different from the south and central regions. SIMPER analysis revealed the species which contributed to the separation between shore levels and regions. It has also given important information on the geographical decline in abundance of species.

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Problem

The amount of literature concerning distribution patterns of rocky shore organisms is vast. Classical descriptive works include the universal scheme of zonation proposed by Stephenson & Stephenson (1949, 1972), the extensive study of zonation patterns on the British Isles by Lewis (1961, 1964), and the similar approach for the Mediterranean by Pérès & Picard (1964). Simultaneously with the descriptions of patterns of distribution (*e.g.*, Lewis, 1964; Brattström, 1980; Norton, 1985; Russell, 1991) marine ecologists started to investigate the influence of physical and biological factors on marine intertidal communities (*e.g.*, Southward, 1958; Ballantine, 1961; Connell, 1972; Underwood, 1981; McQuaid & Branch, 1984; Hawkins & Hartnoll, 1985). Experimental approaches to understand the functioning of rocky shores encompassed disturbance and succession, competition, grazing, predation and recruitment fluctuations (*e. g.*, Connell, 1961; Paine, 1966; Dayton, 1971; Paine, 1974; Branch, 1976; Menge, 1976; Lubchenco, 1978, 1980; Menge 1978a, 1978b; Lubchenco & Menge, 1978; Underwood, 1978, 1984; Denley & Underwood, 1979; Sousa, 1979, 1984; Menge & Lubchenco, 1981; Hawkins & Hartnoll, 1982, 1983; Dethier, 1984; Farrell, 1991; Menge, 1991; Benedetti-Cecchi & Cinelli, 1993; Benedetti-Cecchi *et al.*, 1996; Jenkins *et al.*, 1999a, 1999b). An extensive literature has recently been synthesised by Paine (1994), Little & Kitching (1996) and Raffaelli & Hawkins (1996).

Much less attention has been given to rocky shores of the Portuguese coast. Early studies conducted in the early 20^th^ century were mainly devoted to the biology of certain taxonomic groups (*e. g.*, Cúmano, 1939; Nobre, 1940; Palminha, 1951). To date most of the published information has concerned a specific biological group or the communities of a restricted area of the coast (*e. g.*, Almaça, 1960; Monteiro Marques *et al.*, 1982; Santos & Melo, 1984; Guerra & Gaudêncio, 1986; Lopes, 1989; Marques *et al.*, 1993; Sacarrão, 1994; Cruz, 1999), although Saldanha (1974) has made an important contribution for the study of littoral communities of the entire Arrábida coast and Santos (1994a) has studied in detail the intertidal communities of the northern Portuguese coast. A few broadscale studies have been made on the geographical distribution patterns of several species, including the work of Fischer-Piette (1957, 1958, 1963) and Ardré (1970). More recently, however, the recognition that the study of distribution patterns and the development of experimental ecology may play a crucial role in understanding the organisation of rocky intertidal communities of the Portuguese coast has promoted of several national and European research projects.

The present study aims to describe vertical distribution patterns along the Portuguese coast and to compare quantitatively the patterns of community composition in the mid-shore zone. The qualitative descriptive study provides a useful framework of reference in terms of major zones, dominant organisms at different levels on the shore, and geographical changes of fauna; such an attempt has never been done for the entire Portuguese coast. Such a large scale study is particularly important considering that Portugal is the southern geographical limit for many boreal species and the northern or western limit of subtropical and Mediterranean species (Fischer-Piette, 1957, 1958, 1963; Ardré, 1970; Saldanha, 1974). Hence, it forms a baseline for measuring the response of species distribution to global climatic change. There is also the necessity to provide background studies for management and conservation programmes on intertidal rocky shores (see Underwood, 1991). Intertidal resources are heavily exploited, and with increasing pollution in coastal areas, in particular frequent oil spills, major impacts have been recorded on the rocky shore ecosystem (see Southward & Southward, 1978; Crowe *et al.*, 2000). Additionally, this study provides an observational basis for current and future experimental work. The quantitative comparison of distribution patterns on the lower and upper mid-shore zone along the Portuguese coast will give an insight into the structure of intertidal communities. Despite the profusion of studies in intertidal ecology, few quantitative studies have analysed large-scale patterns of distribution. No such attempt has ever been made for the whole Portuguese coast.

Our specific aims were:

(1) To qualitatively describe the vertical patterns of distribution along the entire Portuguese coast;

(2) Based on the stratification derived from (1), concentrate on the mid-shore region using quantitative multivariate methods to: (a) compare the composition and structure of the upper and lower levels of the mid-shore communities; (b) test for differences between the northern, central and southern regions of Portugal;

(3) For the dominant mid-shore grazing limpets, test for differences in abundance with level and spatial scales (shores and regions).

Material and Methods

1. Study sites

The present study was carried out on the Portuguese continental coast, which extends for more than 800 km. In order to test for any variation in species distribution and abundance along the intertidal rocky shores of the Portuguese coast a total of 27 shores were sampled (Fig. 1).

Santos (1994b) has synthesised relevant aspects of the coastal oceanography of continental Portugal. Frequent upwelling of cold water occurs in the summer. Sea surface temperature on the western Portuguese coast shows marked seasonality, varying between 13 and 15 °C during winter, and reaching 20 °C or more during summer. Temperatures on the south coast are in general slightly higher (approx. 1–1.5 °C) due to the influence of warmer currents. Three directional wave stations installed along the Portuguese coast (Costa, 1995) showed that the mean wave conditions do not differ much along the west coast, which is exposed to the prevailing northwest oceanic swell. Higher swell occurs during winter, reaching values over 5 m on the west coast and over 3 m on the south coast. On the south coast the wave conditions are less severe because it is not exposed to the swell generated in the North Atlantic. The most frequent storms are from WNW along the west coast and from SW along the south coast (Costa, 1995). The tidal regime in the Portuguese coast is semidiurnal. The extreme tidal range of spring tides is approximately of 3.5 to 4 m, and spring low tides occur in the morning and in the evenings.

The morphology of the Portuguese coast is marked by the presence of several capes along the coast, particularly south of Nazaré, and several larger rivers on the north and central coast (Santos, 1994b). Three main rocky shore zones (north, centre and south), separated by wide-ranging soft sediment areas, can be identified in Portugal. Rock types that form intertidal substrates in each of these zones vary (Carvalho, 1992). In the northern region, from Moledo do Minho until Aguda, rocky shores are typically granite, except Vila Chã, where rock platforms consist of shales. The central zone is composed of limestone and sandy limestone with smooth to irregular surfaces. Shales make up most of the bedrock on the south west coast and part of the south coast, being replaced by sandy limestone towards the east of the south coast. The last rocky shore ledges on the south coast are located in Olhos d'Água. Sampling stations were restricted to open bedrock, with areas near sandy beaches and boulder shores being avoided whenever possible.

