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1 **Differences in spatial and seasonal patterns of macrophyte assemblages between a**  
2 **coastal lagoon and the open sea**

3  
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5  
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15  
16 **Abstract**

17  
18 Although benthic macrophytes must be considered in monitoring programs to establish  
19 the ecological status of transitional and coastal waters in the European Union, the  
20 patterns of variability in species composition of macrophyte assemblages in  
21 Mediterranean coastal lagoons has scarcely been studied. In this work the spatial (both  
22 vertical and horizontal) and seasonal dynamics of macrophyte assemblages in a coastal  
23 lagoon (Mar Menor) are compared with those of open coastal assemblages in the SW  
24 Mediterranean to analyze any biological variability in lagoon assemblages and the  
25 factors that determine such variability. Different assemblages, characterized by well  
26 defined groups of species, can be described according to their isolation from the open  
27 sea and the type of substratum; at the same time, a vertical zonation pattern, similar to  
28 that found in all marine communities but more compressed, exists. This implies that  
29 when applying the EU Water Framework Directive or assessing environmental impact,  
30 a lagoon should not be considered spatially uniform and unique unit but as a mosaic of  
31 assemblages.

32  
33 **Keywords:** macrophyte assemblages; coastal lagoons; spatio-temporal variability;  
34 environmental impact assessment; Mar Menor

35  
36 **1. Introduction**

37  
38 Coastal lagoons have traditionally been considered as transitional systems between  
39 continental and marine domains (Bianchi, 1988 a), a consideration that has gained in  
40 importance in the context of the *Water Framework Directive (WFD)* of the European  
41 Union. The *WFD* requires scientific and biological criteria to establish the basis for

42 typifying coastal ecosystems and transition waters (lagoons and estuaries). In the case of  
43 the former, such criteria have long been established, while for transitional waters they  
44 do not exist. The proposed criteria are not the same for both categories and, while there  
45 is no doubt about the nature of estuaries, there is some controversy as to whether  
46 lagoons should be treated as coastal or transitional waters.

47

48 Furthermore, in accordance with the *WFD*, the ecological status of a water body must be  
49 evaluated using biological indicators, including macroalgae and seagrasses in the  
50 context of hydromorphological and physico-chemical conditions (Ballesteros et al.,  
51 2007). In general, benthic macrophytes are considered good indicators of water quality  
52 and different indices and methodologies based on them have been proposed for  
53 assessing the ecological status of coastal and transitional waters in the context of the  
54 *WFD* (Pasqualini et al., 2006; Austoni et al., 2007; Ballesteros et al., 2007; Pinedo et al.,  
55 2007; Wells et al., 2007). However, their application to transitional waters presents  
56 difficulties as a consequence of changes in species composition along the natural  
57 gradients of environmental conditions in these ecosystems (Wilkinson et al., 2007).  
58 Some recent proposals look at the problem in estuarine transitional waters but explicitly  
59 exclude lagoons (Wilkinson et al., 2007).

60

61 Coastal lagoons undergo frequent physical and chemical disturbances and fluctuations  
62 (Unesco, 1981) and are consequently naturally stressed habitats (Barnes, 1980). They  
63 are characterized by particular features, such as shallowness, relative isolation from the  
64 open sea, usually as a result of coastal barriers that maintain some communication  
65 channels or inlets, and the presence of boundaries with strong physical and ecological  
66 gradients (Unesco, 1981). Due to their shallowness, bottoms are usually well irradiated,  
67 while currents and hydrodynamics are closely conditioned by bottom topography and  
68 wind affects the entire water column, promoting the resuspension of materials and  
69 nutrients from the sediment surface layer. Because of these characteristics, coastal  
70 lagoons are usually among the marine habitats that show the greatest biological  
71 productivity (Alongi, 1998).

72

73 Pérès and Picard (1964) considered Mediterranean lagoon systems as a well  
74 differentiated and unique homogeneous community, the so-called euryhaline and  
75 eurythermal biocenoses. This consideration was maintained by later authors, such as  
76 Augier (1982) and Guelorget and Perthuisot (1983), and in the habitat lists of  
77 conservation agreements, including OSPAR, Barcelona and Eunis. Although benthic  
78 macrophytes must be considered in monitoring programs to establish the ecological  
79 status of transitional and coastal waters (European Union, 2000), and despite a number  
80 of papers that study species composition in transitional waters, the patterns of variability  
81 of macrophyte assemblages in coastal lagoons have scarcely been studied in the  
82 Mediterranean. A few studies have explicitly characterized different communities or  
83 phytocoenoses according to the water characteristics in one or several lagoons (Lovric,  
84 1979; Zouali, 1979; Chassany de Casabianca, 1980) or described vertical zonation  
85 patterns (Cecere *et al.*, 1988, Sfriso, 1987). However, some papers that analyze the

86 differences in species distribution or biomass related to environmental variables such as  
87 salinity or trophic conditions (Sfriso et al., 2003; Curiel et al., 2004; Lin and Hung,  
88 2004), do not consider the possibility of several communities existing in lagoons,  
89 similar to those existing in coastal marine habitats, or, when referring to heterogeneity,  
90 assume a single algal community for the whole lagoon (Cecere et al., 1992). In general,  
91 and in accordance with the proposal of Péres and Picard (1964), benthic macrophytes  
92 are considered to constitute a single assemblage within each lagoon (Chassany de  
93 Casabianca, 1979; Nagy, 1979; Skolka and Tiganus, 1985; Cecere et al., 1991; Bachelet  
94 et al., 2000; Mouillot et al., 2005). Because of this, such habitats are managed as units,  
95 with decisions adopted at lagoon scale, whereas different areas of each lagoon might  
96 require different management options (De Biasi et al., 2003).

97  
98 Inter-lagoon variability has been attributed to many biotic and abiotic factors (Ross and  
99 Epperly, 1985; Yañez-Arancibia et al., 1985) and, as regards the functioning of coastal  
100 lagoon ecosystems, several proposals have been made using different criteria to classify  
101 and typify these environments. Among these proposals, some of the most important use  
102 salinity as the main parameter (Anonymous, 1959; Petit, 1953; Por, 1972). Using  
103 salinity as a descriptor involves considering autoecological criteria as a classification  
104 basis, making the use of indicator species feasible (Bianchi 1988a, 1988b).

