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Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast

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Abstract

Geographical patterns in the distribution of epifaunal crustaceans (Amphipoda, Isopoda and Tanaidacea) occurring with dominant macroalgal species were investigated along the Portuguese rocky coast. Three regions, each encompassing six shores, were studied. Algal species were selected according to their geographical distribution: *Mastocarpusstellatus* and *Chondrus crispus* (north); *Bifurcariabifurcata* (north-centre); *Plocamiumcartilagineum* and *Cystoseiratamariscifolia* (centre-south); *Corallina* spp. and *Codiumtomentosum* (entire coast). Multivariate techniques were used to test for differences in crustacean assemblage composition between sub-regions and host algal species. A clear gradient of species substitution was observed from north to south. Differences in abundance and diversity of epifaunal crustaceans were observed between southern locations and the remaining sites. Four species were recorded for the first time in the Portuguese coast. Among the 57 *taxa* identified, southern distribution limits were observed for three species and northern distribution limits were observed for four species. Interestingly, the observed geographical patterns in epifaunal abundance and diversity were not related with geographical changes in the indentity of the dominant algal species.

Introduction

Understanding the causes driving species distribution is a major challenge of modern biogeography. The analysis of the relation between patterns of distribution of organisms and physical or biological factors is usually the first step towards this goal (Hoffman & Blows, 1994). In the marine environment, most large to medium scale studies were primarily focused on the importance of physical factors in the distribution of species (van den Hoek, 1984; Cambridge et al., 1987; Zacharias & Roff, 2001).

Marine algae are known to provide habitats for a wide range of animal species (Williams & Seed, 1992). Several studies addressed the role of seaweeds as determinants of epifauna diversity (Kitching, 1981; Kelaher et al., 2001; Parker et al., 2001; Chemello & Milazzo, 2002; Christie et al., 2003). However, few attempts have been made to investigate the relation between geographical changes in algae composition and patterns of macroinvertebrate diversity (Arrontes & Anadón, 1990a; Russo, 1997).

A considerable number of both cold- and warm-water algal species reach their distributional limits within the Portuguese coast (Ardré, 1971). In the lower eulittoral, northern shores are dominated by large macrophytes, such as *Himanthalia elongata* (Linnaeus) S.F. Gray, and the red algae *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Stackhouse). Towards the south, these species are replaced by *Cystoseira tamariscifolia* (Hudson) and other red algae become dominant, especially *Plocamium cartilagineum* (Linnaeus) (Ardré, 1970, 1971). Despite these differences, no attempts have been made to couple such information with the patterns of distribution of the associated fauna. Recent biogeographical studies in the Portuguese coast addressed solely the distribution and abundance of conspicuous animals (see Boaventura et al., 2002). In contrast, smaller organisms, including those inhabiting seaweeds, have been poorly studied. The information available on these *taxa* often comes from unpublished academic theses, and in most cases is of limited geographic scope.

The purpose of this study was to: (1) provide a description of the patterns of distribution of algal-dwelling crustaceans (Amphipoda, Isopoda and Tanaidacea) along the Portuguese rocky coast and (2) make a preliminary attempt to test the relationship between patterns of distribution of crustacean epifauna and conspicuous macroalgal species.

Material and methods

Study area

The study area encompassed the whole continental Portuguese coast and was divided in three regions (North, Centre and South), corresponding to the main stretches of rocky coastline (Fig. 1). Within each region, six shores with similar geomorphology and wave exposure were selected. Samples of the dominant macroalgae were collected from each shore.

Sampling procedures

Algal species were selected according to their geographical distribution. *M. stellatus* and *C. crispus* are abundant in the north of Portugal, becoming rare or absent towards the south. *Bifurcaria bifurcata* R. Ross is characteristic of northern and central shores. *P. cartilagineum* and *C. tamariscifolia* are abundant in the centre and south. *Corallina* spp. (*C. elongata* J. Ellis & Solander and *C. officinalis* Linnaeus) and *Codium tomentosum* Stackhouse are common along the entire study area. For further details see Figure 2.

