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Biogeographical patterns of algal communities in the Mediterranean Sea: *Cystoseira crinita*-dominated assemblages as a case study

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ABSTRACT

Aim The aim of this study was to describe the composition, community structure and biogeographical variation of subtidal algal assemblages dominated by the brown alga *Cystoseira crinita* across the Mediterranean Sea.

Location The Mediterranean coast, from Spain (1°25' E) to Turkey (30°26' E).

Methods Data on the species composition and structure of assemblages dominated by the species *C. crinita* were collected from 101 sites in nine regions across the Mediterranean Sea. Multivariate and univariate statistical tools were used to investigate patterns of variation in the composition of the assemblages among sites and regions, and to compare these with previously defined biogeographical regions. Linear regressions of species richness versus longitude and versus latitude were also carried out to test previously formulated hypotheses of biodiversity gradients in the Mediterranean Sea.

Results The main features characterizing *C. crinita*-dominated assemblages across the Mediterranean included a similar total cover of species, a similar cover of *C. crinita*, and consistency in the presence of the epiphyte *Haliptilon virgatum*. Biogeographical variation was detected as shifts in relative abundances of species among regions, partly coinciding with previously described biogeographical sectors. A significant positive correlation was found between species richness and latitude, while no significant correlation was detected between species richness and longitude.

Main conclusions The patterns of variation in community structure detected among the studied regions reflected their geographical positions quite well. However, latitude seemed to contribute more to the explanation of biological patterns of diversity than did geographical distances or boundaries, which classically have been used to delimit biogeographical sectors. Moreover, the positive correlation between species richness and latitude reinforced the idea that latitude, and possibly temperature as a related environmental factor, plays a primary role in structuring biogeographical patterns in the Mediterranean Sea. The lack of correlation between species richness and longitude contradicts the notion that there is a decrease in species richness from west to east in the Mediterranean, following the direction of species colonization from the Atlantic.

Keywords

Algal assemblages, biodiversity, biogeographical patterns, *Cystoseira crinita*, latitude, Mediterranean Sea, species richness, temperature.

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INTRODUCTION

Biogeography is the study of distributional patterns in biodiversity, and the examination of affinities and/or differences in the biotas present in different regions (Bianchi & Morri, 2000). Although in the marine environment connectivity among regions is usually greater than that in terrestrial systems (Carr *et al.*, 2003), distinct marine biogeographical regions have been described at a variety of spatial scales (Golikov *et al.*, 1990; Longhurst, 1998; Shears *et al.*, 2008). Among the factors underlying biogeographical patterns in the marine realm, temperature seems to be pivotal (Breeman, 1988; Cambridge *et al.*, 1990; Adey & Steneck, 2001; Blanchette *et al.*, 2008), but other factors such as salinity, currents, upwelling and tides may also play a role in determining patterns of diversity at regional scales (Adey & Steneck, 2001; Phillips, 2001). Finally, history has been invoked as a key factor in the distribution of diversity at large scales (Barber *et al.*, 2000; Phillips, 2001; Kerswell, 2006).

Most of the biota present in the Mediterranean Sea stems from geologically recent times, as the Mediterranean basin became desiccated around 6 Ma, during the Messinian salinity crisis, and refilled 5.3 Ma (Hsu *et al.*, 1973; Krijgsman *et al.*, 1999; García-Castellanos *et al.*, 2009). Despite its relatively young age, the Mediterranean is considered to be a hotspot of species diversity, holding more than 17,000 species (Coll *et al.*, 2010), and with a macroalgal flora placed amongst the world's richest (Bolton, 1994). The Mediterranean is divided into several sub-basins (Coll *et al.*, 2010) which, coupled with basin-scale water circulation and other oceanographic factors (Béthoux, 1979; Hopkins, 1985; Malanotte-Rizzoli & Hecht, 1988; Bosc *et al.*, 2004), has led to the recognition of distinct biogeographical areas (Pères & Picard, 1964; Giaccone, 1971a; Bianchi & Morri, 2000; Bianchi, 2007; Spalding *et al.*, 2007). The presence/absence of species in different areas has been considered as the essential means of defining Mediterranean biogeographical regions, and a pattern of decrease in biodiversity from north-west to south-east has been observed (e.g. Boudouresque, 2004; Bianchi, 2007; Coll *et al.*, 2010). Recent efforts have been directed towards summarizing current knowledge on Mediterranean biodiversity, including identifying spatial patterns in species occurrences and in species diversity (Coll *et al.*, 2010). The examination of general patterns in marine biodiversity at a regional scale has also been carried out using the MacroBen database, which holds data on the biodiversity of invertebrates inhabiting soft sediments from various regions across Europe (Sommerfield *et al.*, 2009). We know of no studies, however, that address patterns in Mediterranean biodiversity at the level of whole assemblages in habitats dominated by macroalgae.

Macroalgae of the genus *Cystoseira* C. Agardh are the primary structural species in Mediterranean sublittoral rocky marine systems (Feldmann, 1937; Giaccone, 1973; Ballesteros, 1988, 1990a,b, 1992; Ballesteros *et al.*, 1998, 2009). This contrasts with the majority of other temperate marine systems, where species of kelp play this role (Steneck *et al.*, 2002).

Assemblages dominated by *Cystoseira* species rank amongst the most productive in the Mediterranean (Ballesteros, 1989) and provide habitat for a considerable number of other algae and invertebrate species (Molinier, 1960; Boudouresque, 1972; Ballesteros, 1992; Ballesteros *et al.*, 2009). Although some *Cystoseira* species are very restricted in their spatial distribution, others are distributed throughout the entire Mediterranean Sea (Cormaci *et al.*, 1992; Ribera *et al.*, 1992), thus providing a good basis for examining patterns in biogeography at the assemblage/community level. Moreover, macroalgal beds dominated by *Cystoseira* spp. are declining in several Mediterranean areas as a consequence of coastal development and deteriorating water quality (Munda, 1982; Thibaut *et al.*, 2005; Airoldi & Beck, 2007; Mangialajo *et al.*, 2008).