105  
106 However, intra-lagoon variability also exists and has been related to depth (Sfriso,  
107 1987; Pasqualini et al., 2006), type of substratum (Pérez-Ruzafa et al., 1989, 2006) and,  
108 especially, confinement gradient *sensu* Guelorget and Perthuisot (1983) an indicator of  
109 the degree of marine influence on lagoon ecosystems (Mariani, 2001).

110  
111 Kjerfve (1994) also sub-divided coastal lagoons into three geomorphic types (choked,  
112 restricted and leaky), which the author considered as three points along a spectrum of  
113 water exchange with the coastal sea. The rate and magnitude of oceanic exchange  
114 reflects both the dominant forcing functions and the time-scale of hydrological  
115 variability.

116  
117 The physical gradients within the lagoon environment arising from these exchange rates  
118 have been related to biological gradients in species richness, abundance and  
119 productivity. In the early 1980's, Guelorget and Perthuisot (Guelorget and Perthuisot,  
120 1983; Guelorget et al., 1983) rejected salinity as an essential parameter for explaining  
121 the observed gradients in density, biomass, species richness and diversity and proposed  
122 that zonation patterns and species distribution inside the lagoons were determined by  
123 the degree of confinement, a parameter which represents the turnover time of marine  
124 water and the impoverishment in some oligo-elements of marine origin. Later, as  
125 regards the structure of faunal lagoon assemblages, Pérez-Ruzafa and Marcos (1992,  
126 1993) suggested that, rather than vitamin and oligo-element recycling, the main factor  
127 explaining them along a confinement gradient would be colonization rates by marine  
128 species. The species composition in each lagoon site will be the result of equilibria, in  
129 the context of interspecific competition between marine and lagoon species.

130

131 According to this, lagoon assemblages would be the result of complex environmental  
132 and biological interactions, and not only a response to the extreme physico-chemical  
133 conditions or to a single horizontal gradient. The structure and composition of lagoon  
134 communities would be better described by sinecological criteria and the same structural  
135 parameters as in open coastal areas. In this way, multifactorial approaches and structural  
136 indices of lagoon assemblages could be used to describe the ecological status of a  
137 particular lagoon site and community.

138

139 In this work, we study the spatial (both vertical and horizontal) and seasonal dynamics  
140 of macrophyte assemblages in a coastal lagoon, compared with those of open coastal  
141 assemblages in the SW Mediterranean, to analyze biological variability in lagoon  
142 assemblages, the factors that determine this variability, and the degree of differentiation  
143 between lagoon and open coastal macrophyte assemblages. The data used for this work  
144 pre-date the changes that have occurred in the trophic status of the Mar Menor waters in  
145 the last ten years (Pérez-Ruzafa et al., 2002) so that they are useful for the establishment  
146 of reference conditions in this lagoon for the implementation of the WFD.

147

## 148 **2. Material and methods**

149

### 150 *2.1. Study area*

151 The Mar Menor is a hypersaline coastal lagoon, with a surface area of 135 km<sup>2</sup> located  
152 on the southwestern Mediterranean coastline (37°42'00" North – 00°47'00" West) (Fig.  
153 1) with a mean depth of 3.6 m and maximum of about 6 m. The salinity of the lagoon  
154 waters range from 42 to 46. The bed sediment grain size composition is predominantly  
155 muddy and sandy, with some areas of natural rocky bottoms around islands and some  
156 calcareous and volcanic outcrops. Muddy bottoms, which cover both the whole central  
157 area of the lagoon and the shallow zones showing lower hydrodynamism, are covered  
158 by a dense meadow of the algae *Caulerpa prolifera* (Forsskål) J.V. Lamouroux or  
159 patches of the sea grass *Ruppia cirrhosa* (Petagna) Grande. Sandy bottoms (with sand  
160 content up to 89%) are located at the margins of the basin and in the small bays  
161 surrounding the islands, in which sparse patches of the phanerogame *Cymodocea*  
162 *nodosa* (Ucria) Asch. grow.

163

### 164 *2.2. Sampling methods*

165 To study the spatial and seasonal patterns of lagoon macrophyte assemblages, three  
166 localities (two inside the lagoon and another on the Mediterranean coast) were sampled  
167 monthly from June 1995 to October, 1996. Sampling sites were located where there was  
168 no significant waste input from human activity based on our knowledge of the main  
169 sources of agricultural runoff inputs (Pérez-Ruzafa et al., 2000), the available  
170 information on the distribution of urban wastes, coliform bacteria and heavy metals in  
171 sediments and organisms (Marcos, 1991) and visual survey. The outer locality was  
172 located at Cala Fría in the Cabo de Palos Marine Reserve, close to the Mar Menor  
173 lagoon (Fig. 1), in a relatively wind-protected area to avoid excessive differences in

174 wave exposure compared with the lagoon localities. Of the two inner localities, one was  
175 close to the main channel through which water exchange takes place, and the other one  
176 was located in the southern basin, considered the most isolated and confined area of the  
177 lagoon (Pérez-Ruzafa, 1989; Pérez-Ruzafa et al., 2004, 2005a, 2005b).

178

179 Macrophyte assemblages were sampled monthly by diving. All macrophyte species  
180 were hand-collected in a square of 400 cm<sup>2</sup> (20 x 20 cm), a size considered  
181 representative for midlittoral and infralittoral Mediterranean macrophyte communities  
182 (Cinelli et al., 1977; Cecere et al., 1988; Ballesteros, 1992, 1993). Two replicates,  
183 randomly distributed, were taken for each sample and the species were determined at  
184 specific level. One of the samples was used for biomass estimations for this work and  
185 the second was used for pigment extraction. Sampled open coastal assemblages include  
186 midlittoral photophilous algae on rock (MPhR), infralittoral photophilous algae on rock  
187 (IPhR), infralittoral sciaphilous assemblage on rock (IScR) and *Posidonia oceanica*  
188 meadow (PM). Inside the lagoon, samples were taken of MPhR a few centimetres under  
189 the mean water level and at 1.5 m depth, both in well illuminated (IPhR) and in  
190 sciaphytic environments (IScR). Furthermore we sampled the *Cymodocea nodosa*  
191 meadow (CyM) on sand and the *Caulerpa prolifera* meadow (CaM) on mud.