Algae were collected either individually (*Cystoseira*, *Codium* and *Bifurcaria*) or by scraping 20 × 20 cm quadrats of monospecific stands (*Corallina*, *Chondrus*, *Mastocarpus*, *Plocamium*). Samples were preserved in formalin (10%). Extraction of animal species was made by washing the algae in flow water through a set of sieves (5 mm to 250 μm mesh). The fraction retained in the 250 μm sieve was sorted under the binocular miscroscope (10× magnification). In addition, the algae were also inspected under a binocular microscope to pick any remaining organisms. All animals were counted and identified to the lowest possible *taxon*. Due to the different structure of the selected algal species, the density of animals was expressed as number of individuals per volume of algae. After removal of macroinvertebrates the algae were dried for 2 h. They were then inserted into a graduated cylinder with a fixed amount of water, and the volume of algae was estimated as the difference between the initial and final volume.

Data analysis

Multivariate analyses were carried out with the PRIMER package (Clarke & Warwick, 1994). Non-parametric multidimensional scaling (nMDS) ordination of samples (alga/site) was performed using Bray–Curtis similarity coefficient. Transformation of animal abundances into presence–absence was chosen in order to minimise data variability. To determine a possible correlation between epifaunal assemblages and algal species a Mantel test (Sokal & Rohlf, 1995) was carried out using distance matrices for sites based on presence-absence of animal and algal species. One-way ANOSIM analyses to test for differences in epifaunal assemblages of algal species were made separately for each region to overcome the problem related to the lack of orthogonality of the two factors involved (regions and algal species).

One-way ANOSIM analyses were also employed to test for differences in species composition between the three regions. In order to avoid confounding effects between regions and algae, only species which span along the entire coast were used (*Corallina* spp. and *C. tomentosum*). To achieve an overall Type I error rate of $\alpha = 0.05$ in multiple tests, a Bonferroni correction was used (Quinn & Keough, 2002).

