Chorotypes of seaweeds from the western Mediterranean Sea and the Adriatic Sea: An analysis based on the genera

*Audouinella* (Rhodophyta), *Cystoseira* (Phaeophyceae) and *Cladophora* (Chlorophyta)

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SUMMARY

The aim of the present paper is to identify the possible existence of groups of species in the genera *Audouinella* (Rhodophyta), *Cystoseira* (Phaeophyceae) and *Cladophora* (Chlorophyta) with significantly similar distribution patterns (chorotypes), in the western Mediterranean Sea and the Adriatic Sea. Of the 98 species studied, 59 were grouped into 11 chorotypes, whereas 39 species remained ungrouped. Thirty-eight species were included in a generalist chorotype, whereas 6 chorotypes were monospecific. The relationships with the environmental factors that could explain the chorotypes are discussed.

Key words: Adriatic Sea, *Audouinella*, biogeography, *Cladophora*, *Cystoseira*, Mediterranean Sea.

INTRODUCTION

Analytical biogeography is focused on studying the distribution of organisms by applying a deductive–hypothetical approach; for this reason, it has been considered as the most objective way to study the distributional patterns of organisms (Ball 1975). Other alternative methodological approaches to biogeographic studies are the descriptive method (usually faunistic and floristic studies) and the narrative approach, which try to explain the observed results by applying an inductive method. The analytical approach has been scarcely used in studies on the biogeography of seaweeds. Objective methods have been applied to discriminate biogeographic areas (Furnari 1984; Ribera et al. 1984; Flores & Conde 1987; Álvarez et al. 1988, 1989; Prud’homme van Reine & van den Hoek 1990) or to study geographic gradients of species richness (Álvarez et al. 1988, 1989). However, in these studies the possible significance of the groupings derived from the classification analyses was not tested and, therefore, their conclusions must be carefully scrutinized.

The geographic relationships among the distribution patterns of several species might result in a continuum gradient, that is, a gradual substitution of species in space, or in a discrete pattern, that is, a set of similar distributions spatially differentiated from other sets of similar distributions (Mayr 1965; Austin & Smith 1989; Hengeveld 1990). These two kinds of patterns could coexist for different groups of species, and it is necessary to test which type of pattern is followed by each species. Baroni-Urbani et al. (1978) propose the term ‘chorotype’ to define the pool of species that share a similar geographic distribution, but whose ranges are significantly different from those of other species. A chorotype can show the geographic area where the pool of species could potentially occur but are not necessarily found at the present time. Chorotypes have two different components: the geographic element, which is the whole area covered by any distribution of the chorotype; and the biotic element (*sensu* Birks 1987), which is the group of species whose distributions belong to the same chorotype. In this way, chorotype and biotic element are related, but are different concepts that refer to discrete biogeographic patterns. When chorotypes cannot be operatively obtained for some species, then they might be assumed to follow a continuous pattern. The identification of chorotypes is one of the topics that is advisable to study using the objective methods from analytical biogeography (Birks 1976), because other possible approaches do not allow removal of the subjective contribution to categorize the overlap in the distributions of organisms. As far as we know, no analysis of chorotypes of seaweeds has yet been carried out. To identify significant levels in the groupings of taxa, Vargas et al. (1997) propose an objective method that allows distinguishing, in the clas-
sification analysis, pools of taxa associated with a higher frequency than that corresponding to a random probability and, therefore, to identify chorotypes.

With the aim of studying the distribution patterns of seaweeds, the present paper analyzes the possible existence of chorotypes in the genera *Audouinella* (Rhodophyta), *Cystoseira* (Phaeophyceae) and *Cladophora* (Chlorophyta) in the western Mediterranean Sea and the Adriatic Sea using a deductive–hypothetical approach. The present study is a complement to the studies carried out to identify biogeographic areas (Báez et al. 2004) and to analyze the species richness (Báez et al. 2005) of the same taxa in this geographic area. In these three previous studies, as well as the present study, typical objective methods from analytical biogeography were followed.

**MATERIALS AND METHODS**

**Study area and selected taxa**

The study area was restricted to the western Mediterranean Sea and Adriatic Sea because of the scarcity of floristic studies in the eastern Mediterranean Sea. A total of 98 species (43 in *Audouinella*, 29 in *Cystoseira* and 26 in *Cladophora*) were considered in the present study, as compiled in Báez et al. (2004). According to recent molecular systematic research, *Audouinella* and *Cladophora* are not natural, monophyletic groups (Bakker et al. 1994; Hanuyda et al. 2002; Harper & Saunders 2002). However, monophyly of the taxa to be studied in analytical biogeography is not necessary; moreover, this is also true in the studies of chorotypes, because every species corresponds to an independent bit of data, and the relationships among the species do not modulate the patterns of chorotypes.