192

193 Macrophyte samples were kept in a cool-box and taken to the laboratory, where samples  
194 were washed using clean sea water to remove sediments and then spread out in a tray  
195 containing sea water to estimate the percentage of cover for each species according to  
196 Cox (1981). After species level identification, the standing crop biomass for each  
197 species was measured in terms of both dry weight (DW) and ash free dry weight  
198 (AFDW). DW determination was made by drying to constant weight (24 h) in an oven  
199 at 110°C, and subsequently AFDW was determined by burning in a furnace at 450°C for  
200 6 h. Weight was calculated with a precision of ± 0.0001 g. The classification and  
201 nomenclature in this study follows that adopted by Guiry and Guiry (2007).

202

203 Key hydrographic (hydrodynamism, nutrient concentration in water column, pH,  
204 temperature and salinity) and sediment characteristics were recorded monthly at the  
205 three stations during the study period.

206

207 The water column is well mixed and there were no significant differences in  
208 temperature or salinity with depth (Pérez-Ruzafa, 1989), so that water samples for  
209 environmental variables were taken at an approximate depth of 1 m with a Niskin bottle,  
210 or by pumping. Samples for nutrient analysis were kept in the dark at 4°C in the field  
211 and stored at -28 °C. Nitrate (NO<sub>3</sub>-N), nitrite (NO<sub>2</sub>-N), ammonium (NH<sub>4</sub>-N) and  
212 phosphate (PO<sub>4</sub>-P) were determined, following the methods described by Parsons et al.  
213 (1984). To determine salinity a Beckman RS 7B salinometer was used, while pH  
214 measurements were made with a pre-calibrated meter.

215

216 At each site, hydrodynamism (as represented by wave exposure) was estimated  
217 according to Keddy (1983) as follows:

218

219 Wave Exposure =  $\sum$  (mean wind velocity<sub>22.5°</sub> \* wind frequency<sub>22.5°</sub> \* effective fetch<sub>22.5°</sub>)

220

221 where the effective fetch ( $F_e$ ) is the direct fetch ( $F$ ), or distance in kilometres along  
 222 which the wind blows from each direction, corrected by fetches in directions of less  
 223 than 45° using the equation,

224

225  $F_e = [F_{(\alpha)} * \cos \alpha + F_{(\alpha + 22.5)} * \cos (\alpha + 22.5) + F_{(\alpha - 22.5)} * \cos (\alpha - 22.5)] / [\cos \alpha + 2 * \cos (\alpha + 22.5)]$

226

227 where  $\alpha$  is equal to 0 for each  $F_e$  calculated.

228

229 Sediment samples were taken by diving in the communities on soft substrata, such as  
 230 sandy bottoms with *Cymodocea nodosa* or *Posidonia oceanica* meadows, and muddy  
 231 bottoms covered by *Caulerpa prolifera* meadows. Samples were hand taken from the  
 232 top 10 cm of the substrata using a shovel, stored and transported in darkness and cold in  
 233 polyurethane bags. At the laboratory they were dried at room temperature. During this  
 234 process they were stirred to break lumps before being sifted to a size of 2 mm. Grain  
 235 size distribution was determined in sub-samples by the Bouyoucos hydrometer method  
 236 (Soil Conservation Service, 1973) after dispersion of clusters by mechanical stirring in a  
 237 sodic-hexametaphosphate and  $\text{Na}_2\text{CO}_3$  solution. Previously, salts were eliminated by  
 238 washing and centrifugation and organic matter was eliminated by hydrogen peroxide  
 239 treatment. Grain size classification was made according to the International Association  
 240 for Soil Science (Duchafour, 1975). Organic carbon was determined by the Walkley-  
 241 Black method (Buchanan, 1984) and total nitrogen by the Kjeldahl method (Bremmer,  
 242 1965).

243

244 

### 245 2.3. Data analyses

246 Macrophyte assemblage structure was specified for each sample according to its species  
 247 richness and species composition, abundance (percentage of cover and biomass), and  
 248 Shannon-Wiener's diversity  $H'$ . For each species we estimated its relative dominance  
 249 (% D) in each assemblage and frequency of occurrence ( $f$ ), classifying them into  
 250 frequent (F) ( $f \geq 40\%$  corresponding to more than 7 months during the study period),  
 251 seasonal (S) ( $18\% \leq f < 40\%$ ) and occasional (O) ( $f < 18\%$ ) species.

252

253 To study the affinity between samples, Jaccard's coefficient (Day et al., 1971; Margalef  
 254 1974) was applied using presence-absence data. Spatial and temporal variations in the  
 255 structure of the vegetation assemblages were assessed by non-metric multi-dimensional  
 256 scaling (MDS) and analyses of similarities (ANOSIM), using the statistical software  
 257 PRIMER 5.0 (Clarke and Warwick, 2001) and similarity matrices based on the Bray-  
 258 Curtis similarity coefficient generated with biomass (DW) data. Values were square-  
 259 root transformed before the analyses so that each species contributed fairly evenly to  
 260 each analysis (Clarke and Green, 1988). Pairwise ANOSIM comparisons were made  
 261 between all groups, using 10000 simulations in each case. Furthermore, site ordination



262 was also conducted using detrended correspondence analysis (DCA) on the records of  
263 biomass (DW) of each species using the CANOCO 3.15 (ter Braak, 1997).

264

265 To explore the spatial variation of macrophyte assemblages in relation to environmental  
266 characteristics, we performed a Canonic Detrended Correspondence Analysis (DCCA) (ter  
267 Braak and Prentice 1988) using both square-root transformed cover and biomass (DW  
268 and AFDW) data. This analysis was applied because the length of the gradient covered  
269 by the first axis, when a Detrended Correspondence Analysis was performed on the  
270 species matrix, was higher than 2 in units of standard deviation, and so the response of  
271 the species to the environment gradient could not be considered linear (Jongman et al.,  
272 1987). The ordination results of are displayed by scaling the axes and adjusting the  
273 species' scores to the species' variance: the resulting scores are correlations between  
274 species and eigenvectors. The relative contribution of each variable to the ordination  
275 established by the DCCA was evaluated by Monte Carlo permutation test after  
276 performing a forward selection of variables at the 0.1% level of significance. All these  
277 calculations were made using the CANOCO v. 3.15 package (ter Braak, 1990).

278

279 To quantify the spatial and temporal variation in macrophyte assemblages, data for  
280 biomass (total, and per species), species richness, diversity and habitat descriptors were  
281 analysed using 3-factor analysis of variance (Underwood, 1997), under the null  
282 hypothesis that each variable tested is homogeneous across the different localities,  
283 assemblages and time. Monthly data were considered as replicates in each season.