This study aims to add to our knowledge of the biogeography of *Cystoseira*-dominated assemblages in the Mediterranean Basin. Our analysis focuses upon assemblages dominated by *Cystoseira crinita* Duby, a Mediterranean endemic species that forms dense stands in shallow, rather sheltered, well-illuminated areas (Feldmann, 1937; Molinier, 1960; Pizzuto, 1997; Sales & Ballesteros, 2009, 2010). Assemblages dominated by *C. crinita* were described by Molinier (1960) as characteristic of shallow rocky habitats in Corsica (north-west Mediterranean) and were assumed by Giaccone (1968, 1971b) and Giaccone *et al.* (1994) to be representative of shallow rocky habitats for the entire Mediterranean. Ballesteros (1992) and Pizzuto (1999) studied seasonal variation in the composition and structure of *C. crinita*-dominated assemblages from Catalonia and Sicily, while Sales & Ballesteros (2010) investigated long-term fluctuations of these assemblages in Corsica. All of these studies were made at local scales. Given the key role that *C. crinita* plays in structuring assemblages, it is important to undertake a fuller description of the species composition of the assemblages dominated by this species across the Mediterranean. Quantitative study of a single habitat across the Mediterranean can be used to verify classical biogeographical regions that previously have been defined only qualitatively, as well as to provide a test of the currently accepted pattern of a decrease in biodiversity from north-western to south-eastern areas across the Mediterranean Sea.

The specific objectives of the study are: (1) to describe the composition of assemblages of algal and invertebrate species occurring in *C. crinita*-dominated habitats across the Mediterranean Sea; (2) to compare the composition of assemblages in these habitats from several areas across the Mediterranean using a quantitative approach; and (3) to compare the observed patterns of biodiversity in these assemblages with previously defined biogeographical regions and biodiversity gradients for the Mediterranean Sea.

MATERIALS AND METHODS

Study area

The Mediterranean Sea is the biggest enclosed sea in the world, with a coastline of 46,000 km in length and a surface area of

2.5 million km² (Boudouresque, 2004). It is a warm-temperate sea (Zabala & Ballesteros, 1989); however, it has many features that distinguish it from open temperate oceans: extreme reduction of tides, oligotrophy, and relatively high temperature and salinity (the former especially in summer) (Ros *et al.*, 1985). The Mediterranean is geographically and oceanographically very heterogeneous (Béthoux, 1979; Bosc *et al.*, 2004); as a consequence, up to 13 distinct biogeographical sectors have been recognized (Pérès & Picard, 1964; Bianchi & Morri, 2000; Bianchi, 2007).

Sampling

Cystoseira crinita-dominated assemblages were surveyed at 101 sites in nine regions across the Mediterranean Sea ranging in longitude from Spain (1°25' E) to Turkey (30°26' E) and spanning latitudes from the northern Adriatic (45°22' N) to Rhodes (36°03' N; Fig. 1). The regions surveyed were Catalonia (*n* = 1), Minorca (*n* = 14) and Formentera (*n* = 3) (Spain); Corsica (*n* = 36) (France); Sardinia (*n* = 14) (Italy); Istria (*n* = 26) (Croatia); Dodecanese (*n* = 2) and Cyclades

islands (*n* = 2) (Greece); and Lycia (*n* = 3) (Turkey). These regions correspond to three previously defined biogeographical sectors according to Bianchi (2007) and Spalding *et al.* (2007): the Central Western Mediterranean (CWM), the Adriatic (A) and the Aegean (AE).

To avoid potential seasonal differences, all samples were collected during late spring of 2007 or 2008. All the samples were collected from coves, bays or shallow areas with a low to medium degree of exposure, and little or no obvious human-induced impact. The depth at which the samples were obtained ranged from 0.2 to 1 m. At each site, a sample measuring 25 × 25 cm (625 cm²) was collected, with the whole community removed with a hammer and chisel (Boudouresque, 1971). This sampling area is greater than the minimum sampling area recommended for Mediterranean infra-littoral assemblages (Coppejans, 1980; Ballesteros, 1992). After collection, all algae and sessile invertebrates were identified to species level. The relative amounts of each species present were measured as horizontal coverage in centimetres squared by spreading specimens/individuals over a laboratory tray to form a thin layer (Ballesteros, 1986). Therefore, species cover was not