Continental shelves close to hydrographical basins and islands were selected as operative geographical units (OGU, Fig. 1). Geographical boundaries of the OGU are explained in Table 1.

**Probabilistic classification analysis to recognize chorotypes**

Real et al. (1992a) applied the approach of McCoy et al. (1986) to develop a probabilistic procedure for recognizing chorotypes. Following this approach, we obtained a matrix of geographic similarities between the distributions of each pair of species a and b using the Baroni-Urbani and Buser’s (1976) index (BUB):

$$BUB = \frac{\sqrt{(CD) + C}}{\sqrt{(CD) + A + B - C}}$$

where A is the number of OGU where species a is present, B is the number of OGU where species b is present, C is the number of OGU where both species a and b are present, and D is the number of OGU where both species are absent.

To group the species into chorotypes, the Unweighted Pair-Group Method using the Arithmetic

![Fig. 1. Operative geographical units (OGU) from the western Mediterranean Sea and Adriatic Sea. Key to OGU: 1, Ibero-Mediterranean; 2, Ebro; 3, Balearic Islands; 4, Corsica and Sardinia; 5, Sicily; 6, Rhone; 7, Po; 8, Tyrrenian; 9, Italo-Adratic; 10, Balkano-Adratic; 11, Tunisia; 12, Algeria; 13, Morocco. Boundaries of each OGU are explained in Table 1.](image)
Averages (UPGMA) procedure was selected (Sneath & Sokal 1973).

Using the critical values in Baroni-Urbani and Buser (1976), the similarity matrix was transformed into a matrix of significant similarities, in which each value of the BUB index was transformed to ‘+’, ‘–’ or ‘0’, depending on whether the values of BUB were higher than, lower than, or similar to that expected at random, respectively (Real et al. 1992b; Márquez et al. 1997).

We considered chorotypes to be those clusters that best combined the following characteristics: a high proportion of significant similarities (+) within the cluster; a low proportion of significant dissimilarities (–) within the cluster; and a low proportion of significant similarities (+) between the distributions of the cluster and the distributions of its most similar cluster. The degree to which a distribution cluster M combines these conditions is provided by the parameter \( DW(M \times M) \) (McCoy et al. 1986). For the mathematical expansion of this parameter, see Báez et al. (2004), who used it to discriminate biogeographic areas rather than chorotypes. In this way, we computed the \( DW(M \times M) \) values for every branch of the dendrogram. A cluster was considered a chorotype if: (i) \( DW(M \times M) = 0.7071 \); that is, the maximum possible value; or (ii) \( DW(M \times M) \) was positive, higher than those of the other clusters including the distributions involved, and a \( G \)-test of independence, which yielded the parameter GS, showed that the proportion of ‘–’ signs was significantly higher between the chorotypes than within them; otherwise the segregation was weak. The parameter GS and \( GW(M \times M) \) follow the \( \chi^2 \) distribution with one degree of freedom.

**Environmental characterization of the chorotypes**

Logistic regressions were performed to test the possible relationships of the chorotypes with environmental or historical factors. For this purpose, we used the environmental variables included in Table 2. We selected the best significant fit in accordance with the \( \chi^2 \)-test (Sokal & Rohlf 1995). An image analysis system was used to obtain the distance values from a given OGU to the Strait of Gibraltar and the surface area of the photic zone. The minimum distance from the Strait of Gibraltar to the OGU was defined as the distance from a given OGU to the Strait of Gibraltar along the course of the main current of the Mediterranean Sea. The surface area of the photic zone of a given OGU was defined as the surface area delimited by the shoreline and the 50 m depth isobath. Overall mean values of surface current flow, latitude, mean temperatures in August and February, salinity and solar radiation were calculated in every OGU using the figures shown in different areas included in the OGU. The values of runoff were

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**Table 1.** Operative geographical units (OGU) used in the present study, and their respective geographic boundaries. Numbers correspond to those used in Figure 1