284

285 All factors, community ( $c=2$ , photophilous midlittoral and infralittoral), season ( $s=5$ ,  
286 from summer 1995 to summer 1996, both included) and locality ( $l=3$ , Cabo de Palos,  
287 Estacio and El Ciervo island) were fixed orthogonals. For the *Caulerpa prolifera*  
288 meadow, two factor (season and locality) analysis of variance was performed. Prior to  
289 analysis, homogeneity of variances was checked using Cochran's test.

290

291 When the results of the analyses were significant, Tukey's Honestly Significant difference  
292 (HSD) tests were performed in order to identify the significantly different means.

293

### 294 **3. Results**

295

#### 296 *3.1. Variation of environmental parameters*

297

298 The environmental conditions of the three localities differed (Fig. 2, Table 1). Although  
299 water temperature and the suspended solids content were similar, they differed in  
300 salinity, wave exposure and nutrient concentration (Table 2). Temperature showed a  
301 marked seasonal pattern, with maximum temperatures in August (28 °C at El Estacio  
302 and El Ciervo island, and 26°C at Cabo de Palos) and minimum in January and February  
303 (13 °C at Cabo de Palos and 10 and 9 °C at El Estacio and El Ciervo island,  
304 respectively). Water transparency was high, Secchi disc visibility reaching the bottom in  
305 all localities. Suspended solids ranged between 0.01 and 0.18 g/L, with no seasonal

306 pattern, and did not differ greatly between localities. The greatest difference in salinity  
 307 was between Cabo de Palos (39-40) and the two lagoon localities (44-47 at El Ciervo  
 308 island; 42-47 at El Estacio). There was also some time lag in the minimum salinity in  
 309 the three localities, Cabo de Palos reaching minimum levels in November, El Ciervo  
 310 island in December-January and El Estacio in February.

311

312 Wave exposure was higher in Cabo de Palos than in the lagoon localities, and the  
 313 interaction Locality \* Season ( $p < 0.0001$ ) was significant as a consequence of seasonal  
 314 changes in wind regime and because the three localities did not have the same  
 315 orientation.

316

317 In general, waters were oligotrophic in Cabo de Palos and had a slightly higher nutrient  
 318 concentration in the lagoon. Nitrate was the main nitrogen compound, ranging between  
 319 0.10 and 0.39  $\mu\text{M}$  in Cabo de Palos, 0.02 and 0.72  $\mu\text{M}$  in El Ciervo island and, 0.34 and  
 320 3.18  $\mu\text{M}$  at El Estacio. Maximum values were recorded in summer in the Mar Menor  
 321 localities in the two sampled years and in summer (1995) and autumn (1996) in Cabo de  
 322 Palos. Minimum values were reached in winter at all sites. The differences between  
 323 localities were significant ( $p < 0.0001$ ), and the interaction Locality \* Season ( $p < 0.05$ )  
 324 indicated that seasonal patterns differed among localities.

325

326 Phosphate showed highest values at El Ciervo island (0.67 – 2.38  $\mu\text{M}$ ), while the lowest  
 327 values were found in Cabo de Palos (0.19 - 0.66  $\mu\text{M}$ ). El Estacio showed intermediate  
 328 values of 0.23-0.99  $\mu\text{M}$ . Differences were significant for the factors Locality  
 329 ( $p < 0.0001$ ) and Season ( $p = 0.01$ ) but not for the interaction, indicating that all localities  
 330 showed the same seasonal pattern.

331

### 332 3.2. Macrophytobenthic species composition at the sampling localities

333 Midlittoral and infralittoral communities on rocky, muddy and sandy substrata from the  
 334 Mediterranean (Cabo de Palos), and the Mar Menor coastal lagoon (El Estacio and El  
 335 Ciervo Island) differed both in species composition and dominance. In total, 72 species  
 336 (23 Chlorophyta, 17 Ochrophyta, 29 Rhodophyta, 1 Cyanophyta and 2 Magnoliophyta)  
 337 were recorded (Tables 3, 4). The highest floristic richness was found in Cabo de Palos  
 338 (56 spp), while 25 species were found at El Ciervo island and 21 at El Estacio. A depth-  
 339 related gradient was observed in the assemblage composition of the three sites. The 0 m  
 340 level at Cabo de Palos possessed the highest number of species (43), while the lowest  
 341 number (4) was observed in the *Caulerpa* beds from both El Estacio and El Ciervo  
 342 island. 26 species (37.68 %) were exclusive to the sea, while 13 (18.84%) (*Anotrichium*  
 343 *tenuis*, *Boergeseniella fruticulosa*, *Caulerpa prolifera*, *Chaetomorpha linum*,  
 344 *Cladophora albida*, *Cymodocea nodosa*, *Cystoseira foeniculacea* f. *tenuiramosa*,  
 345 *Liebmannia leveillei*, *Polysiphonia subulata*, *Spyridia filamentosa*, *Ulva compressa*,  
 346 *Ulva clathrata* and *Valonia aegagropila* were present in the Mar Menor samples only.  
 347 Among these, *Boergeseniella fruticulosa*, *Chaetomorpha linum*, *Cymodocea nodosa*,  
 348 *Cystoseira foeniculacea* f. *tenuiramosa* and *Spyridia filamentosa* were exclusive to El

349 Ciervo Island and *Anotrichium tenue*, *Polysiphonia subulata*, *Ulva compressa* and *Ulva*  
350 *clathrata* were exclusive to El Estacio channel.

351

352 In terms of biomass, the *Posidonia* meadow showed the highest mean monthly value  
353 (143.80 g DW/400 cm<sup>2</sup>) while the minimum corresponded to the *Caulerpa prolifera*  
354 meadow (11.97 g DW/400 cm<sup>2</sup>) and the midlittoral photophilous assemblage on rock  
355 (12.70 g DW/400 cm<sup>2</sup>) at El Ciervo Island.

356

357 At Cabo de Palos the two shallower levels were dominated by *Stypocaulon scoparium*  
358 and *Haliptilon virgatum*, the latter becoming less frequent with depth. Neither was  
359 present in the lagoon. At 1.5 m depth, but only in shadow sites, *Peyssonnelia squamaria*  
360 was the dominant species. In the deepest water *Posidonia oceanica* was the dominant  
361 seagrass.