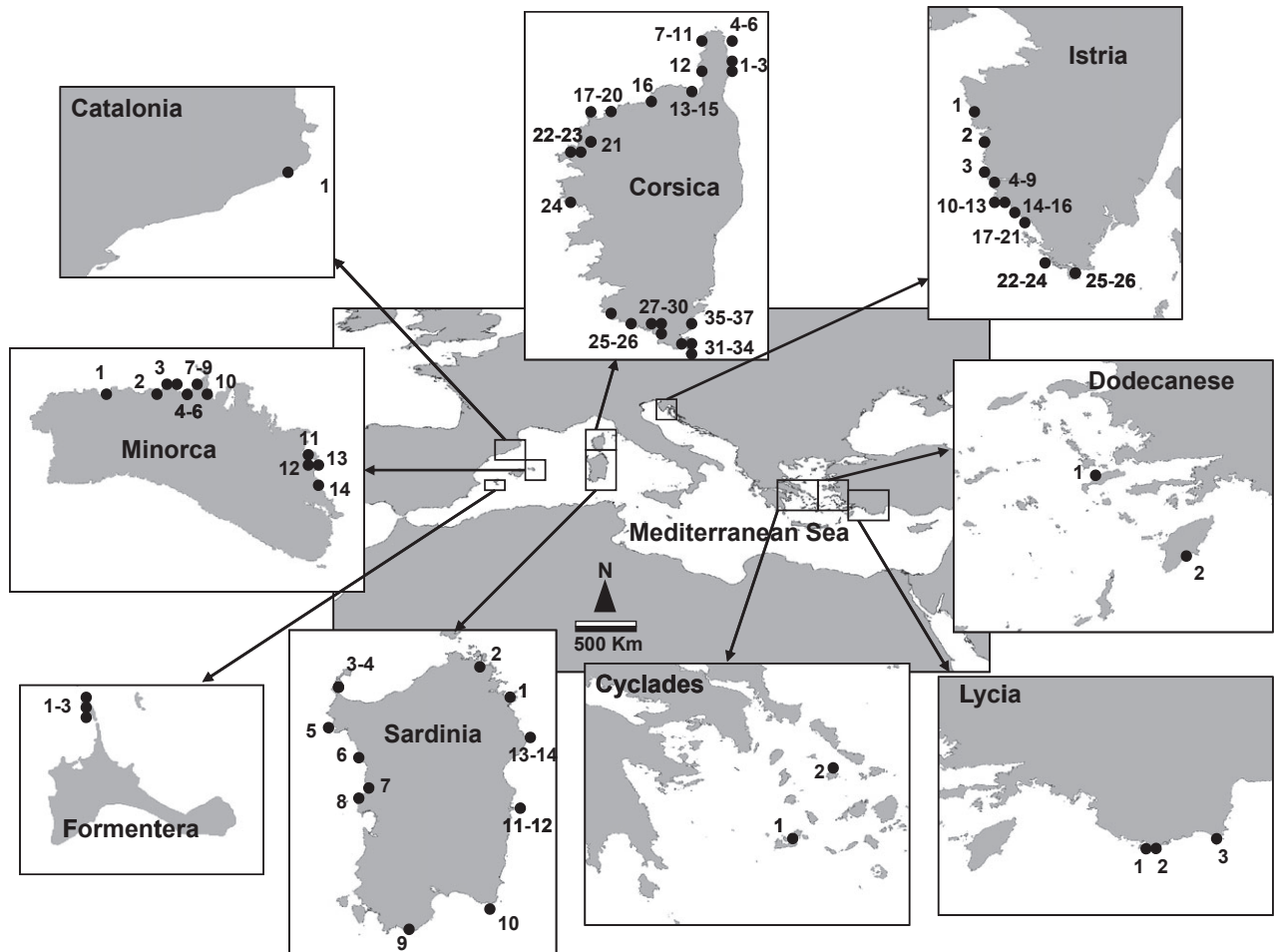


Figure 1 A map of the Mediterranean Sea, showing the locations of the 101 sites from where *Cystoseira crinita*-dominated assemblages were sampled.

measured as a percentage of substrate occupied by each species, as is often the case, but as the area covered by each species when placed horizontally. This measure is quite closely related to the ash-free dry weight of algal species (Ballesteros, 1992). From here on, we will use the word 'cover' to refer to horizontal cover in centimetres squared. Species that could not be identified in the field were preserved in 4% formalin in seawater and identified later in the laboratory.

Describing patterns in community structure

Several multivariate analytical procedures were used to investigate patterns of variation in the composition of assemblages among samples and regions. First, the data matrix of species coverage was fourth-root-transformed. A reasonably severe transformation was appropriate in order to reduce the contribution of the most abundant species, especially the dominant alga *C. crinita*. Next, a Bray–Curtis similarity (Bray & Curtis, 1957) matrix was constructed for the full set of data (all samples) and also on the basis of the average coverage of species in each of the nine geographical regions. Non-metric multidimensional scaling (NMDS) ordination (Kruskal & Wish, 1978) was undertaken to visualize patterns of community similarities among the 101 sites and also, separately, among the averages for the nine regions. A hierarchical group-average agglomerative clustering method accompanied by similarity profiles, the SIMPROF test (with 9999 permutations, and using a 0.1% significance level; Potter *et al.*, 2001; Clarke *et al.*, 2008), was used to explore potential grouping structures among the samples. The previously articulated hypotheses of decreasing richness from west to east and from north to south were tested by linear regressions of species richness (number of species per sample) versus longitude and also versus latitude.

Characterizing biodiversity in different regions

Although there were nine identifiable geographical regions in this study, as described, sampling was more concentrated in essentially five geographical areas (omitting the single sample obtained from Catalonia), namely: the Balearic Islands (merging Minorca and Formentera), Corsica, Sardinia, Istria and the Southern Aegean Sea (merging Cyclades, Dodecanese and Lycia; see Fig. 1). Analysis of similarities (ANOSIM; Clarke, 1993) was used to test the null hypothesis of no differences among the communities obtained from these five areas. Furthermore, we characterized these more intensively sampled areas in terms of their biodiversity and the taxa or species with the greatest areal coverage. Univariate analyses (one-way ANOVA), followed by *post-hoc* Tukey tests, were used to compare the five areas for some specific aspects of the community, namely: total cover, cover of *C. crinita*, cover of Chlorophyta (green algae), and cover of sessile invertebrates. One-way ANOVA tests (comparing areas) were also carried out on the number of species per sample (species richness, *S*) and Simpson's evenness ($1 - \lambda'$; Simpson, 1949). Finally, the average coverage of the 10 species constituting the greatest

areal coverage of each region was represented graphically to help to describe similarities and/or differences in community structure among these five areas. STATISTICA 6 was used for all univariate analyses, and PRIMER 6 (Clarke & Gorley, 2006) with the PERMANOVA+ add-on package (Anderson *et al.*, 2008) for all multivariate analyses.

Comparison of grouping models for assemblages

There were several potential ways that sites could be grouped, given the above multivariate analyses (see Results) and previous studies. These included: a 3-group model, corresponding to previously defined biogeographical regions (CWM, A and AE); a 5-group model, suggested by clusters of sample points in the 2-D NMDS plot; a 7-group model, corresponding to an arbitrary slice in the dendrogram arising from the cluster analysis at a Bray–Curtis similarity of 40%; and an 11-group model, corresponding to the groups in which there were no statistically significant structural differences among samples as determined by SIMPROF. We wished to compare these potential groupings quantitatively for their goodness-of-fit to the observed data and also their parsimony, given the number of parameters (groups) in each model. Three criteria were used to compare the models: (1) the ANOSIM *R* statistic (Clarke, 1993); (2) a pseudo-multivariate 'effect size' (in Bray–Curtis units), as measured by the square root of the among-group component of variation from a one-way PERMANOVA model (e.g. Anderson *et al.*, 2005, 2008); and (3) a pseudo-multivariate information criterion, a direct analogue to the univariate small-sample-corrected Akaike information criterion (AIC_c) (Hurvich & Tsai, 1989), as calculated using the DISTLM routine in the PERMANOVA+ add-on package (see Chapter 4 in Anderson *et al.*, 2008 for details). All three of these criteria are potentially appropriate for comparing models having different numbers of parameters, as they take into account the differing degrees of freedom associated with each model fit.

RESULTS

Patterns in community structure

In total, 234 species were identified from the samples, consisting of 5 cyanobacteria, 194 macroalgae and 35 sessile invertebrates. A common structure was present across the entire study area, with the species divided into four layers: canopy, turf-forming, encrusting and epiphytic. The canopy layer was always dominated by *C. crinita*, although other *Cystoseira* species were also occasionally abundant. The encrusting layer consisted mainly of the coralline alga *Neogoniolithon brassica-florida*, except in Catalonia (northern Spain), where the encrusting layer was represented mainly by *Lithophyllum incrustans*, another coralline alga. The brown alga *Pseudolithoderma adriaticum* was an important component of the encrusting layer in Corsica, Sardinia and Minorca. A turf-forming layer of primarily the red algae *Corallina elongata* and

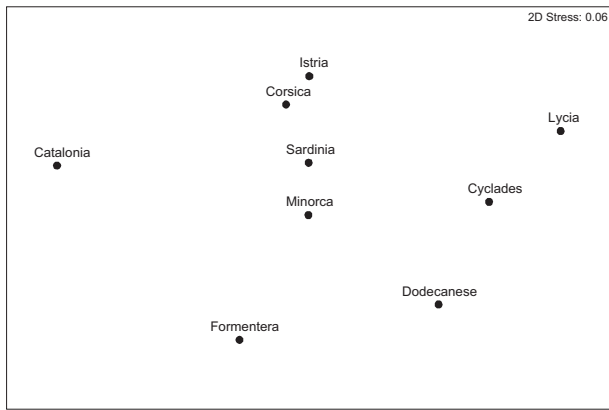


Figure 2 Non-metric multidimensional scaling (NMDS) of *Cystoseira crinita*-dominated assemblages, based on the Bray–Curtis resemblance measure for species cover data after transforming to fourth roots and averaging the values for each variable for each of the nine geographical regions sampled throughout the Mediterranean Sea. The horizontal axis is axis 1 and the vertical is axis 2.