<table>
<thead>
<tr>
<th>OGU</th>
<th>Number</th>
<th>Geographical boundaries</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ibero-Mediterranean</td>
<td>1</td>
<td>From the Strait of Gibraltar to the north of Castellón (Spain)</td>
</tr>
<tr>
<td>Ebro</td>
<td>2</td>
<td>From the north of Castellón (Spain) to the Pyrenees</td>
</tr>
<tr>
<td>Balearic Islands</td>
<td>3</td>
<td>From the Pyrenees to the Gulf of Genoa</td>
</tr>
<tr>
<td>Corsica and Sardinia</td>
<td>4</td>
<td>From Ancona (Italy) to the Gulf of Trieste</td>
</tr>
<tr>
<td>Sicily</td>
<td>5</td>
<td>From the Gulf of Genoa to Catanzaro (Italy)</td>
</tr>
<tr>
<td>Rhone</td>
<td>6</td>
<td>From Catanzaro (Italy) to Ancona (Italy)</td>
</tr>
<tr>
<td>Po</td>
<td>7</td>
<td>From the Gulf of Trieste to the Strait of Otranto</td>
</tr>
<tr>
<td>Tyrrenian</td>
<td>8</td>
<td>From the Gulf of Gabès to Tizi-Ouzzou (Algeria)</td>
</tr>
<tr>
<td>Italo-Adriatic</td>
<td>9</td>
<td>From Tizi-Ouzzou (Algeria) to Mostaganem (Algeria)</td>
</tr>
<tr>
<td>Balkano-Adriatic</td>
<td>10</td>
<td>From Mostaganem (Algeria) to the Strait of Gibraltar</td>
</tr>
<tr>
<td>Tunisia</td>
<td>11</td>
<td>From the Strait of Gibraltar to the north of Castellón (Spain)</td>
</tr>
<tr>
<td>Algeria</td>
<td>12</td>
<td>From Castellón (Spain) to the Pyrenees</td>
</tr>
<tr>
<td>Morocco</td>
<td>13</td>
<td>From the Pyrenees to the Gulf of Genoa</td>
</tr>
</tbody>
</table>
calculated as the difference between rain precipitation and evaporation, computing the overall mean as was explained above for other variables. Single tidal amplitudes were obtained only for two of the OGU, and an overall mean amplitude of 15 cm was assumed in the remaining OGU because no significant tides occur in the Mediterranean Sea (Rodríguez 1982). Data sources of all variables are shown as references in Table 2.

RESULTS AND DISCUSSION

Fifty-nine species were distributed in 11 chorotypes (Fig. 2), whereas 39 species were not pooled in significant groups. Thirty-eight species were included in chorotype IV, with an extensive geographic distribution in the study area. The other species were distributed in 10 different chorotypes, 6 of them monospecific.

Chorotype I (Fig. 3)

This chorotype includes Audouinia alariae (Jönsson) Wolkerling, Audouinia gracilis (Børgesen) Jaasund, Audouinia gynandra (Rosenvinge) Garbary, Cystoseira abies-marina (S. G. Gmelin) C. Agardh, Cystoseira hyblaea Giaccone, and Cystoseira susanensis Nizamud-din. No environmental explanations were deduced for this chorotype by applying logistic regression.

Chorotype II (Fig. 4)

This chorotype includes Audouinia endozoica (Darbishire) P. S. Dixon, Cystoseira foeniculacea (Linnaeus) Greville, Cystoseira mauritanica Sauvageau and Cystoseira nodicaulis (Whithering) M. Roberts. A significant relationship ($\chi^2 = 11.162, P = 0.0008$) was found between this chorotype and the lowest values of salinity in the geographic area. The chorotype is restricted to the western Mediterranean Sea, including the Ibero-Mediterranean and Morocco OGU.

Chorotype III (Fig. 5)

This monospecific chorotype includes only Cladophora vadorum (J. Areschoug) Kützing. No environmental explanation was deduced for this chorotype by applying logistic regression.

Chorotype IV

This chorotype includes Audouinia alariae (Jönsson) Wolkerling, Audouinia gracilis (Børgesen) Jaasund, Audouinia codii (H. M. Crouan et P. L. Crouan) Garbary, Audouinia daviesii (Dillwyn) Woelkerling, Audouinia duboscquii (J. Feldmann) Garbary, Audouinia hauckii (Schiffnerr) Ballesteros, Audouinia humilis (Rosenvinge) Garbary, Audouinia leptonema (Rosenvinge) Garbary, and Audouinia mediterranea (Rosenvinge) Garbary. This chorotype includes 38 species, 13 in the genus Audouinia (Audouinia codii (H. M. Crouan et P. L. Crouan) Garbary, Audouinia daviesii (Dillwyn) Woelkerling, Audouinia duboscquii (J. Feldmann) Garbary, Audouinia hauckii (Schiffnerr) Ballesteros, and Audouinia humilis (Rosenvinge) Garbary, Audouinia leptonema (Rosenvinge) Garbary, and Audouinia mediterranea (Rosenvinge) Garbary). This chorotype was included in the study area. The other species were distributed in 10 different chorotypes, 6 of them monospecific.