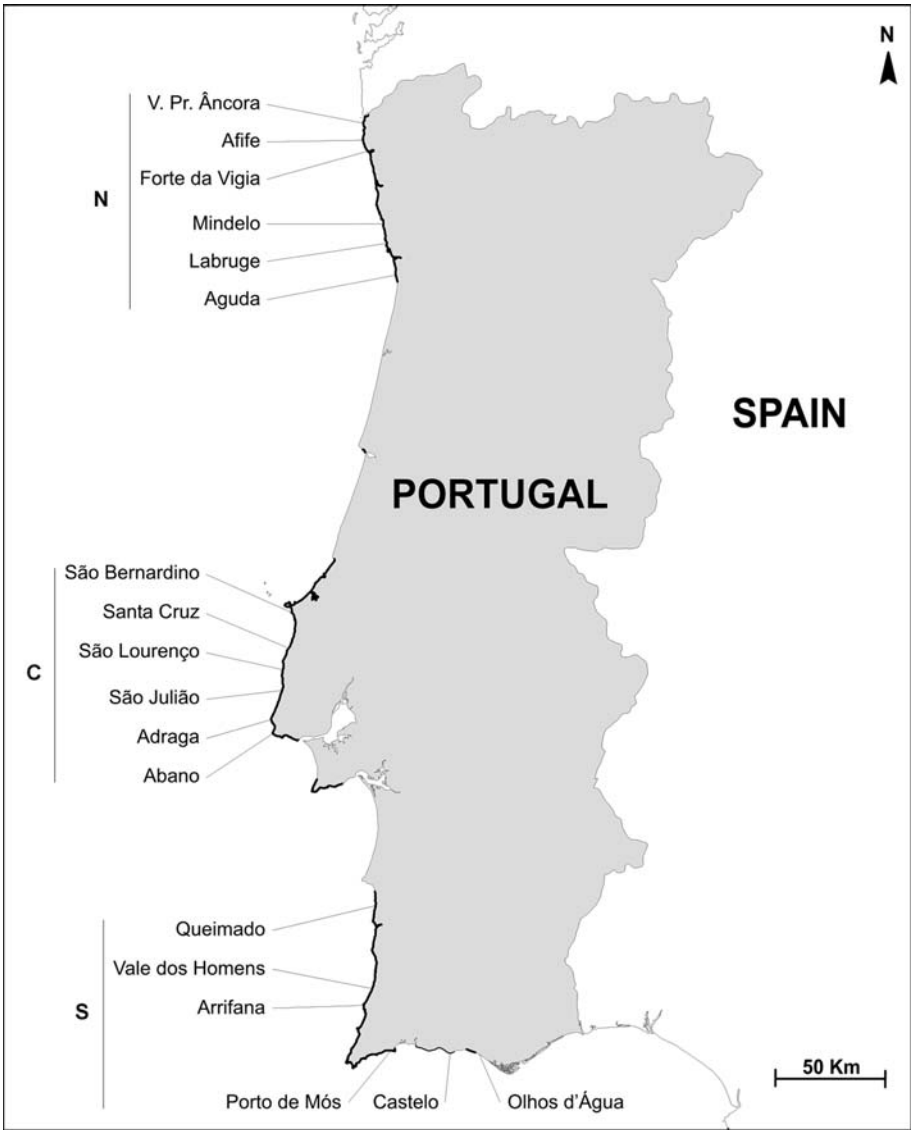

Figure 1. Location of the studied shores in the Portuguese coast. The main stretches of rocky coastline are depicted in black. sampled location. N: 1 – Vila Praia de Âncora, 2 – Afife, 3-Forte da Vigia, 4 – Mindelo, 5 – Labruge and 6 – Aguda; C: 7 – São Bernardino, 8 – Santa Cruz, 9 – São Lourenço, 10 – São Julião, 11 – Adraga and 12 – Abano; S: 13 – Queimado, 14 – Vale dos Homens, 15 – Arrifana, 16 – Porto de Mós, 17 – Castelo and 18 – Olhos d'Água.

Results

A total of 57 *taxa* were identified (34 amphipods, 19 isopods and four tanaids). Most *taxa* occurred with more than one algal species (32% of the *taxa* were observed at least in five algae). Seven species were seaweed-specific (five were found in *Corallina* and two in *Cystoseira*). From these, only *Biancolina algicola* Della Valle (found in *Cystoseira*) occurred consistently in more than one site.

The nMDS ordination (Fig. 3) revealed a significant interspersion of samples. No clear pattern between regions or algal species was observed. Furthermore, the stress value (0.2) suggests that too much reliance should not be placed on the detail of the plot (Clarke & Warwick, 1994).

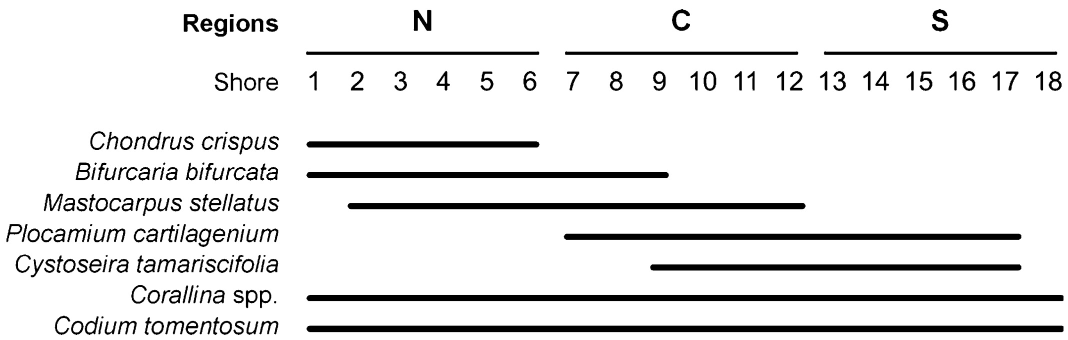

Figure 2. Shores where the algae species were sampled. For locations names see Figure 1.

Differences in macroinvertebrate assemblages were found between regions (ANOSIM $R = 0.209$; $p < 0.05$). Multiple tests revealed significant differences between all regions. A clear latitudinal gradient of substitution was shown plotting macroinvertebrate species against sampled sites. Figure 4 depicts this gradient in more detail.