Laurencia spp. appeared frequently in almost all the regions. The brown alga *Halopteris scoparia* and various species from the family Dictyotaceae were other important components of the turf-forming stratum. Finally, the green algae *Dasycladus vermicularis*, *Flabellia petiolata*, *Valonia utricularis* and various *Cladophora* species appeared frequently in the understory turf community. *Cystoseira* thalli were usually covered by epiphytes, with *Haliptilon virgatum* and *Sphacelaria cirrosa* being the most common and abundant. Despite being low in cover, some *Dasya* and *Ceramium* species were also found as epiphytes on *Cystoseira* (see Appendix S1 in Supporting Information).

Sessile invertebrates generally represented less than 1% of the total coverage of the assemblages. The most common species were the hydrozoan *Aglaothenia kirchenpaueri*, the bryozoans *Amathia lendigera*, *Turbicellepora magnicostata* and *Scrupocellaria* sp., the ascidians *Cystodites dellechiaiei* and various species from the family Didemnidae, and the sponges *Ircinia fasciculata* and *I. variabilis* (see Appendix S1).

The NMDS on averaged species data showed patterns of resemblances in community structure among the regions that reflected their relative geographical positions (Fig. 2). There was a clear pattern of variation from west to east along the first (horizontal) NMDS axis, with the maximum distance represented in the NMDS between Catalonia (Spain) and Lycia (Turkey). Variation from north to south was apparent along the second (vertical) NMDS axis. The three regions of Spain were quite well separated, with the island of Minorca appearing more similar to Corsica (France) and Sardinia (Italy) than to Formentera or Catalonia. Although there was a clear east–west gradient in community structure (Fig. 2), this was not reflected in patterns of species richness. The correlation between longitude and species richness was very low and not statistically significant (Fig. 3). There was, however, a positive and significant correlation between latitude and species richness (Fig. 3).

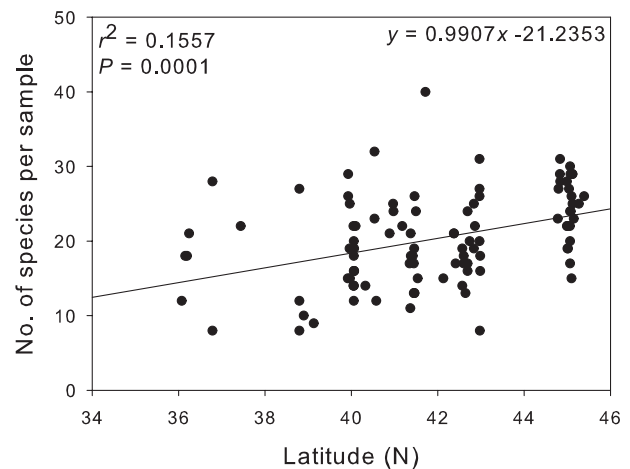
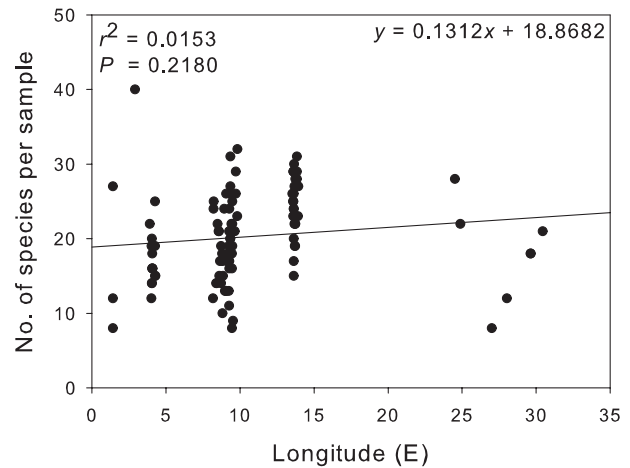


Figure 3 Relationship between richness (number of species per sample) and either longitude (top panel) or latitude (lower panel), using the whole data set for the *Cystoseira crinita*-dominated assemblages sampled throughout the Mediterranean ($n = 101$ sites). The linear regression line and associated results are shown.

Characterizing regional biodiversity

ANOSIM indicated statistically significant differences between all pairs of the more intensively sampled areas, except for Corsica and Sardinia (Table 1). Univariate (one-way ANOVA) analyses of the total cover and of the cover of *C. crinita* showed no significant differences among these five areas (Balearic Islands, Corsica, Sardinia, Istria and the Southern Aegean; see Table 2 and Fig. 4). However, there was a significantly higher cover of green algae in Istria than in the Balearics and a significantly higher cover of sessile invertebrates in Istria and in the Southern Aegean than in the other areas (Table 2, Fig. 4). The number of species per sample was significantly higher in Istria than in the Balearic Islands, Corsica and the Southern Aegean (Table 2, Fig. 5). There were no significant differences, however, in the evenness of assemblages among these five areas (Table 2, Fig. 5).

The plots of the 10 species having the greatest average cover per area demonstrated that the most distinctive region was the

Table 1 Results of analysis of similarity (ANOSIM) tests comparing composition and relative coverage of species in *Cystoseira crinita*-dominated assemblages from the five more intensively sampled geographical areas (Balearic Islands, Corsica, Sardinia, Istria and the Southern Aegean) across the Mediterranean Sea. Significant values are written in bold.