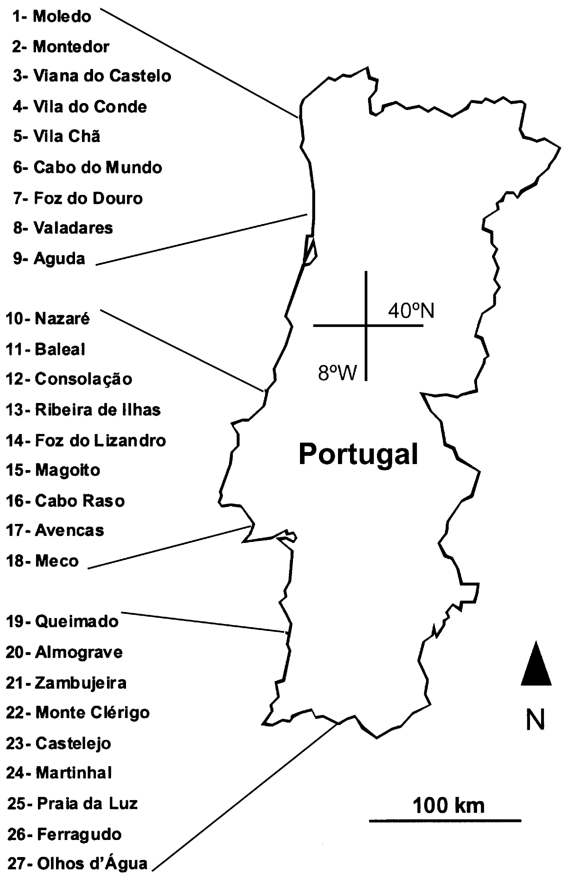

Fig. 1. Study sites.

2. Experimental design

Due to logistic constraints, each of the 27 shores was only visited once during the spring of 1997. The coast was divided in three main regions: north, centre and south. Nine shores were sampled in each of these main regions. Previous observations on the rock platform indicated that different organism assemblages were distributed at different levels on the shore. These could be broadly classified according to zonation schemes as a lower algal bed zone (sub-littoral fringe), an animal-dominated eulittoral zone and a littoral fringe (after Lewis, 1964). These three main zones were qualitatively described in the present study. The lower algal zone has a relatively high number of species with respect to the time available for sampling during low tide. Conversely, the diversity in the littoral fringe is considerably reduced compared with that in lower levels on the shore. Therefore, it was decided to concentrate the quantitative sampling effort on the mid-shore zone. Thus, the factor "level on the shore" included the lower mid-shore zone where mussels and encrusting algae occur, and the upper mid-shore zone mainly dominated by barnacles. Five replicate quadrats of 50 × 50 cm were sampled in each level.

3. Sampling methods

Qualitative description. To assess the major distribution patterns in each of the 27 locations the shore was levelled and qualitatively sampled along each transect. The main biotic assemblages and zones were identified, their extent measured, and the upper and lower limit of each zone measured in relation to chart datum using a level. A simple device based on water in a tube with both ends tied to a ruler was used. The differences between the height of the water in the rulers correspond to the vertical difference in the height of the ground. Height measurements were taken along the shore transects, at successive intervals, from the water line at the time of low water. Positions in relation to chart datum were later calculated by adding of the height between low water and chart datum.

Quantitative sampling. Non-destructive methods (point intersection) (see Hawkins & Jones, 1992, for a review) were used within the lower and upper mid-shore area in moderately exposed shores along the Portuguese coast. Five replicate plots were counted in each of the two mid-shore areas using a quadrat of 50×50 cm with 49 intersection points. The percentage cover of algae and sessile animals was estimated and the total numbers of limpets and other mobile animal species were counted. The species present inside the plot but which did not match any intersection point were recorded. Whenever large algae were present, sampling was stratified in different layers and canopy cover was distinguished from substrate cover. The quadrats were photo-documented with a Nikon F70 (35–80 mm lens). Sampling was stratified by considering only open, freely draining rock.

4. Study organisms

The identification of organisms was done *in situ* whenever possible. In case of taxonomic uncertainty the specimen was collected and identified in the laboratory. Considering the high diversity of the intertidal communities, sampling focussed on conspicuous species that were either common in terms of percentage cover or density, or were important in a biogeographic context for the Portuguese coast. Note that the scale of observation and studied organisms was also conditioned by the use of non-destructive methods. The adopted methodology entailed sampling species whose identification and quantification in quadrats was reliable. Very small organisms (*e. g.*, amphipods) and/or highly motile species (*e. g.*, crabs) were not quantified. Species whose differentiation in the field was difficult, such as certain algal epiphytes (*e. g.*, species of the genus *Ceramium* or *Polysiphonia*), were identified and quantified only to the genus. The term "lithothamnia" was used to designate calcareous crust species, which are difficult to differentiate in the field (see Hawkins & Jones, 1992).

5. Data analyses

Vertical distribution patterns were depicted by diagrams for each location. The height above chart datum was used as the vertical scale. This enabled description of the main zonation patterns on a broad geographic scale.

Multidimensional scaling was used to analyse quantitative data on species abundance and distribution. Due to the high total number of quadrats, the 5 replicate quadrats sampled in each shore level were averaged prior to multidimensional analysis. A matrix of similarities between each pair of samples was calculated using the Bray-Curtis similarity coefficient (Bray & Curtis, 1957). This coefficient was adopted since it is not affected by joint absences and is sufficiently robust for marine data (Field *et al.*, 1982). Percentage cover values and abundances were used simultaneously in the same matrix. According to Anderson & Underwood (1997), there is no mathematical reason for not calculating similarity coefficients between samples of mixed data (*i. e.* data made up of abundances, percentage cover and presence/absence information for different variables), provided that the interpretation of the results takes into account the potential difference in contribution or weight of certain variables because of their scale (Anderson & Underwood, 1997). In this study, the fourth-root transformation of data was used in order to preserve information concerning relative abundance or percentage cover of species across samples, but also to minimise differences in scale (and therefore relative weight) among variables (Clarke, 1993; Anderson & Underwood, 1997). Non-metric multidimensional scaling was used as an ordination technique for graphical representation of community relationships (Clarke, 1993). Although it uses a complex algorithm this method has several advantages. Some of its strengths are its dependence only on a biologically meaningful view of the data, since it works on the sample dissimilarity matrix and not on the original data array, and its distance-preserving properties by constructing a configuration where distances between points have the same rank order as the correspondent dissimilarity between samples (Clarke, 1993). Hierarchical agglomerative clustering was performed on the same similarity matrix using group average linking to cross-check the results obtained with the MDS. This procedure is particularly advised for stress values close to 0.2 (Clarke, 1993). The one-way ANOSIM permutation test was used to assess the significant differences between pre-defined groups of sample sites in the multidimensional analyses (Clarke, 1993). Two different null hypotheses were tested: (i) there is no difference between the two studied shore levels, (ii) there are no differences between regions. The second hypothesis was tested separately for the lower and upper mid-shore. The Similarities Percentages procedure (SIMPER) (Clarke, 1993) of fourth-root transformed macrobenthonic abundances was used to determine the contributions from individual species to the Bray-Curtis dissimilarities between levels and regions. Graphical descriptors in the form of K-dominance curves were plotted for species abundance for each level and region.

Univariate analyses of community structure included the distribution of limpet species. Analyses of variance on limpet density along the Portuguese coast were done using a three-way mixed model. The design included three factors: factor "level on the shore" (orthogonal, fixed with two levels), factor "regions" (orthogonal, fixed with three levels), factor "shore" (nested in regions, random with 9 levels). The analysis tested the null hypotheses of no differences in *Patella* species density in the two levels and any of the considered spatial scales.

All multidimensional analyses and calculation of biodiversity indices were done using the PRIMER for windows v5.0 computer program (Plymouth Marine Laboratory, UK). Analyses of variance, tests of homogeneity, and SNK (Student-Newman-Keuls*) a posteriori* comparison tests were done using GMAV5 for Windows Statistical Software (Institute of Marine Ecology, Sydney, Australia).