362

363 At El Estacio, the 0 m level was dominated by *Cladophora* spp and *Ulva clathrata*,  
364 while *Chondrophycus tenerrimus* dominated this level at El Ciervo island. At depth,  
365 over hard substrata the community was dominated by *Chondrophycus tenerrimus*, and  
366 *Cystoseira foeniculacea* f. *tenuiramosa* and *Cystoseira compressa*. *Jania rubens* was  
367 the more important epiphyte algae. At El Ciervo island *Cymodocea nodosa* meadows  
368 (mixed or not with the green alga *Caulerpa prolifera*, or in patchy outgrowths between  
369 boulders) were dominant at all depths, while at El Estacio, a *Caulerpa prolifera* mono-  
370 specific meadow was dominant at greater depths.

371

### 372 3.3. Vegetation assemblage structure

373 The hierarchical clustering of presence/absence data performed on a Jaccard matrix for  
374 mean seasonal biomass at each sampling site (assemblage) showed a clear separation  
375 between sea and lagoon assemblages, with the midlittoral samples from El Estacio and  
376 the 1995 summer sample from El Ciervo island close to them (Fig. 3).

377

378 At a second level, 10 well defined groups corresponded to the main midlittoral and  
379 infralittoral assemblages both in the sea and lagoon environments. Group 1 included all  
380 midlittoral Mediterranean samples; group 2 included spring and summer sciaphilous  
381 communities on rock at Cabo de Palos; group 3 included Mediterranean infralittoral  
382 photophilous samples on rock, except the winter sample, which joined the *Posidonia*  
383 meadow samples, and autumn and winter sciaphilous communities on rock (group 4).  
384 Groups 5 to 10 corresponded to lagoon assemblages: El Estacio midlittoral samples  
385 (G5), *Cymodocea nodosa* meadows (G6), autumn and winter midlittoral samples at El  
386 Ciervo island (G7), infralittoral photophilous assemblages on rock at El Ciervo island,  
387 including spring midlittoral assemblages at this locality (G8), El Estacio infralittoral  
388 photophilous assemblages (G9) and *Caulerpa prolifera* meadows at both El Estacio and  
389 El Ciervo island (G10).

390

391 The MDS ordination plot based on biomass (DW) data confirmed these results and  
392 clearly separated the samples into localities and assemblages (Fig. 4). This indicated

393 that the presence/absence of species, rather than their abundance, separates the different  
 394 groups, and confirms the existence of different assemblages. ANOSIM indicated that  
 395 these vegetation assemblages differed significantly. Global tests for differences between  
 396 locality groups showed significant differences between El Ciervo island and Cabo de  
 397 Palos ( $R$ -statistic=0.6,  $p<0.0001$ ) and between El Estacio and Cabo de Palos ( $R$ -  
 398 statistic=0.5,  $p<0.0001$ ), but no significant differences were found between El Estacio  
 399 and El Ciervo island. These differences became significant for all the pairwise  
 400 comparisons between localities when only midlittoral and infralittoral photophilous  
 401 assemblages on rock (present in all the three localities) were considered ( $R$ -  
 402 statistic=0.91,  $p<0.0001$ ;  $R$ -statistic=0.996,  $p<0.0001$ ;  $R$ -statistic=0.739,  $p<0.0001$ ;  
 403 respectively). When comparisons were made between assemblages, the global test was  
 404 significant (Global  $R$ -statistic= 0.938,  $p<0.0001$ ). Pairwise tests were all significant at  
 405  $p<0.01$  level ( $R$ -statistic $\geq 0.5$ ) except between midlittoral and infralittoral photophilous  
 406 assemblages, on rock at El Ciervo Island, which were significantly different at  $p<0.05$   
 407 level ( $R$ -statistic=0.238).

408  
 409 The diversity values reached by midlittoral assemblages were the highest of all sampled  
 410 assemblages. Cumulative diversity was 3.26 bits indiv.<sup>-1</sup> at Cabo de Palos and 2.53 and  
 411 2.54 bits indiv.<sup>-1</sup> at El Estacio and El Ciervo island, respectively.

412  
 413 According to this, the different assemblages were characterized by well defined groups  
 414 of species at each locality.

#### 415 416 *Cabo de Palos*

417 At Cabo de Palos, midlittoral photophilous assemblages (CP\_MPhR) were dominated  
 418 by the frequent species *Haliptilon virgatum* and *Stypocaulon scoparium*, which  
 419 represented 29.5 and 25.5 %, respectively, of the total biomass. *Dictyota fasciola*, *Jania*  
 420 *rubens* var *corniculata* and *Padina pavonica* together constituted an additional 21.9 %.  
 421 Infralittoral Photophilous assemblages on rocky substrata (IPhR) were dominated by  
 422 *Cladostephus spongiosus* (11.7 %), *Stypocaulon scoparium* (60.9 %) *Haliptilon*  
 423 *virgatum* (10.6 %), *Padina pavonica* (6.0 %) and *Jania rubens* var *corniculata* (2.8 %),  
 424 all of them frequent species.

425 Infralittoral sciaphilous assemblages on rocky substrata (IScR) was only present at Cabo  
 426 de Palos locality since in the Mar Menor, rocky substrata are hard volcanic crusts with  
 427 only small holes and crevices (El Ciervo Island) or artificial boulders used to build  
 428 breakwaters (El Estacio) with too little space and illumination to permit conspicuous  
 429 algal development. The dominant species were *Peyssonnelia squamaria* (51.6 %,  $f=100\%$ ),  
 430 *Halopteris filicina* (19.8 %,  $f=100\%$ ), *Haliptilon virgatum* (3.8 %,  $f=64.7\%$ ),  
 431 *Flabellia petiolata* (3.1 %,  $f=100\%$ ), *Halimeda tuna* (2.1 %,  $f=76.5\%$ ) and *Amphiroa*  
 432 *rigida* (1.58 %,  $f=41.2\%$ ). Seasonally or occasionally, *Corallina elongata* (8.2 %,  $f=5.9\%$ )  
 433 and *Mesophyllum lichenoides* (2.23 %,  $f=23.5\%$ ) also contributed to the  
 434 assemblage biomass.

435 *Posidonia oceanica* meadows (PM) was also exclusive to the open coastal  
 436 Mediterranean bottoms. In terms of biomass the community was monospecifically

437 dominated by *Posidonia oceanica*, which contributed to 99.5% of the total biomass  
438 ( $f=100\%$ ). *Halopteris filicina* (0.3 %,  $f=41.2\%$ ) was the only other frequent species in  
439 the samples from this assemblage.