Low similarity within regions was found (32–45%), denoting a high heterogeneity between replicate shores. The *taxa* with higher contribution to the dissimilarity between regions were found after SIMPER analysis: *Jassa* spp., *Idotea pelagica* Leach and *Dynamene bidentata* (Adams) for North vs. Centre; *Idotea granulosa* Rathke, *Dexamine spiniventris* (Costa) and *Synisoma capito* (Rathke) for North vs. South; *Dexamine spiniventris* (Costa), *I. pelagica* Leach and *Jassa* spp. for Centre vs. South. Although most species were found along the entire coast, several were present exclusively in the northern or southern regions. In most cases, these species were represented by one or few individuals found in one type of seaweed at a single shore and did not contribute in a consistent way to the differences between sub-regions.

ANOSIM analyses did not reveal any significant differences in epifaunal assemblages between algal species for the southern and central regions (ANOSIM $R = 0.048$, $p > 0.05$ and $R = 0.306$, $p > 0.05$ respectively). For the northern region differences were found between *B. bifurcata*, *Corallina* spp. and the remaining algae (ANOSIM $R = 0.445$, $p < 0.05$). The Mantel test revealed a low, but statistically significant, correlation between algae and epifauna ($r = 0.2429$; $p < 0.05$).

Discussion

Broad geographical differences in crustacean epifauna diversity were found along the continental Portuguese coast. A statistically significant difference in crustacean assemblage composition was found between the three regions. The species gradient supports the idea that the Portuguese coast acts as a region of contact between warm-water (from north Africa and the Mediterranean Sea) and cold-water species (from the North Sea and the Arctic) as described in earlier works (Ardré, 1970, 1971).

Four species were recorded for the first time in the Portuguese coast: two amphipods, *Caprella mitis* Mayer and *B. algicola*, one isopod, *S. capito*, and one tanaid, *Leptochelia savignyi* (Kroyer). Previously, the first three species were only recorded in the Mediterranean Sea. Not surprisingly, southern distribution limits were also detected in the studied area: *Amphitolina cuniculus* (Stebbing), *I. pelagica* and *I. granulosa*. The two idoteids were thought to be limited to northern Spain (Arrontes & Anadón, 1990b), but their range extends as far as southern Portugal.

Apparently, the observed geographical differences in epifaunal crustaceans were not related with differences in dominant algal species. These observations differ from those described by Arrontes & Anadón (1990a) for northern Spain, who found that several isopod species responded to geographical changes in algal composition. Interestingly, the three idoteid species were closely associated with algae that displayed geographical changes in abundance. This is certainly not the case in the Portuguese coast. *Idotea granulosa* and