Results

1. Qualitative description

Vertical distribution patterns were examined on the rocky shores of the north, centre and south coast of Portugal. An example of a zonation diagram of each region is represented in Fig. 2 (for more details see Santos, 1994a; Boaventura, 2000). Three major zones were readily discernible based on the conspicuous species, although some species occur in more than one and the boundaries can be blurred in places (cf. Lewis, 1964). The lichen *Verrucaria maura* and the gastropod *Melaraphe neritoides* are the most common forms in the uppermost zone of the shore, the littoral fringe. The extension and position of this assemblage in relation to chart datum varies with exposure to wave action, being broader and reaching higher levels – above extreme high water of spring tides (EHWS) – on more exposed shores (*e. g.*, Moledo, Montedor, Cabo Raso). Despite the fairly constant species composition of the littoral fringe some variations occurred. The annual *Porphyra umbilicalis* was observed in the lower part of the littoral fringe on some shores from the northern region (*e. g.*, Montedor, Viana do Castelo, Vila do Conde). Further south, and/or in less exposed shores (*e. g.*, Avencas, Meco), *Verrucaria maura* may be absent. Under these circumstances, the grey upper zone is generally composed of cyanobacteria and *Melaraphe neritoides*. This zone can be dominated by ephemeral green algae such as *Enteromorpha* sp. (*e. g.*, Avencas, Monte Clérigo), particularly if it is close to freshwater runoff from the cliff, or if the shore topography is likely to retain water for a longer period. In this situation other gastropod species like the pulmonate *Siphonaria pectinata* were observed here. *Pelvetia canaliculata* straddles the boundary with the eulittoral on northern shores.

The eulittoral zone is dominated by a variety of animal and algal species. A high percentage of space is occupied by sessile filter feeders such as barnacles and mussels. The barnacle *Chthamalus* spp. (mainly *Chthamalus montagui*) dominates on the upper mid-shore zone starting immediately below the littoral fringe. The extension of the zone dominated by *Chthamalus* spp. varied from shore to shore and its limits were sometimes hard to define since the barnacles may be sparse on both their upper and lower limit of distribution and also overlap with other organisms (*e. g.*, mussels), forming mosaic patterns. Numerous species can also cover the barnacles, usually in patches. The lichen *Lichina pygmaea* often covers the barnacles in the upper mid-

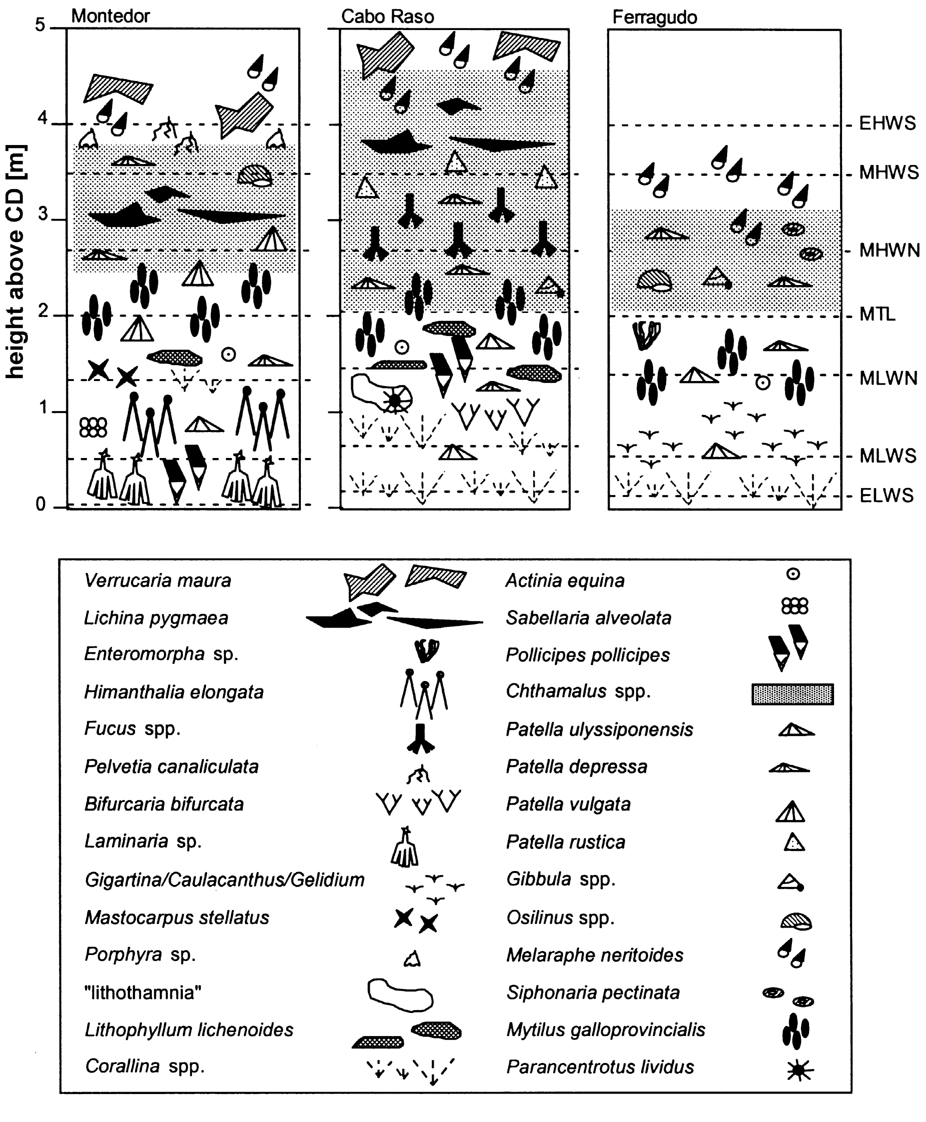

Fig. 2. Example of zonation diagrams of one shore from the north (Montedor), centre (Cabo Raso) and south (Ferragudo).

shore zone above mean high water of neap tides (MHWN). Unlike *Pelvetia canaliculata* which was confined to the northern region, this lichen was found along the entire coast. A band of *Fucus spiralis* was also observed covering the middle of the barnacle zone. Although present in the north and south, this algae was notably abundant on some shores of the central region between mean high water of spring tides (MHWS) and mean tide level (MTL). Small areas of rock within the barnacle zone can also be covered with encrusting algae species such as *Ralfsia* sp., *Petrocelis* sp. and *Hildenbrandia rubra*.

Mussels occur in the lower mid-shore zone of more exposed shores. In the northern region *Mytilus galloprovincialis* can extend up to MHWN, whilst in the central and southern regions intertidal mussels generally occur below MTL. *Corallina* spp., *Caulacanthus ustulatus, Mastocarpus stellatus*, among other algal species, can occur together with mussels as well as certain red algal crusts like *Lithophyllum lichenoides* or "lithothamnia". Throughout the eulittoral zone many gastropod species are present and several of these species are important in a biogeographic context. *Littorina saxatilis* occurs amongst the barnacles in the upper mid-shore zone. This species was most abundant on the northern shores and becomes occasional or rare further south. *Osilinus* spp. (*O. lineatus* and *O. collubrina*) and *Gibbula* spp. (mostly *G. umbilicalis*) are common on the whole mid-shore level whereas *Nucella lapillus* occurs lower on the shore amongst the mussel beds. The latter progressively decreases in abundance from north to south. Amongst grazing limpets all four species – *Patella vulgata, Patella rustica, Patella depressa* and *Patella ulyssiponensis* – inhabit the eulittoral zone along the Portuguese coast. *Patella ulyssiponensis* is more abundant in the sublittoral fringe but can also occur in the lower mid-shore zone together with the mussels and *Lithophyllum lichenoides* patches. *Patella rustica* is a southern species that was absent from the northern shores. In the central and southern regions it is more abundant in the upper barnacle zone. In contrast, *Patella vulgata* is a northern species that is less abundant in the centre and south. Finally, *Patella depressa* is widely distributed and abundant along the entire coast. It occurs, like *Patella vulgata*, throughout the eulittoral zone. The pulmonate gastropod *Siphonaria pectinata* was more abundant towards the south.