	ANOSIM R	ANOSIM P
Global test	0.531	0.0001
Pairwise tests		
Balearics, Corsica	0.217	0.002
Balearics, Sardinia	0.183	0.001
Balearics, Istria	0.772	0.0001
Balearics, S Aegean	0.755	0.0001
Corsica, Sardinia	0.09	0.105
Corsica, Istria	0.696	0.0001
Corsica, S Aegean	0.893	0.0001
Sardinia, Istria	0.722	0.0001
Sardinia, S Aegean	0.811	0.0001
Istria, S Aegean	0.934	0.0001

Table 2 Results of one-way ANOVA tests to compare the five more intensively sampled areas (Balearic Islands, Corsica, Sardinia, Istria and the Southern Aegean) across the Mediterranean for several specific components of *Cystoseira crinita*-dominated assemblages. Total cover: horizontal projection of all algae and sessile invertebrates constituting the assemblage in cm²; Cover of *C. crinita* in cm²; Cover of Chlorophyta in cm²; Cover of invertebrates in cm²; Number of species per sample (richness); Simpson's evenness ($1 - \lambda'$; Simpson, 1949). The transformations (Transf.) applied to the original data values, when necessary, are indicated: log, base 10 logarithmic; sqrt, square root; 4th root, fourth root. Significant values are written in bold.

Variable	Transf.	ANOVA F	ANOVA P
Total cover	log	1.323	0.267
Cover of <i>C. crinita</i>	sqrt	1.987	0.103
Cover of Chlorophyta	sqrt	3.670	0.008
Cover of invertebrates	4th root	7.474	0.0001
Number of species (richness)	4th root	6.583	0.0001
Simpson's evenness	None	1.122	0.351

Southern Aegean, which, apart from *C. crinita*, shared only two species with the other sampled areas (Fig. 6). These were the epiphyte *Haliptilon virgatum* and the encrusting coralline alga *Neogoniolithon brassica-florida*. The average cover of *H. virgatum* apparently increased from north to south ($I < C < S < B < SA$). *Neogoniolithon brassica-florida* had a greater average coverage in Corsica and Sardinia than in the Balearic Islands, Istria and the Southern Aegean. Moreover, the Southern Aegean was the only area in which an invertebrate (the hydrozoan *Aglaophenia kirchenpaueri*) appeared in the list of the 10 species having the greatest cover. Apart from *H. virgatum*, two other epiphytes appeared as important components of *C. crinita*-dominated assemblages from the Balearic Islands, Corsica, Sardinia and Istria: the brown alga *Shpacelaria cirrosa* and the encrusting coralline *Hydrolithon*

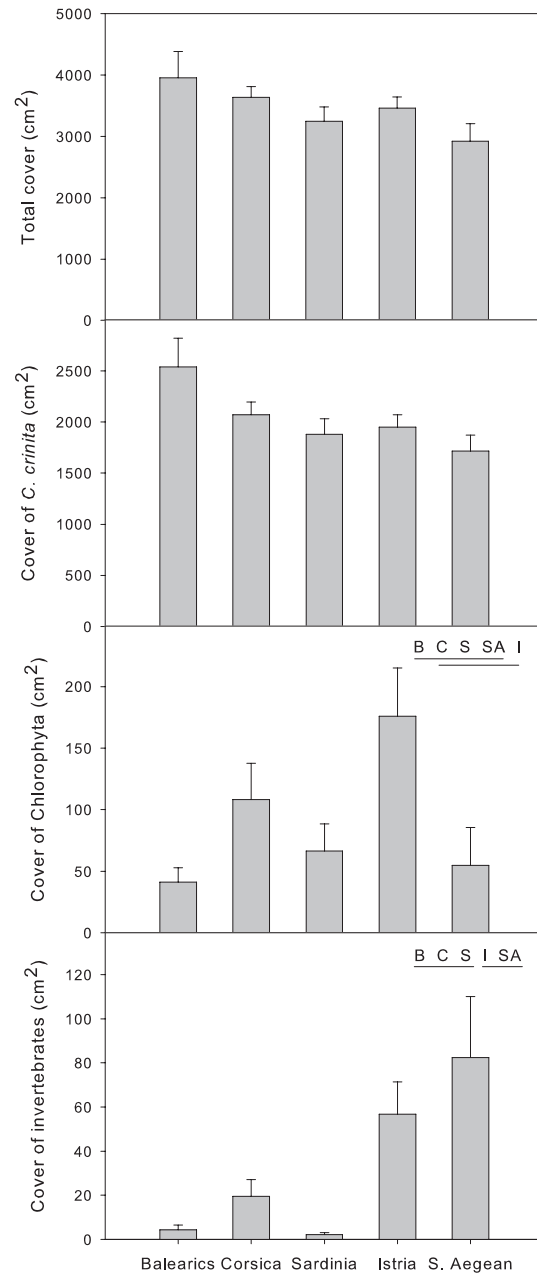


Figure 4 Mean (± 1 SE) cover of several components of the *Cystoseira crinita*-dominated assemblages for each of the five more intensively sampled areas across the Mediterranean (Balearic Islands, $n = 17$; Corsica, $n = 36$; Sardinia, $n = 14$; Istria, $n = 26$; Southern Aegean Sea, $n = 7$). For those showing statistically significant differences by ANOVA, the results of the *post-hoc* Tukey tests are shown in the upper right-hand corner of each graph (B, Balearic Islands; C, Corsica; S, Sardinia; I, Istria; SA, Southern Aegean). Letters with a common underlining denote areas that are not statistically significantly different from one another in their mean values ($P > 0.05$).

farinosum. The epiphyte *S. cirrosa* apparently decreased in average cover from northern to southern areas ($I > C > B > S$), while *H. farinosum* showed the opposite pattern ($I < C < B \sim S$). In the Southern Aegean, the red filamentous