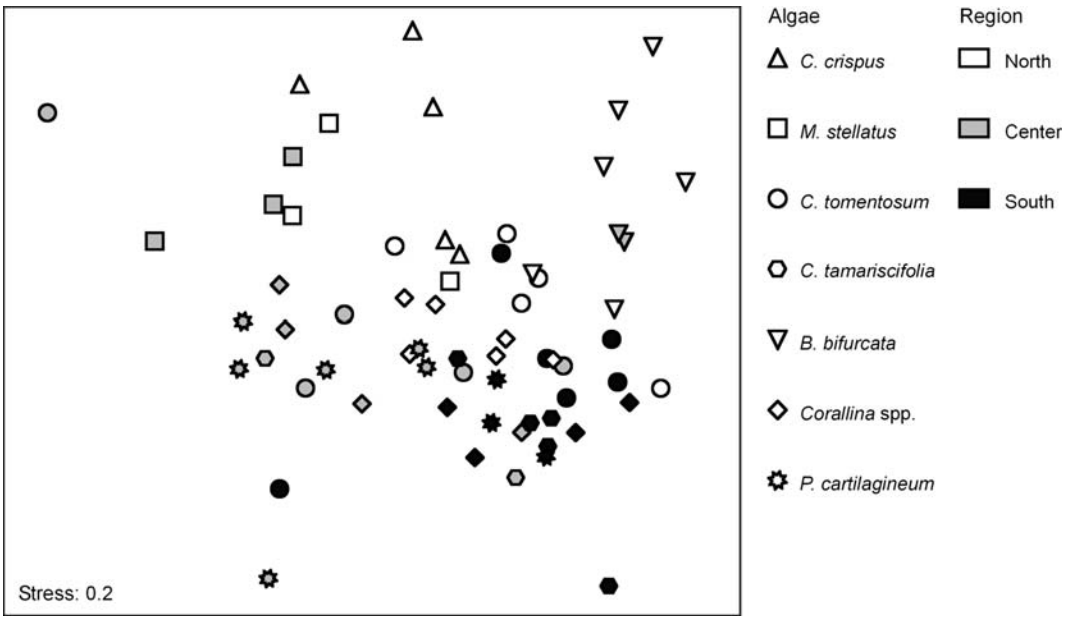

Figure 3. nMDS ordination of the samples (algae/site). Regions are depicted by different grades of shade, and algal species by different shapes.

I. pelagica were commonly found in *Corallina* (which ranges from north to south) and in both northern (*Chondrus* and *Mastocarpus*) and southern (*Cystoseira* and *Plocamium*) algal species.

Most *taxa* displayed no preference for a particular alga, occurring in association with different macroalgae species at different geographical locations. Only *B. algicola* was found consistently in *Cystoseira* at two different sites. The lack of a strict host specialisation by epifauna has been reported by several authors (Russo, 1990; Parker et al., 2001).

Algal architecture might play a more important role in determining epifaunal diversity and abundance (e.g. Crisp & Mwaiseje, 1989; Chemello & Milazzo, 2002; Kelaher, 2003). In the present study, finely branched macroalgae (*Cystoseira*, *Plocamium* and *Corallina*) exhibited a more diversified and abundant epifauna, when compared with the other five species, which have a less complex architecture. *Mastocarpus* and *Chondrus*, the only algae with blade-like structure, presented the lowest diversity values. These findings prompt for a more detailed analysis with a sampling strategy aimed towards algal complexity rather than algal species. In the present study, many non-dominant, but common, algal species were left out. Yet, when contiguous to the dominant plants, they may also account for a large proportion of the epifauna, especially when highly mobile organisms are considered (Gunnill, 1982).

Some of the species recorded in this study are probably transient in the lower shore. This is the case of *Phtisica marina* Slabber, *Synisoma acuminatum* (Leach), *Idotea baltica* (Pallas) and *Campecopea hirsuta* (Montagu), which are known to occur along the entire Portuguese coast, but appeared sporadically on some samples. The first three are mainly sublittoral species, whilst the latter is typically found in the upper midshore among barnacles and in *Lichina pygmaea* (Lightfoot) Agardh (Arrontes & Anadón, 1990b, for the isopod species). Other species are also abundant in non-algal substrates. In the present study *I. pelagica* was more common in the centre and southern Portuguese coast, but in fact it is one of the most abundant species found among mussels in the northern shores (A. M. Santos, unpublished data). Removal of such species from the data did not alter the final outcome of the analysis.

Analysis of temporal and small-scale spatial variability was not addressed in the present study due to logistic constraints given the large sampling area. However, both sources of variation are known