The sublittoral fringe is characterised by a profusion of macroalgae which are only occasionally not submerged. This assemblage can extend up to mean low water of neap tides (MLWN) and corresponds to the zone of the shore with a highest number of species. The sublittoral fringe of northern rocky shores differs considerably from that of the centre and south regions. Most northern shores are distinguished by the presence of large brown algae (*e. g., Laminaria* spp., *Saccorhiza polyschides, Himanthalia elongata*), which generally occur below mean low water of spring tides (MLWS). The red algae *Mastocarpus stellatus* was also more abundant here. The sublittoral fringe of the centre and south regions is typically dominated by a red algal turf composed of *Corallina* spp., *Plocamium cartilagineum, Caulacanthus ustulatus, Gelidium* spp., *Laurencia pinnatifida*, among others. On more exposed shores *Corallina* spp. dominates over the other algal species and, together with red encrusting algae, forms a pink band on the low-shore. On more sheltered shores non-calcareous turf-forming algae appear in higher proportions. In some central shores (*e. g.*, Nazaré, Ribeira de Ilhas) the algae *Bifurcaria bifurcata* can cover extensive areas in the upper sublittoral fringe. The lower eulittoral and sublittoral zone of Martinhal exhibited a different pattern, being dominated essentially by ephemeral green algae. Abundant animal species in the sublittoral fringe are, for example, *Patella ulyssiponensis, Paracentrotus lividus* and *Sabellaria alveota*. *Pollicipes pollicipes* occurs throughout the Portuguese coast, particularly on exposed shores.

2. Comparative analyses of distribution patterns in the lower and upper mid-shore zone

The MDS configuration that resulted from the abundance matrix shows a separation of levels (Fig. 3). Samples that correspond to the average of replicate plots taken on the upper mid-shore are located in the left side of the figure whereas those taken in the lower mid-shore zone are positioned towards the right. Exceptions to this are the low mid-shore zone of Zambujeira and Baleal, which appear on the left side of the figure. The low mid-shore level of Martinhal in the south, which appears at the top of the figure, seems to differ considerably from all the other samples (Fig. 3); this was due to an extremely high abundance and dominance of ephemeral green algae at this level. The distinction between levels was confirmed by the ANOSIM test. There was a significant difference, r = 0.53 (P = 0.1 %), between the low mid-shore zone where mussels occur and the upper zone dominated by barnacles.

Although the lowest stress value of 0.13 still indicated a potentially useful 2-dimensional picture, these results were cross-checked by cluster analysis (Fig. 4). Hierarchical representation showed a clear separation of lower and upper mid-shore levels. The lower mid-shore samples most similar to the upper mid-shore zone were those from Baleal, Zambujeira, Praia da Luz and Almograve shores. These results confirm the trends shown in the MDS (Fig. 3). The cluster also confirms the separation of the Martinhal lower level from all the other shores.

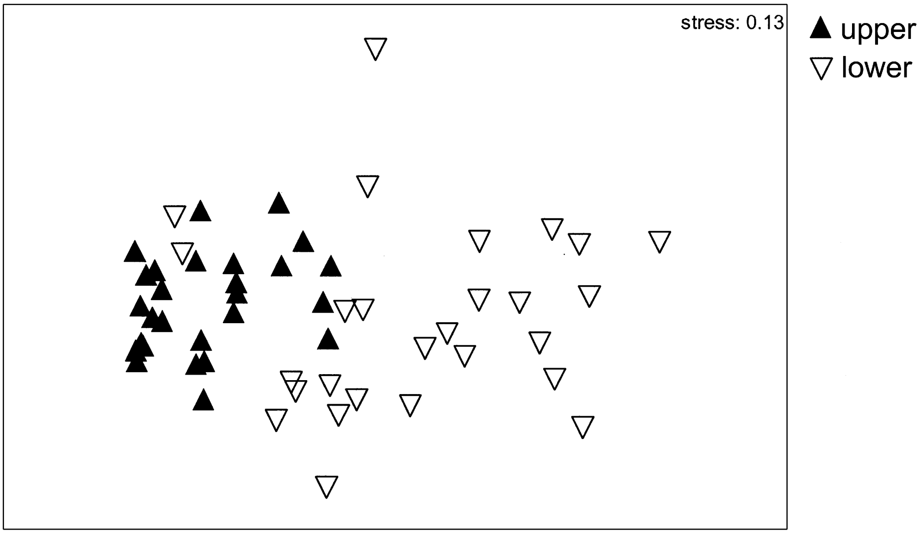

Fig. 3. MDS ordination of Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) for the factor level (upper and lower mid-shore).

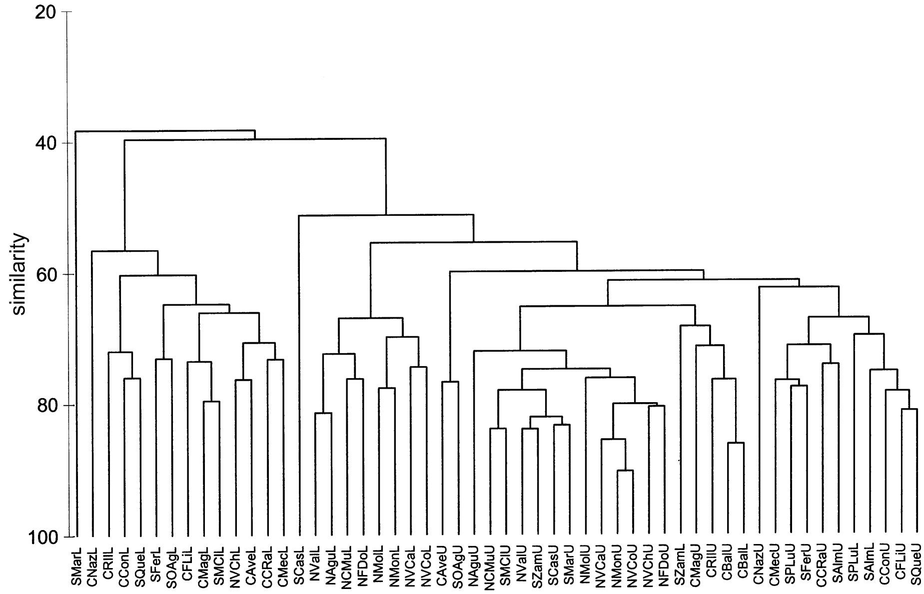

Fig. 4. Dendrogram from Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) with group average linking (N. . . : north; C. . . : centre; S. . . . : south; . . .U: upper; . . .L: lower). Shore names are abbreviated (cf. Fig. 1).