Table 2. Variables considered in the present study, and mean values of the variables in every operative geographical unit (OGU) (key of OGU as explained in Table 1).

<table>
<thead>
<tr>
<th>Variable (units)</th>
<th>OGU</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from an OGU to the Strait of Gibraltar (km) †</td>
<td>0 2250 2325 1375 1625 1825 6875 1988 6625 5875 750 400 0</td>
<td>Lacombe and Tchernia (1972)</td>
</tr>
<tr>
<td>Current flow ($\times 10^{-9}$ m$^3$ year$^{-1}$)</td>
<td>52.4 37.8 37.8 23.9 20.5 31.9 32.0 22.8 22.8 22.8 49.0 51.7 52.4</td>
<td>Rodríguez (1982)</td>
</tr>
<tr>
<td>Latitude (degrees N)</td>
<td>38.3 41.4 39.4 40.8 37.5 43.5 44.8 41.2 42.0 42.8 35.5 37.0 35.5</td>
<td>Espenshade et al. (1980)</td>
</tr>
<tr>
<td>Mean temperature in August ($°C$)</td>
<td>23.0 23.5 24.5 23.5 25.5 22.0 24.5 24.0 25.0 24.5 24.0 24.0 23.0</td>
<td>Lüning (1990), Verlaque (1994)</td>
</tr>
<tr>
<td>Mean temperature in February ($°C$)</td>
<td>13.5 13.0 13.0 12.5 13.0 12.5 10.0 13.0 11.6 11.6 14.0 13.5 14.0</td>
<td>Lüning (1990), Verlaque (1994)</td>
</tr>
<tr>
<td>Salinity (%)</td>
<td>36.4 38.0 38.0 37.7 37.8 38.0 38.6 38.0 38.6 38.6 37.0 36.0 36.0</td>
<td>Rodríguez (1982)</td>
</tr>
<tr>
<td>Runoff (mm)</td>
<td>52.4 37.8 37.8 23.9 20.5 31.9 32.0 22.8 22.8 22.8 49.0 51.7 52.4</td>
<td>Rodríguez (1982)</td>
</tr>
<tr>
<td>Solar radiation ($kJ cm^2 year^{-1}$)</td>
<td>663 600 636 580 604 548 533 581 574 583 652 638 696</td>
<td>Sawyer Hopkins (1989)</td>
</tr>
<tr>
<td>Surface area of the photic zone ($\times 10^3$ km$^2$)</td>
<td>24.2 5.9 9.7 20.2 12.1 15.4 9.6 23.7 69.0 30.8 106.2 4.8 8.4</td>
<td>Espenshade and Morrison (1980)</td>
</tr>
<tr>
<td>Tidal amplitude (cm)</td>
<td>15 15 15 15 15 15 100 15 15 15 200 15 15</td>
<td>Rodríguez (1982)</td>
</tr>
</tbody>
</table>

† Measured along the course of the main current of the Mediterranean Sea.
Chorotypes of seaweeds

Fig. 2. Significant chorotypes for the species of the genera *Audouinella*, *Cystoseira* and *Cladophora*, in the western Mediterranean Sea and the Adriatic Sea. Key of operative geographical units (OGU): 1. Ibero-Mediterranean; 2, Ebro; 3, Balearic Islands; 4, Corsica and Sardinia; 5, Sicily; 6, Rhone; 7, Po; 8, Tyrrhenian; 9, Italo-Adratic; 10, Balkano-Adratic; 11, Tunisia; 12, Algeria; 13, Morocco. Boundaries of each OGU are explained in Table 1.

Fig. 3. Geographical distribution in the western Mediterranean and the Adriatic Sea of chorotype I, formed by *Audouinella alariae*, *Audouinella gracilis*, *Audouinella gynandra*, *Cystoseira abies-marina*, *Cystoseira hyblaea* and *Cystoseira susanensis*.
Fig. 4. Geographical distribution in the western Mediterranean and the Adriatic Sea of chorotype II, formed by Audouinella endozoaica, Cystoseira foeniculacea, Cystoseira mauritanica and Cystoseira nodicaulis.