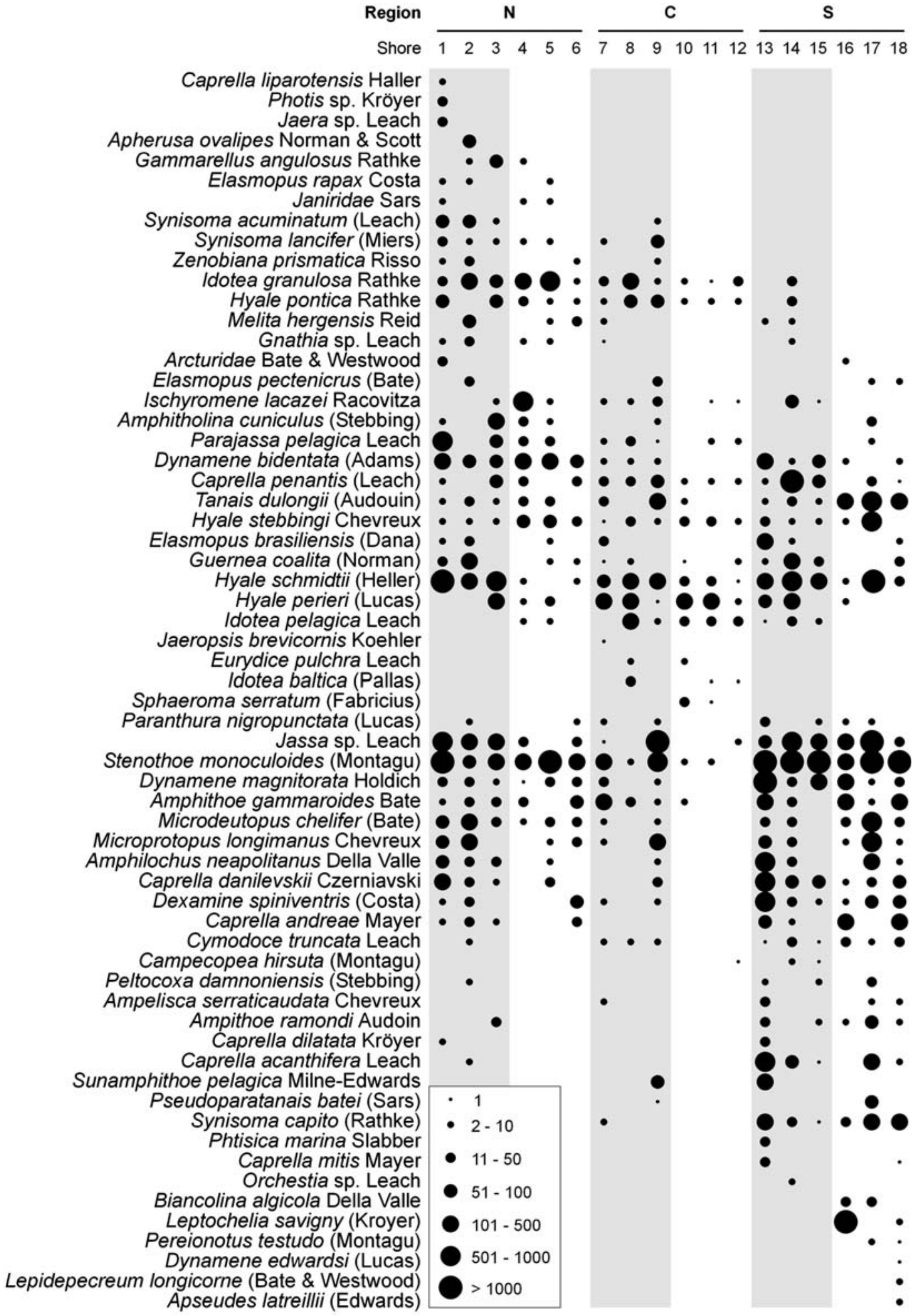

Figure 4. Graphical representation of macroinvertebrate abundance vs. sampled location. Abundances are expressed as number of individuals per 1000 cm^3 of algae. For locations names see Figure 1.

to be important (Kelaher et al., 2001). Futhermore, some species may exploit distinct habitats in different phases of their life-cycle. For example, Arrontes & Anadón (1990a) found that many isopod species displayed marked seasonal variation in algal occurrence, with macroalgae providing a habitat for juvenile stages, while adults occurred elsewhere. Other traits, such as feeding behaviour, vagility or response to predators, may also contribute to the high variation in epifaunal abundance and composition observed among different algal species (Williams & Seed, 1992) or even different thalli of the same or similar species (Gunnill, 1982; Kelaher et al., 2001). Therefore, replication at these small-scale levels is mandatory to distinguish wandering organisms from true host-plant specialists, which are more likely to be affected by changes in the distribution of their host.

The present study found that epifaunal crustacean assemblages display marked geographical differences along the Portuguese coast. Northern and southern limits of distribution were detected for several of the 57 *taxa* identified. In addition, four new species were recorded outside their previously known distribution range. Biogeographical patterns of epifauna seem not to be related with geographical changes in dominant algal species. Instead, physical factors, such as temperature, water currents and wave exposure, or biological factors, such as algal architecture, might play a more important role as determinants of epifaunal distribution and should be investigated in detail.

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