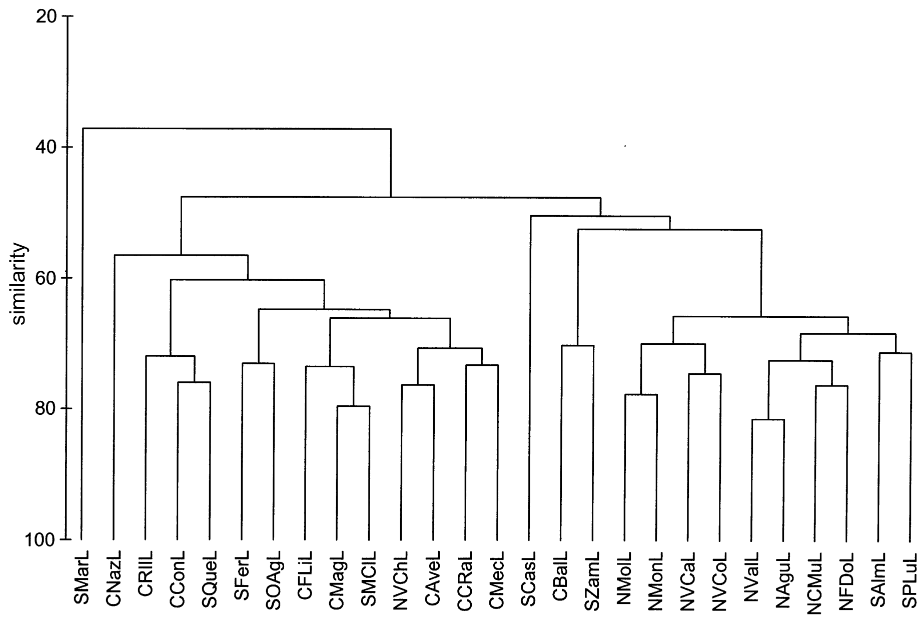

Fig. 5. Dendrogram from Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) with group average linking for the lower mid-shore level (N. . . : north; C. . . : centre; S. . . . : south; . . .U: upper; . . .L: lower). Shore names are abbreviated (cf. Fig. 1).

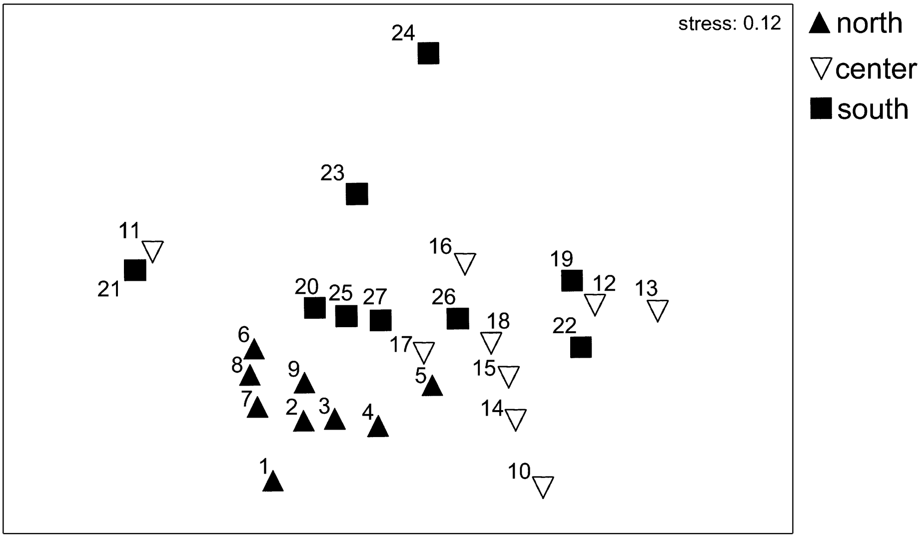

Fig. 6. MDS ordination of Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) for the lower mid-shore level. Different regions are represented by symbols and shore numbers are indicated (cf. Fig. 1).

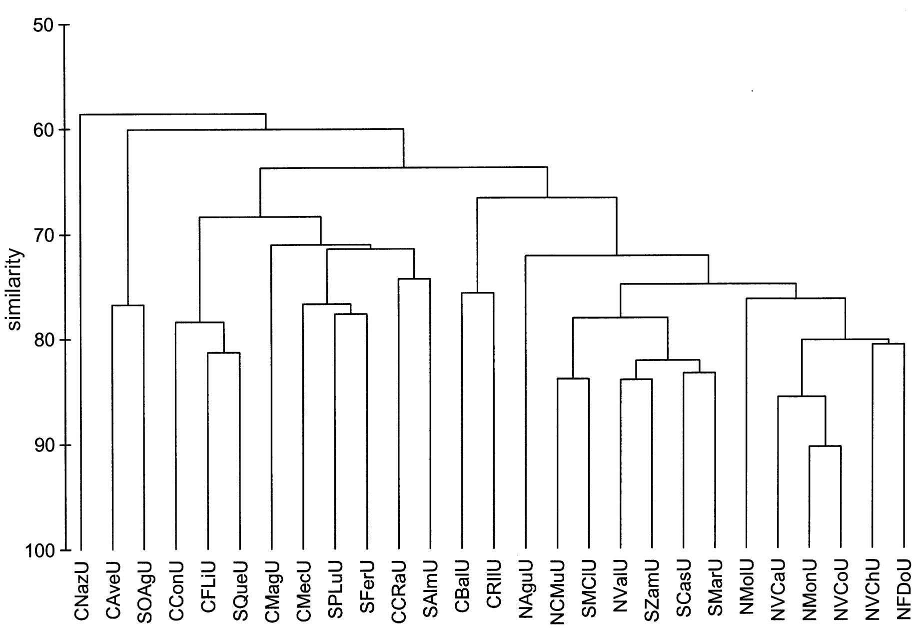

Fig. 7. Dendrogram from Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) with group average linking for the upper mid-shore level (N. . . : north; C. . . : centre; S. . . . : south; . . .U: upper; . . .L: lower). Shore names are abbreviated (cf. Fig. 1).

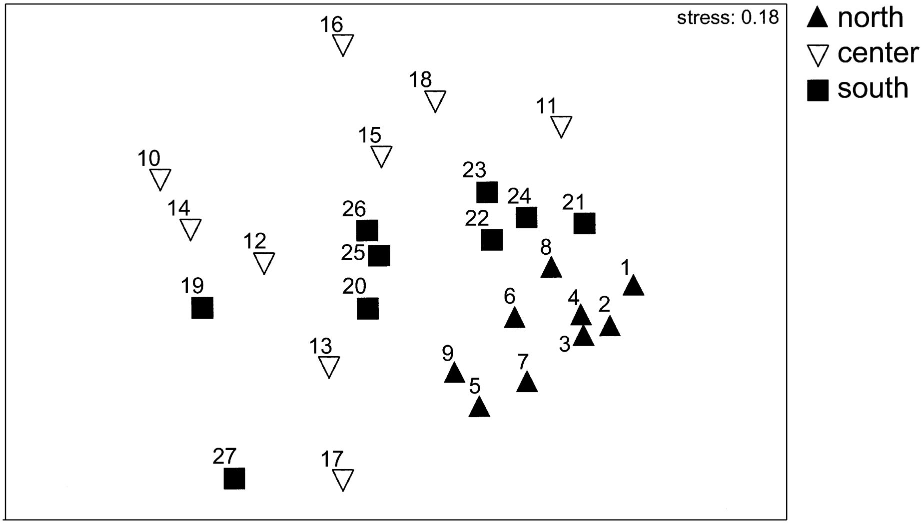

Fig. 8. MDS ordination of Bray-Curtis similarity matrix of species abundance data (fourth-root transformed) for the upper mid-shore level. Different regions are represented by symbols and shore numbers are indicated (cf. Fig. 1).

Given the differences between levels and, since the MDS algorithm places most weight on the large distances, possible geographical variations in species communities were analysed separately for each level.