440

#### 441 *El Estacio*

442 At El Estacio, midlittoral assemblages (EE\_MPhR) were dominated by *Cladophora*  
443 *albida* (37.2 %), *Jania rubens* (25.9 %) and *Ulva clathrata* (12.1 %). However, except  
444 the first one, which was frequent, the others can be considered seasonal. *Cladophora*  
445 *coelothrix* represented only 5.2 % of the total mean biomass but was present during  
446 most of the year ( $f=52.9\%$ ).

447 IPhR assemblages were dominated by a nearly mono-specific cover of *Jania rubens*  
448 which represented 84.7 % ( $f=100\%$ ) of the total assemblage biomass. Other frequent  
449 species were *Caulerpa prolifera* (6.8 %), *Valonia aegagropila* (2.5 %) and  
450 *Chondrophyucus tenerrimus* (0.5 %). Seasonally, *Ceramium ciliatum* (2.1% of the total  
451 mean biomass), *Cladophoropsis modonensis* (1.6 %), *Padina pavonica* (0.8 %) and  
452 *Acetabularia acetabulum* (0.28 %) made significant contributions to the assemblage  
453 biomass.

454

#### 455 *El Ciervo Island*

456 At El Ciervo Island, the dominant species in midlittoral assemblages (IC\_MPhR) were  
457 *Chondrophyucus tenerrimus* (45.3 %) and *Cladophora albida* (23.5 %), both frequent,  
458 followed by *Cystoseira compressa* (8.6 %) and *Jania rubens* (6.7 %). *Cystoseira*  
459 *compressa*, being a perennial species, overcomes the unfavourable season with basal  
460 parts only and shows a pronounced seasonal cycle at this midlittoral level.

461 Infralittoral photophilous assemblages on rocky substrata were dominated by  
462 *Chondrophyucus tenerrimus* (58.2%), *Cystoseira compressa* (15.6 %) and *Cystoseira*  
463 *foeniculacea* f. *tenuiramosa* (6.7%), all them with high frequencies of occurrence  
464 ( $f=100\%$ ). Also frequent but with a lower contribution to the total biomass were  
465 *Caulerpa prolifera* (3.3 %,  $f=88.2\%$ ), *Padina pavonica* (4.0,  $f=94.1\%$ ) *Cymodocea*  
466 *nodosa* (3.1 %,  $f=76.5\%$ ) and *Jania rubens* (4.0 %,  $f=64.7\%$ ).

467

468 *Cymodocea nodosa* (CyM) and *Caulerpa prolifera* (CaM) meadows were only sampled  
469 in the Mar Menor lagoon where the former constituted the most conspicuous  
470 community on sandy bottoms and the latter on muddy bottoms with a high organic  
471 matter content. In terms of biomass, the former was monospecifically dominated by  
472 *Cymodocea nodosa*, which contributed 98.9% to the total biomass ( $f=100\%$ ). Any other  
473 species, such as *Chaetomorpha linum*, *Acetabularia acetabulum* or *Acetabularia*  
474 *calyculus* were occasional and, in the last case, linked to the existence of small stones or  
475 shells.

476 On the other hand the *Caulerpa prolifera* meadow was dominated by this alga which  
477 contributes 99.6 % and 97.2 % to the total biomass at El Estacio and El Ciervo island,  
478 respectively ( $f=100\%$  in both cases). At El Ciervo island there were some seasonal  
479 contributions from *Chaetomorpha linum*.

480

### 481 3.4. Environmental factors explaining the assemblage composition and structure

482 When performing the redundancy analyses (DCCA) on the macrophyte species matrix  
 483 using environmental data as explanatory variables, the cumulative percentage of  
 484 variance of the species-environment relation for the first two axes reached 59.1 % (Fig.  
 485 5). The first axis had an eigenvalue of 0.82 and explained 41.1 % of total variance.

486  
 487 The stepwise forward selection of environmental variables pointed to salinity,  
 488 temperature, organic matter, wave exposure, depth, phosphate, nitrate, and salinity and  
 489 temperature stress as having a significant influence on the assemblage structure (Fig. 6).  
 490 All the samples were distributed in the space defined by the positive parts of axes I and  
 491 II. The first axis represents a gradient from higher wave exposure and lower salinity on  
 492 the left, to little exposed assemblages and highly saline waters on the right. Other  
 493 descriptors related to natural environmental stress (range of salinity and temperature)  
 494 were also related to the positive part of the first axis. The second axis was related with  
 495 depth and nutrient content in the water column, with greater depth and phosphate in the  
 496 positive part and nitrate in the negative part. This axis explained only 18 % of the total  
 497 variance.

498  
 499 According to this, samples were distributed along a gradient from the Mediterranean  
 500 assemblages on the left to the lagoon assemblages on the right. In the lagoon part,  
 501 samples corresponding to El Estacio and to El Ciervo island were well differentiated.  
 502 Both in the Mediterranean and lagoon samples, two gradients corresponding to the two  
 503 axes were well defined within each locality, with deeper assemblages in the upper zone  
 504 and shallower (and environmentally more stressed) assemblages on the right (Fig. 5a).

505  
 506 Thus, the macrophytobenthic species correlated with the positive portion of axis 1 are  
 507 typical lagoon species such as *Cladophora albida*, *Anotrichium tenue*, *Valonia*  
 508 *aegagropila*, *Ulva clathrata* and *Liebmannia leveillei*. The negative part of axis 1 would  
 509 be determined by those species which do not inhabit the lagoon. The other species,  
 510 located in the centre of the plot, can be considered intermediate relative to their salinity  
 511 and temperature preferences. The second axis appears to be related to a gradient of  
 512 decreasing depth and increasing environmental stress. Its negative part was determined  
 513 by *Ulva compressa*, *Ulva clathrata*, *Scytosiphon lomentaria*, *Liebmannia leveillei*,  
 514 *Polysiphonia subulata* and *Anotrichium tenue*. The positive part was determined by the  
 515 phanerogams *Posidonia oceanica* and *Cymodocea nodosa*, in Cabo de Palos and El  
 516 Ciervo island, respectively, and the algae *Cystoseira compressa*, *Cystoseira*  
 517 *foeniculacea* f. *tenuiramosa*, *Chondrophycus tenerrimus*, *Dictyota linearis*, *Taonia*  
 518 *atomaria*, *Palmophyllum crassum* and *Codium bursa*, in both sites (Fig. 5b).