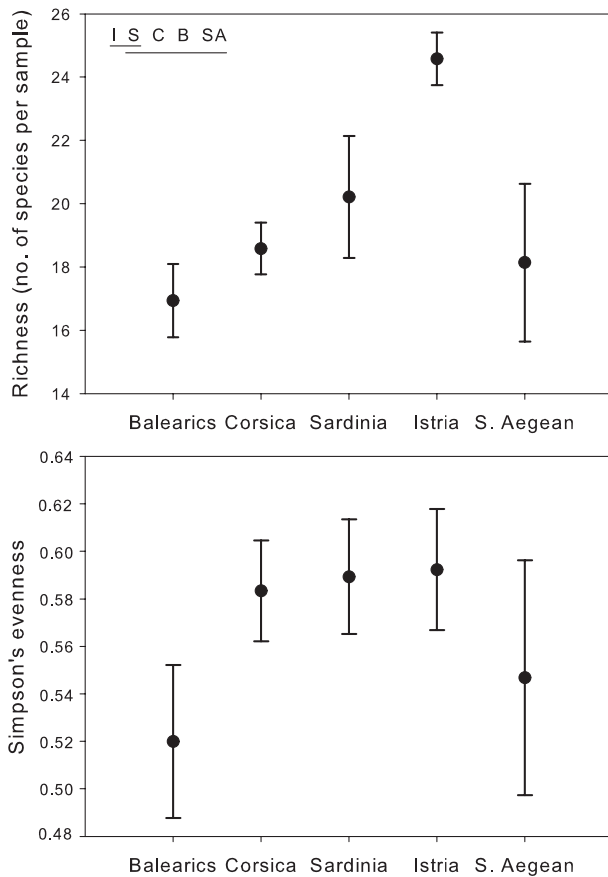


Figure 5 Mean (± 1 SE) richness (number of species per sample) and Simpson's evenness ($1 - \lambda$; Simpson, 1949) of *Cystoseira crinita*-dominated assemblages calculated for each of the five more intensively sampled areas across the Mediterranean (Balearic Islands, $n = 17$; Corsica, $n = 36$; Sardinia, $n = 14$; Istria, $n = 26$; Southern Aegean Sea, $n = 7$). For those showing statistically significant differences by ANOVA, the results of the *post-hoc* Tukey tests are shown in the upper left-hand corner of each graph (I, Istria; S, Sardinia; C, Corsica; B, Balearic Islands; SA, Southern Aegean). Letters with a common underlining denote areas that are not statistically significantly different from one another in their mean values ($P > 0.05$).

algae *Herposiphonia secunda* and *Dasya corymbifera* were among the most important epiphytes. No turf-forming alga occurred, however, in any of these regional lists of the 10 species having greatest cover. The articulated coralline alga *Corallina elongata* appeared in the lists for Minorca, Corsica and Istria; *Rytiphlaea tinctoria* appeared in the lists for Minorca, Corsica, Sardinia and the Southern Aegean; and *Dictyota* spp. appeared only in the lists for Corsica and Sardinia. Finally, in the canopy layer, *Cystoseira barbata* co-occurred with the dominant species *C. crinita* in the lists for Corsica, Sardinia and Istria (see Fig. 6).

Comparison of potential grouping models

All of the models examined here separated the samples from sites in Istria from all other samples (Fig. 7). The single sample

from Catalonia was also quite dissimilar from the other samples, and all but the simple 3-group biogeographical model also separated this sample out from the rest. Both the 5-group and the 7-group model grouped the samples from Corsica, Sardinia and Minorca together into a single group (except for Minorca site 6, which appeared to be more similar to assemblages from sites in the eastern Mediterranean; Fig. 7). Samples from Formentera were also separated out from all other assemblages for the 5-, 7- and 11-group models. Interestingly, the assemblage from one of the sites in the eastern Mediterranean (Dodecanese site 1) was grouped with the assemblages from Formentera by these models. The models differed, however, in the degree to which assemblages from eastern Mediterranean sites (Greece and Turkey) were grouped together, and the 11-group model also introduced splits into the large group of sites comprising the Corsica–Sardinia–Minorca grouping obtained by the simpler models (Fig. 7).

The best models for grouping the samples will have a low value for AIC_c , but high values for the PERMANOVA effect size and the ANOSIM R statistic, both of which measure the degree of separation of the groups of samples in the multidimensional multivariate Bray–Curtis space. These three criteria yielded the same ranking of these models, with the 7-group model obtained by the slice in the dendrogram (at 40% Bray–Curtis similarity) being the best, followed by the 5-group model obtained from clusters seen in the 2-D NMDS ordination, followed by the 11-group SIMPROF model (Table 3). There was little to distinguish the 5-group and 7-group models in terms of these criteria and also regarding the nature of the groupings (Table 3, Fig. 7). However, all of these models were deemed to be substantially better at describing patterns in these data than the simpler 3-group biogeographical model (Table 3).

DISCUSSION

Seaweeds are the primary species of *C. crinita*-dominated assemblages, while invertebrates usually display low coverage in these shallow Mediterranean habitats. The overall consistency in total cover and cover of *C. crinita* in the assemblages from the different regions, and also the presence of the epiphyte *Halitilon virgatum* are the defining characteristics of these assemblages across the Mediterranean as a whole. Other epiphytic species that were present in all or almost all of the studied regions were the red filamentous algae *Herposiphonia secunda* and *Dasya* spp. The turf-forming *Corallina elongata* and *Rytiphlaea tinctoria*, and the encrusting *Neogoniolithon brassica-florida* were also present and abundant across almost all of these regions.

Despite these general features, marked shifts in the relative coverage of species have been detected among the studied regions. The groupings of samples obtained from the quantitative analyses in this study yielded models that fitted the data well and were better (based on independent criteria) than previous models described in the literature, which were based mainly on information regarding the presence/absence of