The cluster obtained for the low mid-shore zone samples separated most of the northern shores from those located in the centre and south (Fig. 5). The MDS configuration, with a stress value of 0.12, showed the same trends (Fig. 6). The MDS reflects also a higher similarity and less variability for the northern stations. ANOSIM analysis confirmed significant differences between the factor regions ($r = 0.334$, $P = 0.1$ %). Pair-wise tests revealed significant differences between north and centre ($r = 0.566$, $P = 0.2$ %), between north and south ($r = 0.377$, $P = 0.2$ %), but no significant differences between centre and south regions ($r = 0.108$, $P = 6.6$ %).

Geographic differences between regions for the upper mid-shore zone also separated the north from the centre and south in the cluster (Fig. 7) and in the MDS with a stress value of 0.18 (Fig. 8). The ANOSIM test revealed significant differences for the region global test ($r = 0.303$, $P = 0.1$ %). Results from pair-wise tests were consistent with those from the lower level and again revealed significant differences between north and centre ($r = 0.61$, $P = 0.2$ %), north and south ($r = 0.306$, $P = 0.2$ %), and no significant differences between centre and south ($r = 0.025$, $P = 57.8$ %).

SIMPER analyses of the transformed abundance data allow the examination of the species which contribute to the dissimilarity between levels and regions (Tables 1 and 2). The upper mid-shore zone is separated from the lower mid-shore zone by a general reduction of red algae species (*e. g., Corallina* spp., “lithothamnia”, *Caulacanthus ustulatus* and *Gelidium* spp.) and the presence of relatively high numbers of a few species including *Chthamalus* spp., *Patella depressa, Siphonaria pectinata* and *Melaraphe*

Table 1. Summary of similarity terms (SIMPER) analysis. Differences (< and >) in average abundances or percentage cover per quadrat of species contributing to dissimilarities between upper and lower mid-shore level (after fourth-root transformation). A cut-off of a cumulative % dissimilarity of 80 % was applied.

species	upper		lower
Mytilus galloprovincialis	1.59	<	39.46
Chthamalus spp.	76.98	>	14.15
Patella ulyssiponensis	0.44	<	12.01
Gibbula spp.	5.50	<	10.37
Corallina spp.	0.04	<	11.13
Patella depressa	47.87	>	22.62
ephemeral algae	0.23	<	5.36
Sabellaria alveolata	0.32	<	2.39
“lithothamnia”	0.20	<	4.00
Actinia sp.	0.13	<	2.95
Siphonaria pectinata	1.82	>	0.57
Patella vulgata	0.80	<	1.56
Melaraphe neritoides	0.67	>	0.21
Ralfsia sp.	0.79	<	0.99
Osilinus spp.	1.04	>	1.00
Littorina saxatilis	1.84	>	0.33
Caulacanthus ustulatus	0.03	<	1.62
Gelidium spp.	0.15	<	0.41
Lithophyllum lichenoides	0.10	<	1.56
Nucella lapillus	0.01	<	1.33

neritoides. Animal species important in characterising lower mid-shore communities include *Mytilus galloprovincialis, Patella ulyssiponensis* and *Sabellaria alveolata* (Table 1).

The northern region is separated from the centre and south regions by a higher average abundance of *Mytilus galloprovincialis, Patella vulgata* and *Littorina saxatilis*. Conversely, in the centre and south regions, there is a higher average abundance of *Corallina* spp., *Patella ulyssiponensis* and *Siphonaria pectinata* (Table 2). Some species showed an abundance gradient along the coast (Table 2) that supported the observations made for zonation patterns. Examples include *Mytilus galloprovincialis* and *Nucella lapillus*, which showed a progressive decrease in average abundance from north to south. The opposite trend, with higher average abundances decreasing from south to north, also occurred, for example in *Siphonaria pectinata*. Discontinuities in average abundance along the coast were also registered. *Patella ulyssiponensis* and *Corallina* spp. have considerably higher abundances in the centre than in either the north or south region. In contrast, *Patella vulgata* is less abundant in the central region.

The K-dominance curves on species abundance for the two studied levels showed that the dominance was higher in the upper mid-shore level (Fig. 9a). Differences in cumulative dominance among regions were not so strong (Fig. 9b).

Table 2. Summary of similarity terms (SIMPER) analysis. Differences (< and >) in average abundances or percentage cover per quadrat of species contributing to dissimilarities between regions (after fourth-root transformation). A cut-off of a cumulative % dissimilarity of 80 % was applied.

species	north		centre		south
Mytilus galloprovincialis	32.45	>	15.57	>	13.56
Patella vulgata	3.34	>	0.00	<	0.19
Gibbula spp.	10.0	>	9.29	>	4.51
Patella ulyssiponensis	2.69	<	11.71	>	4.27
Chthamalus spp.	47.28	>	42.14	<	47.27
Corallina spp.	0.38	<	11.50	>	4.88
Littorina saxatilis	3.07	>	0.04	<	0.14
"lithothamnia"	0.33	<	3.69	>	2.29
Patella depressa	36.48	<	39.51	>	29.76
Actinia sp.	1.19	<	2.63	>	0.80
Sabellaria alveolata	0.32	<	3.08	>	0.66
Osilinus spp.	1.20	>	0.67	<	1.19
Ralfsia sp.	0.43	<	1.04	<	1.19
Siphonaria pectinata	0.00	<	1.28	<	2.31
Melaraphe neritoides	0.54	>	0.52	>	0.25
Fucus spiralis	0.02	<	1.05	>	0.13
ephemeral algae	0.17	<	0.66	<	7.54
Caulacanthus ustulatus	0.00	<	2.20	>	0.27
Nucella lapillus	1.42	>	0.58	>	0.01
Lithophyllum lichenoides	0.06	<	1.93	>	0.50
Gelidium spp.	0.05	<	0.25	<	0.54
Dictyota dichotoma			1.22	>	0.29

The distribution and abundance of mid-shore grazing limpets were compared in particular for *Patella depressa* and *Patella vulgata*. Note that *Patella ulyssiponensis* and *Patella rustica* dominate the lower algal zone and the high shore levels respectively, and these species were not analysed formally.

Patella depressa was widely distributed and relatively abundant in the mid-shore throughout the Portuguese coast (Fig. 10). However, a significant interaction between levels and shores was detected, indicating that the abundance of this limpet in the two zones can vary depending on the shores (Table 3). No significant differences between levels were detected in the northern region, except for Cabo do Mundo, where *Patella depressa* was more abundant in the lower versus upper mid-shore zone (SNK test, SE = 6.91; Fig. 10). In contrast, this limpet was more abundant in the upper mid-shore zone at most shores in the central region. No significant differences in abundance between levels were detected on three southern shores (Zambujeira, Martinhal and Olhos d'Água); the limpet was more abundant in the lower zone only at Almograve, and commoner in the upper zone for the remaining shores.