519

520

### 521 3.5. Spatio-temporal variation in macrophytobenthic assemblage structure

#### 522 3.5.1. Changes in biomass

523 The seasonal variation in vegetation composition and structure of the assemblages and  
 524 in the biomass of individual species showed a different pattern, depending on the

525 assemblage and locality (Fig. 7 and 8). The two-way analysis of variance performed  
 526 considering the factors Season and Local\_Assemblage found significant differences  
 527 between local assemblages but did not show significant differences in biomass between  
 528 seasons (Table 5). However, the three-way analysis performed for photophilous  
 529 assemblages on rock, which were the only ones present in the three localities and so  
 530 permitted a well balanced analysis, showed significant differences between Localities  
 531 ( $p<0.001$ ), Assemblages ( $p<0.001$ ) and the interaction Season\*Locality ( $p<0.05$ ) (Table  
 532 6) but, again, no differences were found between seasons either for the interaction  
 533 Season\*Assemblage or Season\*Locality\*Assemblage. This suggests that the  
 534 assemblages show low seasonal changes in their total biomass and that these small  
 535 changes are dependent on differences in the environmental conditions in the three  
 536 localities that condition the biomass assemblage (Fig. 7 a-c). On the other hand, the  
 537 *Caulerpa prolifera* meadow showed significant differences in biomass between  
 538 localities but they showed the same seasonal pattern (Table 7, Fig. 7d).

539

540 The behaviour of individual species was heterogeneous (Fig. 8). Of the 36 species  
 541 analysed, 15 showed seasonal changes at some significant level ( $p<0.05$ ) (Table 8).  
 542 *Cladostephus spongiosus*, *Cymodocea nodosa*, *Halopteris filicina* and *Peyssonnelia*  
 543 *squamaria* showed significant differences in biomass between assemblages but not  
 544 significant seasonal variations (at  $p<0.05$ ).

545

546 *Ceramium ciliatum* and *Ceramium tenerrimum* (G. Martens) Okamura only showed  
 547 significant temporal patterns, but no differences were found between assemblages.  
 548 *Cystoseira compressa*, *Cystoseira foeniculacea* f. *tenuiramosa* and *Stypocaulon*  
 549 *scoparium* showed significant differences in biomass between assemblages and between  
 550 seasons, but the temporal patterns were the same in all the communities and localities in  
 551 which they were present.

552

553 On the other hand, although *Acetabularia acetabulum*, *Caulerpa prolifera*,  
 554 *Chondrophyucus tenerrimus*, *Dictyota fasciola*, *Dictyota linearis*, *Haliptilon virgatum*,  
 555 *Jania rubens*, *Jania rubens* var *corniculata*, *Padina pavonica* and *Ulva intestinalis* also  
 556 showed significant seasonal variations, the interaction Season\*Local\_Assemblage was  
 557 also significant, indicating that those patterns were different in each local assemblage.

558

559 *Cladophora vagabunda*, *Cladophoropsis modonensis*, *Corallina elongata*, *Dasya*  
 560 *corymbifera*, *Laurencia obtusa*, *Liagora viscida*, *Lyngbia sordida* and *Valonia*  
 561 *aegagropila* showed no spatial or temporal variations at the studied scales.

562

### 563 3.5.2. Changes in community structure

564 The spatial and seasonal variability in species richness and diversity were higher than in  
 565 total biomass. Species richness and diversity showed strongly significant differences  
 566 between local\_assemblages, with the Cabo de Palos midlittoral and the El Ciervo island  
 567 infralittoral photophilous communities being the richest and most diverse and the  
 568 *Caulerpa prolifera* meadows, both at El Estacio and El Ciervo island, the least rich and

569 least diverse. However, seasonal variations showed different patterns for species  
570 richness and for diversity. Species richness showed significant seasonal variations at  
571  $p < 0.05$  level but the Tukey test identified no significant groups. In the case of diversity,  
572 seasonal variations were highly significant ( $p < 0.001$ ), with the highest diversity in  
573 spring and summer and lowest in winter and autumn. However, the fact that the  
574 interaction Season\* Local\_Assemblage was also significant ( $p < 0.001$ ) indicates that  
575 seasonal patterns in diversity were not the same at all the Local\_assemblages (Fig. 7i-1).

576  
577 The ANOVA three-way analysis performed on photophilous assemblages on rock gave  
578 similar results (Table 6). In the case of species richness, differences were significant for  
579 Season ( $p < 0.005$ ) and for Locality ( $p < 0.001$ ), and for the interactions between  
580 Locality\*Assemblage ( $p < 0.001$ ). In the case of diversity, differences were also  
581 significant for Season ( $p < 0.001$ ) and for Locality ( $p < 0.001$ ), and the interactions  
582 between Locality\*Assemblage ( $p < 0.001$ ) and Season\* Locality\* Assemblage  
583 ( $p < 0.005$ ). In both cases, the highest values were reached at Cabo de Palos and the  
584 lowest at El Estacio.

585  
586 In the *Caulerpa prolifera* meadow (Table 7), differences were only significant for  
587 diversity in the case of the factor Locality (IC>EE,  $p < 0.05$ ) and for the interaction  
588 Season x Locality ( $p < 0.05$ ).

#### 589 **4. Discussion and conclusions**

591  
592 Lagoon macrophyte benthic assemblages are diverse, heterogeneous and well  
593 characterized according to the hydrological conditions pertaining to a particular depth  
594 range or substrate or in given wave exposure conditions. This work contributes to  
595 solving the long-standing discrepancies, whether coastal lagoons show similar vertical  
596 zonation patterns to those observed in open coastal areas (as assumed by Mars, 1966;  
597 Bianchi, 1988a, 1988b; Occhipinti et al., 1988) or whether, on the contrary, the lagoon  
598 environment constitutes a uniform system, controlled by extreme physico-chemical  
599 conditions which disguise any small scale pattern. According to our results, the  
600 eurihaline and eurithermal biocenosis proposed by Pérès and Picard (1964) and Augier  
601 (1982) to define coastal lagoon assemblages applies to just one particular assemblage  
602 characteristic from lagoon soft (muddy) bottoms in more or less confined areas.

603  
604 Our results showed that both marine and lagoon assemblages are clearly differentiated  
605 as regards species composition, and that different lagoon assemblages are similarly well  
606 differentiated according to vertical and horizontal zonation patterns. Inside the lagoon,  
607 the macrophyte assemblages showed the same vertical zonation patterns and patch  
608 distribution (according to the nature of the substrata and physico-chemical environmental  
609 conditions) as the equivalent assemblages in open coastal areas.