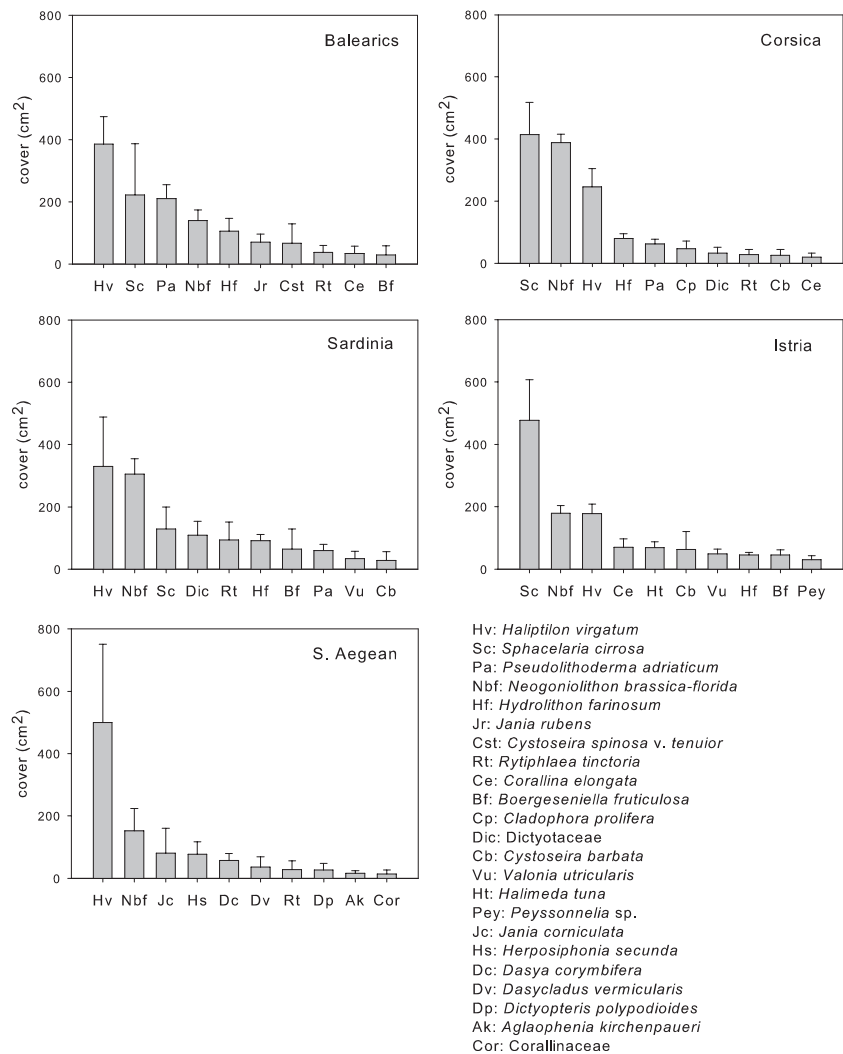


Figure 6 Mean (± 1 SE) cover of the 10 species having the greatest areal coverage (excluding *Cystoseira crinita*) in *Cystoseira crinita*-dominated assemblages for each of the five more intensively sampled areas across the Mediterranean Sea (Balearic Islands, $n = 17$; Corsica, $n = 36$; Sardinia, $n = 14$; Istria, $n = 26$; Southern Aegean Sea, $n = 7$).

species alone (Boudouresque, 2004; Bianchi, 2007; Coll *et al.*, 2010). This result accords with Adey & Steneck's idea (2001) that biogeographical regions should be determined by the relative coverage of species in assemblages. One striking exception to classical biogeographical patterns is the case of Formentera (southern Balearic Islands). The samples from this island were separated from Minorca samples (northern Balearic Islands) and placed relatively close to the samples from Dodecanese (Greece) in the NMDS plot. A similar temperature and trophic regime in the south-western Mediterranean and the eastern Mediterranean (Bosc *et al.*, 2004) could explain this result. The only sites sampled south of the 14 °C February isotherm (Brasseur *et al.*, 1996) were those in Formentera, Cyclades, Dodecanese and Lycia. Bianchi (2007) observed that the 15 °C February isotherm followed quite closely the biogeographical boundary between the western and eastern Mediterranean, and also that the 14 °C isotherm could have some biogeographical relevance. Invertebrate assemblages from the south-western Mediterranean have also been found to be more similar to those from the eastern Mediterranean than to those from the north-western Mediterranean (Bianchi,

2007). Despite this divergence between the northern and southern Balearic Islands, the distances among samples shown by the NMDS did tend to mirror the geographical positions of the regions. Similar findings, showing a high degree of spatial structure of intertidal and sublittoral assemblages at a regional scale, have been reported for the whole of Europe (Arvanitidis *et al.*, 2009), for the western coast of the USA (Blanchette *et al.*, 2008) and for the southern coast of Australia (Connell & Irving, 2008).

The relative positions of the regions in the NMDS plot suggest that longitude and latitude are more important than geographical distances *per se*. For example, Istria (northern Adriatic) appears quite close to Corsica and Sardinia, although the geographical distance by sea is fairly large. Based on the results of the NMDS and ANOSIM, *C. crinita*-dominated assemblages from Istria have more biological affinity with assemblages from the western Mediterranean than with assemblages from the eastern Mediterranean. This seems again to be related to temperature, as the winter temperatures of both the Adriatic Sea and Corsica–Sardinia are below 14 °C. Temperature has been shown to be an important factor