Patella vulgata was clearly more abundant in the north, both in the upper and lower mid-shore zone (Table 4, Fig. 11). No significant differences between levels were obtained in the centre and south region (SNK test, SE = 0.44, $P > 0.05$; Fig 11). In the north, however, where this species occurs in higher densities, *Patella vulgata* was more abundant in the lower mid-shore level (SNK test, SE = 0.44, $P < 0.01$;

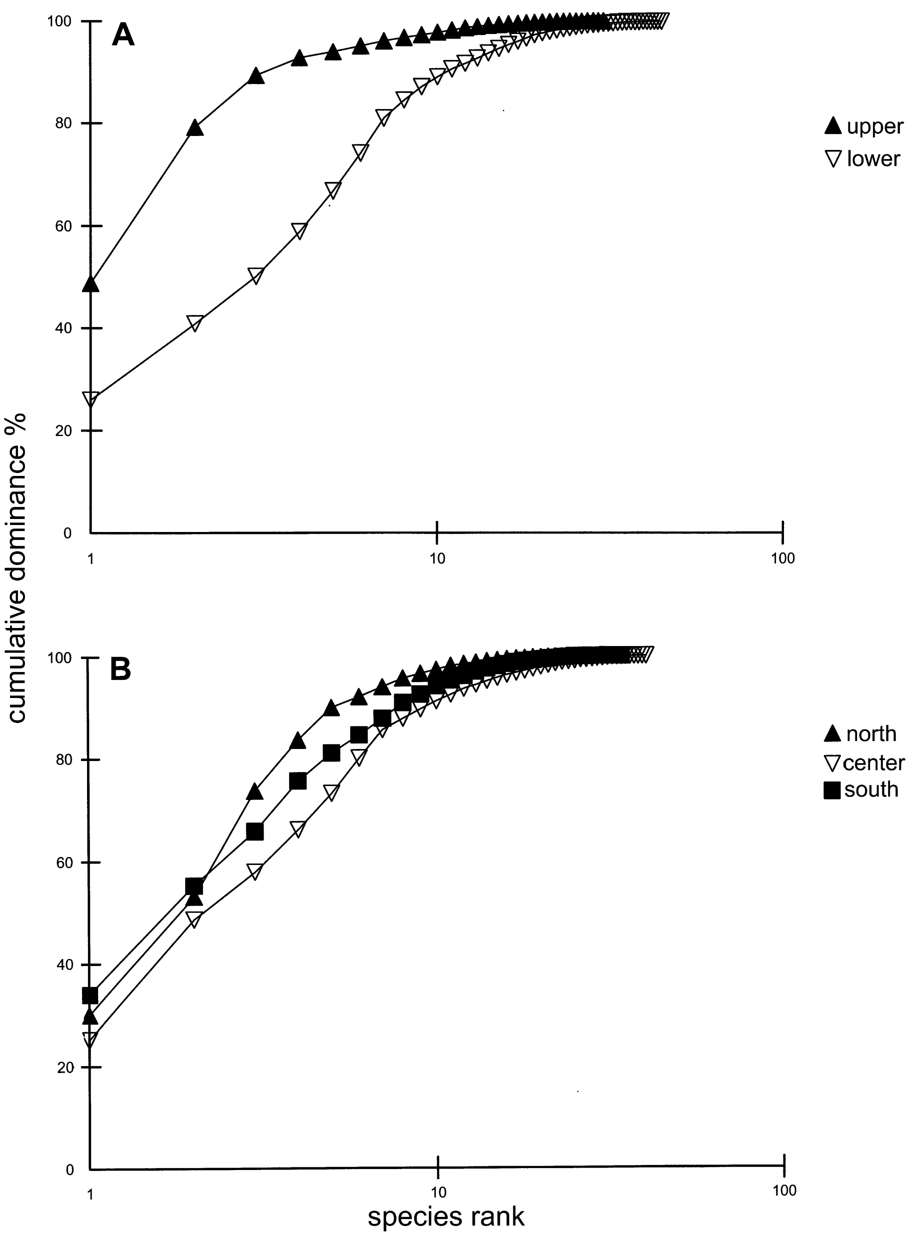

Fig. 9. Cumulative dominance for levels (A) and regions (B).

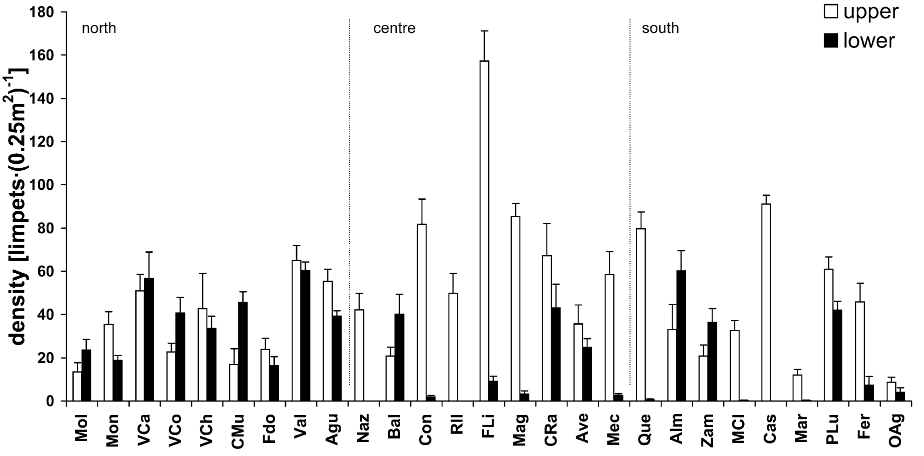

Fig. 10. Mean number of limpets (± SE) of the species *Patella depressa* in each shore (upper and lower mid-shore levels). Shore names are abbreviated (cf. Fig. 1).

Table 3. ANOVA on the number of limpets of the species *Patella depressa*. ns = not significant, *: P < 0.05, **: P < 0.01,***: P < 0.001.

source of variation	df	MS	F
level = Le	1	451 632.20	13.08 **
region = Re	2	2 534.21	0.84 ns
shores (regions) = Sh (Re)	24	3 009.80	12.60 ***
Le × Re	2	16 187.34	4.69 *
Le × Sh (Re)	24	3 452.33	14.45 ***
res.	216	238.94	
Cochran's test		C = 0.10 ns	

Table 4. ANOVA on the number of limpets of the species *Patella vulgata*. ns = not significant, *: P < 0.05, **: P < 0.01,***: P < 0.001.

source of variation	df	MS	F
level = Le	1	38.53	4.40 *
region = Re	2	317.68	7.96 **
shores (regions) = Sh (Re)	24	39.92	4.88 ***
Le × Re	2	35.23	4.02 *
Le × Sh (Re)	24	8.76	1.07 ns
res.	216	8.19	
Cochran's test		C = 0.75,	P < 0.01

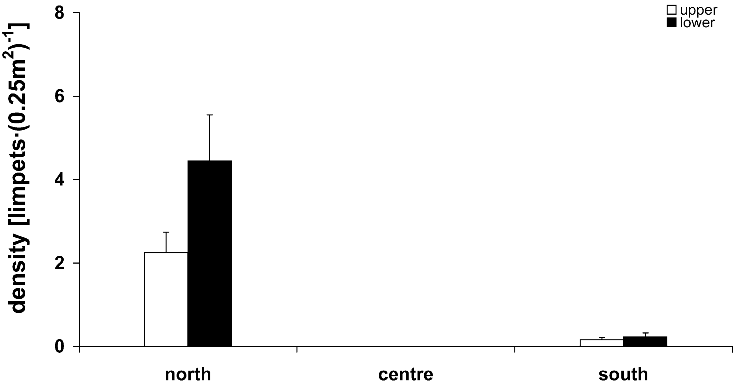

Fig. 11. Mean number of limpets (± SE) of the species *Patella vulgata* in each region (upper and lower mid-shore levels).

Fig. 11). Note that the variances were not homogeneous and that even transformation of the data did not solve this problem. The results presented correspond to the original (non-transformed data) and interpretation of significant results must be made with caution.

Discussion

1. Vertical distribution patterns

The present study has provided qualitative and quantitative information on distribution patterns of intertidal marine organisms along the rocky shores of the continental Portuguese coast. A comprehensive study of zonation patterns along the whole coast and a systematic comparison of organisms abundances along a vertical and horizontal gradient has to date been missing in Portugal. Some constraints were found and much remains to be done. For instance, the quantitative approach was only applied to the upper and lower mid-shore zone, and it was not possible to analyse seasonal variation. These aspects will soon be complemented with the results from a national research project. Nonetheless, the information obtained with the present study has clarified several questions related to the vertical and horizontal distribution of organisms on intertidal rocky shores.