Fig. 5. Geographical distribution in the western Mediterranean and the Adriatic Sea of the monospecific chorotype III formed by Cladophora vadorum.

Cystoseira mediterranea Sauvageau, Cystoseira sau-vageauana G. Hamel, Cystoseira schiffreri G. Hamel, Cystoseira spinosa Sauvageau and Cystoseira zosteroides (Turner) C. Agardh; and 13 in the genus Cladophora (C. aegagropila (Linnaeus) Rabenhorst, C. albida (Nees) Kützing, Cystoseira coelothrix Kützing, Cystoseira dalmatica Kützing, Cystoseira hutchinsiae (Dillwyn) Kützing, Cystoseira laeleviren (Dillwyn) Kützing, Cystoseira lehmanniana (Lindenberg) Kützing, Cystoseira pellucida (Hudson) Kützing, Cystoseira prolifer (Roth) Kützing, Cystoseira ruchingeri (C. Agardh) Kützing, Cystoseira rupestris (Linnaeus) Kützing, Cystoseira sericea (Hudson) Kützing and Cystoseira vagabunda (Linnaeus) van den Hoek). This chorotype is present throughout the geographic area, which suggests that these species do not encounter significant ecologic restrictions in the study area, probably because no relevant environmental gradients are present in the
western Mediterranean (Rodríguez 1982; Cruzado 1989).

**Chorotype V (Fig. 6)**

This monospecific chorotype contains only the Mediterranean endemic *Cystoseira dubia* Valiante; the geographic area of the chorotype is explained by the mean temperature in August ($\chi^2 = 6.076, P < 0.01$). It is distributed in the Tunisia, Sicily and Tyrrenhian OGU, and on the shores of the Adriatic Sea.

**Chorotype VI (Fig. 7)**

This monospecific chorotype contains only the Adriatic endemic *Audouinella extensa* (Ercegovic) F. Conde Poyales, and could be explained by the surface area of the continental shelf ($\chi^2 = 7.051, P < 0.008$). Arrhenius (1921) proposes that species richness increases as the surface area of a given territory increases. Following this reasoning, Lomolino (2001) suggests that as the surface area increases, speciation processes could occur that give rise to endemic taxa.
Chorotype VII (Fig. 8)

This monospecific chorotype corresponds to *Audouinella minutissima* (Zanardini) Garbary, and cannot be explained by the environmental factors used in the present study.

Fig. 8. Geographical distribution in the western Mediterranean and the Adriatic Sea of the monospecific chorotype VII formed by *Audouinella minutissima*.

Chorotype VIII (Fig. 9)

This chorotype is defined by the species *Audouinella caesarace* (J. Feldmann) F. Conde Poyales and *Audouinella porphyrae* (Drew) Garbary. No environmental explanation was deduced for this chorotype by applying logistic regression.

Fig. 9. Geographical distribution in the western Mediterranean and the Adriatic Sea of chorotype VIII, formed by *Audouinella caesarace* and *Audouinella porphyrae*.

Chorotype IX (Fig. 10)

This monospecific chorotype contains only *Audouinella membranacea* (Magnus) Papenfuss, and cannot be correlated with any of the environmental variables used in the present study.
Chorotype X (Fig. 11)

This monospecific chorotype contains only *Cystoseira sedoides* (Desfontaines) C. Agardh, and can be explained by the lowest latitude in the study area ($\chi^2 = 6.178$, $P = 0.01$), because the species is endemic from north-western Africa and adjacent islands (Ribera et al. 1992).

Chorotype XI (Fig. 12)

This chorotype includes *Audouinella floridula* (Dillwyn) Woelkerling, *Audouinella maluina* (Hamel) South et Tittley and *Cystoseira barbatula* Kützing. No environmental explanation was deduced for this chorotype by applying logistic regression.
Validity of the deductive–hypothetical approach

The procedures followed in the present study allow objective methods to be used to identify chorotype patterns, and to correlate the geographic patterns of the chorotypes with several environmental variables. However, clear limitations of the study are linked to the sampling of taxa in every OGU, the lack of homogeneity of taxonomic criteria used by the authors who compiled the floras from each territory, and differences in the intensity of sampling along each shore. Therefore, the conclusions derived from the present study must not be considered definitive, but as a first milestone toward further studies. The strength of conclusions in further analyses will be linked to improvements in floristic studies. Moreover, only 4 of the 11 chorotypes have been explained by the environmental variables considered in the present study, suggesting that new hypotheses about distributions of seaweeds could be generated if other environmental variables were included.

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REFERENCES