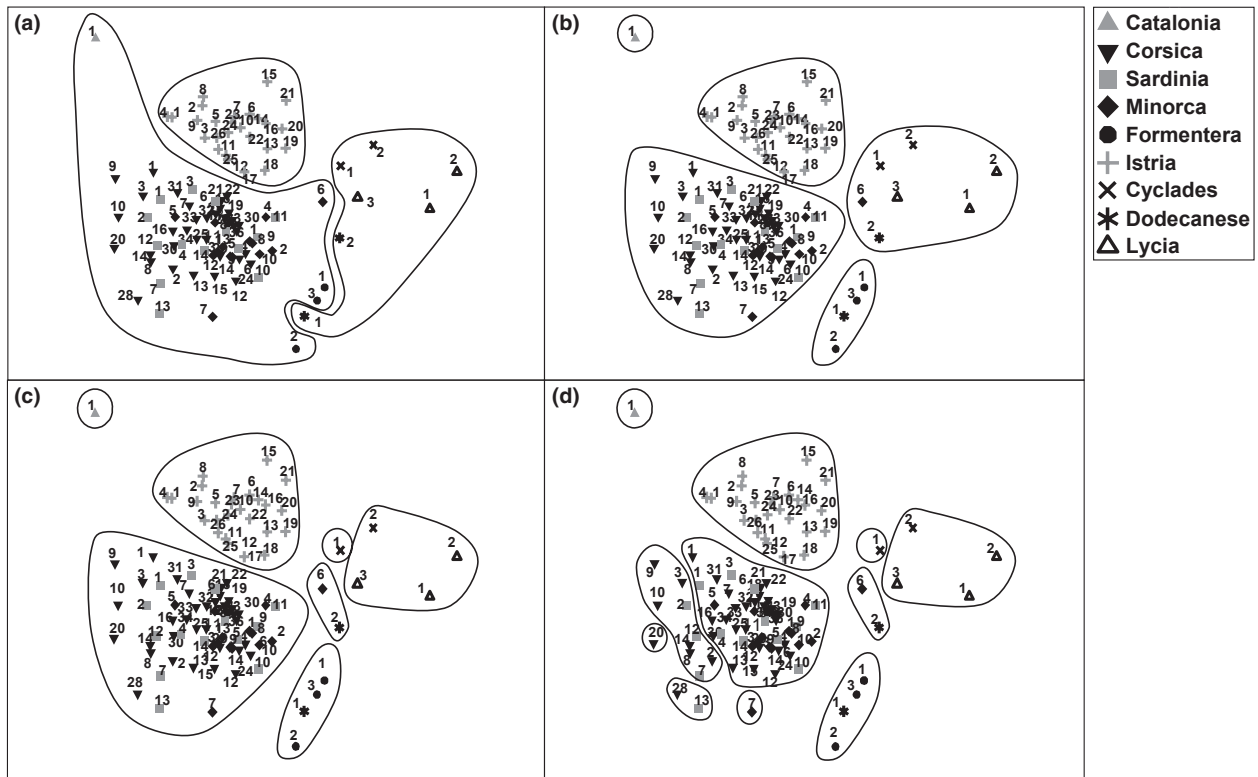


Figure 7 Non-metric multidimensional scaling (NMDS) of individual samples collected in *Cystoseira crinita*-dominated assemblages across the Mediterranean ($n = 101$), numbered by site within each of the nine sampled regions, based on the Bray–Curtis resemblance measure for species cover data after transforming to fourth roots, with groups of samples delineated according to: (a) previously described biogeographical regions (a 3-group model); (b) a 5-group model suggested by apparent separations between subset samples, observed in the NMDS plot itself; (c) a 7-group model obtained by slicing the hierarchical agglomerative group-average dendrogram at the level of 40% Bray–Curtis similarity; and (d) an 11-group model obtained by SIMPROF analysis. The stress for the 2-D NMDS shown in each panel is 0.24, which is quite high. However, the stress for the 3-D NMDS of these samples is 0.17, which is acceptable, and has highly similar patterns to those shown in the 2-D solution.

Table 3 Comparison of possible grouping models of the *Cystoseira crinita*-dominated assemblages sampled throughout the Mediterranean ($n = 101$ sites) [3-group model, previously defined biogeographical regions; 5-group model, as suggested by visual inspection of the 2-D non-metric multidimensional scaling (NMDS) plot, see Fig. 7; 7-group model, obtained by slicing the dendrogram arising from the cluster analysis at a Bray–Curtis similarity of 40%; 11-group model, obtained by SIMPROF analysis]. Values of the various criteria and the ranking assigned to each grouping model are given.

Model	AIC _c	PERMANOVA 'effect size'	ANOSIM <i>R</i>	Ranking
3-group (biogeographical)	736.2	24.07	0.645	4th
5-group (from 2-D NMDS)	731.8	26.33	0.760	2nd
7-group (dendrogram slice)	730.9	27.50	0.782	1st
11-group (SIMPROF)	731.9	26.17	0.748	3rd

AIC_c, the multivariate analogue to the Akaike information criterion corrected for small sample size (Hurvich & Tsai, 1989); PERMANOVA 'effect size', the square root of the estimated among-group component of variation from a one-way PERMANOVA model (Anderson *et al.*, 2005, 2008); ANOSIM *R*, the analysis of similarity (ANOSIM) *R* statistic (Clarke, 1993).

limiting the spatial distributions of seaweeds (Breeman, 1988; Cambridge *et al.*, 1990).

The idea that there is a gradient of species richness that decreases from west to east in the Mediterranean Sea (Boudouresque, 2004) has been reinforced by results obtained by a variety of scientists working on different groups of

organisms (Arvanitidis *et al.*, 2002; Coll *et al.*, 2010). In contrast, we did not find any significant correlation between longitude and species richness in our study. Instead, a general pattern of increasing species richness with latitude was found, reinforcing the idea that temperature (being strongly correlated with latitude) may be a key factor determining macro-

algal diversity patterns. Similarly, Renaud *et al.* (2009) found a slight increase in species richness of invertebrate assemblages with latitude in coastal European environments, which included study sites in the Mediterranean Sea. At a global scale, macroalgal richness peaks at temperate latitudes (Kerswell, 2006). It is possible that the climatic and oceanographic conditions of the northern Mediterranean, with lower temperatures and higher run-off of nutrients from rivers, are similar to those of temperate oceans, where peaks in macroalgal richness are found. Other explanations, such as higher geomorphological complexity, are unlikely, as the southernmost regions sampled in this study included several morphologically complex islands.

The cover of green algae, which is often correlated with nutrient levels (Ballesteros *et al.*, 2007), was significantly higher in Istria than in other regions. In the northern Adriatic, run-off from rivers is relatively high, mainly owing to the River Po, and water circulation is low owing to the narrowness and the shallowness of this area, making it one of the most eutrophic parts of the Mediterranean (Bosc *et al.*, 2004). There is no obvious explanation, however, for the relatively high cover of invertebrates found in the southern Aegean, but our results are consistent with those of Kocatas (1976), who described *C. crinita*-dominated assemblages with high abundance of invertebrate species in the Izmir Gulf (Aegean Sea, Turkey).

Although this study embraced a much wider area than previous, localized, studies on macroalgal assemblages (e.g. Molinier, 1960; Boudouresque, 1972; Ballesteros, 1992; Pizzuto, 1999), it is still far from including all of the potential biogeographical variation occurring in the Mediterranean Sea. Moreover, and unfortunately, the regions of Catalonia, Formentera, Cyclades, Dodecanese and Lycia were less intensively sampled than the other regions. The particular environments sheltering *C. crinita*-dominated assemblages (i.e. rocky platforms situated slightly below mean sea level in places of medium exposure and relatively high sediment loads; Ballesteros, 1992) were fairly rare in these areas, thus reducing the potential for more intensive sampling. Nevertheless, it was also in these particular (under-sampled) areas that we obtained greater variation in the results concerning the nature of appropriate groupings of communities.

We have detected large-scale biogeographical variability in *C. crinita* assemblages across the Mediterranean. We know of no similar work performed in other habitats across the entire Mediterranean Sea, but patterns observed here could possibly occur in many other habitats. A regional conservation plan for *C. crinita* and other vulnerable assemblages/habitats in the Mediterranean should take into account these biogeographical patterns and divergences. Although we did not find a longitudinal gradient in species richness, the strongest pattern in assemblage structure (including relative coverage of species) was differences from west to east (as seen along the horizontal NMDS axis in Fig. 2). Thus, localized protection of *C. crinita* assemblages alone would be insufficient to preserve variation in biodiversity for these habitats across the Mediterranean Sea as a whole.

In conclusion, the variability in species composition and in the relative coverage of species within *C. crinita*-dominated assemblages shows clear geographical patterns. However, we found some exceptions to the classical biogeographical view of the Mediterranean, which identifies a main division located near Sicily to delineate a western and an eastern basin. First, assemblages from the northern Adriatic showed a higher affinity to those from the north-western Mediterranean than to those from the eastern Mediterranean. Second, a strong shift was detected between the northern and southern Balearic Islands. Moreover, species diversity did not decrease from west to east but, rather, from north to south. These results challenge the notion that relatively low diversity is found in the eastern Mediterranean Sea, and also provide important information to assist in future management plans that may seek to preserve the intrinsic biodiversity of these habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Average coverage of species in the various geographical regions included in the study.

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