The existence of a black littoral fringe characterised by the presence of encrusting lichens, small littorinid gastropods and cyanobacteria may be considered as a worldwide feature of the upper zone of intertidal rocky shores (Stephenson & Stephenson, 1972; Raffaelli & Hawkins, 1996). This pattern was also found on most of the Portuguese shores. Some variations, however, did occur. These included the absence of the lichen *Verrucaria maura* and presence of cyanobacteria, which conferred a grey colour to the rock, or the presence of ephemeral green algae. The abundance of *Melaraphe neritoides* was sometimes much reduced.

The eulittoral zone of Portuguese rocky shores is dominated by barnacles and sometimes mussels. Mussels occur in the lower mid-shore zone of more exposed shores. This pattern corresponds to that described for exposed northeast Atlantic shores (Ballantine, 1961; Lewis, 1964; Raffaelli & Hawkins, 1996). Effectively, the whole coast of Portugal is exposed to the Atlantic swell. However, the prevalence of large seaweeds in the more sheltered eulittoral zones, as described for cooler temperate regions (*e. g.*, British Isles), is not common here. With the exception of a few northern shores, where *Pelvetia canaliculata, Fucus* spp. and *Ascophyllum nodosum* were observed, fucoid seaweeds do not occur or tend to be in stunted, small clumps. The only species observed in the centre and south region was *Fucus spiralis*. The lack of dense mid-shore seaweed beds in Portugal, however, is not only related to the exposure and its effects on modifying grazing efficiency (Hartnoll & Hawkins, 1985; Hawkins *et al.*, 1992), but mainly to the geographical distribution of certain species, whose distributional limits are located in the north of Portugal (*e. g., Ascophyllum nodosum, Himanthalia elongata*) (Ardré, 1970).

The distribution patterns in the sublittoral fringe clearly differed between northern shores, where large kelps and *Himanthalia* are present, and central and southern shores, which are essentially dominated by red algal turf species. Hence, the zonation patterns here may be seen as mixture of the patterns described for the northeast Atlantic coasts (Lewis, 1964) and for the Mediterranean (Pérès & Picard, 1964). The present study also confirms the latitudinal variations in zonation patterns described by Hawkins *et al.* (1992). From northern to southern Europe, animal-dominated communities extend further into shelter at more southerly locations. Similarly, southwards, dominance by large brown algae declines low on the shore and red algal turfs become more important (Hawkins *et al.*, 1992).

The quantitative approach used in the present study not only confirmed the trends observed in descriptive work, but also enabled questions to be answered about possible differences in community structure between the upper and lower mid-shore level and across north, centre and south regions. Multidimensional analysis and the ANOSIM test revealed clear differences in the structure of upper and lower mid-shore zone. The separation of two mid-shore zones may be an evidence of the over-simplification of a zonation scheme based only on three major zones. The number of species found in the upper and lower level definitely contributed to the obtained differences. In general, the upper level had a lower diversity and a higher dominance. The lower level at Baleal and Zambujeira was not separated in the general MDS analysis from the upper level stations also due to the lower average number of species recorded there.

SIMPER analyses confirmed the species with the highest contribution to the dissimilarity between the two levels. *Chthamalus* spp., *Patella depressa, Siphonaria pectinata, Melaraphe neritoides, Osilinus* spp. and *Littorina saxatilis* were more abundant in the upper mid-shore level, whilst *Mytilus galloprovincialis, Patella ulyssiponensis, Gibbula* spp., *Sabellaria alveolata, Actinia* sp., *Patella vulgata, Nucella lapillus* and a variety of algal species were more characteristic of the lower level. These results support the vertical distribution patterns described in this study and in the literature (*e. g.*, Lewis, 1964; Stephenson & Stephenson, 1972; Saldanha, 1974).

Multidimensional analysis separated the low shore zone of Martinhal from all the other shores. This was due to an extremely high abundance and dominance of ephemeral green algae at this level, probably related to the irregularity of the substratum, coupled with disturbance associated with boulders (Sousa, 1979).

2. Geographic variation

Portuguese rocky shores provide an excellent location to study biogeographical processes. There is a gradient for many warm-water sub-tropical and Mediterranean species (*e. g., Siphonaria pectinata, Oncidiella celtica, Patella rustica, Caulacanthus ustulatus, Lithophyllum lichenoides*) and boreal, cold-water species (*e. g., Ascophyllum nodosum, Himanthalia elongata, Pelvetia canaliculata, Patella vulgata, Nucella lapillus*) (cf. Fischer-Piette, 1957, 1958, 1963). Some species show a decrease in abundance or have reached their geographic limits along the coast.

The present study included the comparison of the eulittoral community structure across different regions of the Portuguese coast. Within each level, the northern region differed considerably from the south and central regions. SIMPER analysis revealed the species which contributed to this geographical separation. It also yielded important information on the geographical decline in the abundance of species such as *Mytilus galloprovincialis, Nucella lapillus* and *Siphonaria pectinata*. Although present along the entire coast, *Mytilus galloprovincialis* progressively declined in abundance from north to south. This variation may follow a general decrease in exposure. Note also that these data refer to intertidal mussels, but that dense subtidal populations have been described for the Arrábida coast by Saldanha (1974). The abundance of *Nucella lapillus* decreases from north to south and its southern limit of distribution seems to be located on the southern coast (Praia da Luz) as described by Nobre (1940). The occurrence of this gastropod in Portugal is closely related to the existence of mussel beds on which they feed. Mussel populations also provide shelter for *Nucella lapillus*. In contrast, the pulmonate limpet *Siphonaria pectinata* decreased in abundance from south to north. Several species were more abundant in the centre. These included *Patella ulyssiponensis, Corallina* spp., *Fucus spiralis, Bifurcaria bifurcata* and *Lithophyllum lichenoides*.

Limpet distribution was analysed in particular because *Patella* species are important in a geographical comparison context (as shown by SIMPER analyses) and because its effects on community structure are currently under study at several locations in Portugal. *Patella ulyssiponensis* occurs throughout the Portuguese coast in the lower eulittoral and sublittoral fringe. It was more abundant in the central region. *Patella rustica* occurs at higher shore levels, being sometimes abundant on vertical surfaces. This species is more abundant in the centre and south. Formal statistical analyses showed that *Patella depressa* is widely distributed and abundant in all examined mid-shore areas. Its relative abundance in the lower or upper mid-shore zone varied, depending on shore. *Patella vulgata* was more abundant in the north than elsewhere at both mid-shore zones. In the northern region, it was more abundant in the lower mid-shore level.

Conclusions

Distribution patterns in Portugal may be interpreted as a mixture of the patterns described for the northeast Atlantic coasts and for the Mediterranean. The present study also confirms the latitudinal variations from northern to southern Europe, with animal-dominated communities extending further into shelter at more southerly locations. Similarly, southwards, dominance by large brown algae declines low on the shore and red algal turfs become more important. Multidimensional analysis and the ANOSIM test revealed clear differences in the structure of upper and lower mid-shore zone. The number of species found at the two levels contributed to the obtained differences. In general, the upper level exhibited a lower diversity and a higher dominance. Within each level, the northern region differed considerably from the south and central regions. Considering the distribution patterns described for the whole coast, it is likely that differences between regions would have been stronger if quantitative data had also been obtained for the sublittoral fringe. This hypothesis, however, requires further testing.

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