610  
611 However, the boundaries between vertical zonation levels were narrower in the inner  
612 lagoon and some species that are characteristic from the midlittoral in open coastal



613 zones were common in the infralittoral part in the lagoon. While the midlittoral and  
614 infralittoral photophilous assemblages on rock shared 34.0 % and 33.3% of the algae  
615 species at Cabo de Palos and El Estacio, respectively, at El Ciervo island these two  
616 assemblages shared up to 79.2 % of the species. This would explain the structural  
617 similarities and the proximity in the ordination diagrams observed between midlittoral  
618 photophilous assemblages on rock from Cabo de Palos and the infralittoral photophilous  
619 assemblage in El Ciervo island.

620

621 Nineteen species (27.5 %) are shared by the lagoon and open coast marine assemblages  
622 studied in this work and most of the others characterize (Pérès and Picard, 1964;  
623 Augier, 1982) or are common in the different communities in the south-western  
624 Mediterranean (Pérez-Ruzafa, I. and Honrubia, 1984; Pérez-Ruzafa et al., 1991; Flores-  
625 Moya et al., 1995a, 1995b; Conde et al., 1996).

626

627 The main differences observed between assemblages are due to a few exclusive species  
628 from distinct levels and environments and to differences in the dominance relationships.  
629 In the lagoon environment, especially in the most confined areas, the term “paralic”  
630 (*sensu* Frisoni et al., 1983; Guelorget et al., 1983; Guelorget and Perthuisot, 1983, 1992)  
631 referring to typically lagoon species could still be useful.

632

633 Despite the confinement theory (Guelorget et al., 1983; Guelorget and Perthuisot, 1983,  
634 1992), according to which there would be a decreasing gradient in species richness from  
635 the inlets communicating with the open sea to the inner parts (more confined) of the  
636 lagoon, the assemblages at El Estacio showed the lowest number of species and lowest  
637 diversity. In fact, El Estacio only shared 13 species with the open coastal assemblages.  
638 Pérez-Ruzafa (1989) and Pérez-Ruzafa and Marcos (1992, 1993), on the basis of  
639 evidence from faunal assemblage gradients in the Mar Menor, reformulated the  
640 confinement theory in different terms so that, instead of the recycling of “vitamins or  
641 vital elements” and the influence of seawater, the main factor explaining the structure of  
642 lagoon assemblages in a confinement gradient would be the rates of colonization by  
643 Mediterranean species. So, for the fauna, the species composition at each lagoon site  
644 will be the result of equilibria in the context of interspecific competition between sea  
645 and lagoon species, taking into account that lower competition coefficients of  
646 Mediterranean species in the lagoon environment or the partial or complete lack of  
647 reproduction inside the lagoon could be compensated by high immigration rates of  
648 juveniles or adults from outer habitats. However, this mechanism does not seem to be  
649 valid for vegetation. It could apply to some vegetal species – for example, some mats of  
650 *Posidonia oceanica* have occasionally been observed in the inlet-influenced areas of the  
651 Mar Menor and the invasive algae *Caulerpa prolifera* were seen to progressively  
652 colonize the lagoon from the less confined areas to the inner parts of the lagoon (Pérez-  
653 Ruzafa et al., 1989, 2005b) and is now colonizing rocky substrates (unpublished data).  
654 However, according to the results of this work, this does not seem to be applicable to  
655 most macrophyte species and the dispersion and colonization mechanisms of the  
656 vegetation need to be analysed in greater depth.

657

658 El Estacio assemblages can be considered distinct assemblages (well differentiated and  
659 characterized by some exclusive species). The site is not an ecotone between open  
660 coastal and lagoon communities, but a lagoon location with environmental instability  
661 tolerated only by some species. This would explain its lower species richness and  
662 diversity. This instability could not be related to the maximum and minimum  
663 temperature or salinity, or to the medium and long term variation in these parameters,  
664 but with the short term (hours to days) scale determined by the changes in direction of  
665 the current at the inlet (with a mean periodicity of 6 hours) (Arevalo, 1988) and the  
666 alternating influence of Mediterranean and lagoon conditions.

667

668 The different assemblages described in this work could be considered as real biocenoses  
669 *sensu* Margalef (1974), as communities that do not depend on organisms external to  
670 themselves and in which the internal relationships are always stronger than the  
671 interchanges with adjacent ones. In the case of both the vertical and horizontal zonation  
672 of macrophyte assemblages, the different communities can not be understood without  
673 the concepts of *continuum* and *nodum*, *sensu* Boudouresque (1970, 1971), and of  
674 biocenosis (see Ballesteros, 1992 for a general review).

675

676 Many characteristic species showed significant differences in biomass for the factor  
677 Local\_assemblage and for the interaction Locality x Assemblage in the photophilous  
678 rocky assemblages. This would confirm the differences obtained in the ordination  
679 analyses. However, precisely because of the differences existing between the three  
680 localities, a more complete bionomic study would need to replicate each one of the three  
681 environmental situations.

682

683 As regards the total assemblages, biomass is higher in Cabo de Palos than in the lagoon  
684 and in the infralittoral assemblages than in the midlittoral. No significant differences  
685 were found between the same assemblage in the two localities inside the lagoon except  
686 for the *Caulerpa prolifera* meadow, which showed higher biomass in El Estacio than in  
687 El Ciervo island. De Biasi et al. (2003) also found that macroalgae were generally more  
688 abundant in the outer part of the Orbetello lagoon but did not consider vertical zonation  
689 patterns or the influence of depth in their study. These authors rejected the theory of  
690 “confinement” to describe spatial pattern in assemblages in every lagoon because of the  
691 spatial variability that they found over scales of tens to hundreds of metres. However, as  
692 they did not consider the direction of currents and did not analyze any environmental  
693 variable, such a rejection can not be supported.

694

695 Substrate type, nutrient concentration and the influence of sea vs fresh water are among  
696 the main factors affecting the species composition and abundance in macrophyte  
697 assemblages in coastal lagoons (Pasqualini et al., 2006). According to our results, two  
698 additional factors seem to overlap in determining macrophyte biomass: open sea vs.  
699 lagoon environment, and infralittoral vs. midlittoral. Both could be defined as  
700 environmental stress gradients operating at the same time on two different spatial

701 scales: from hundreds of metres to kilometres in the horizontal plane, thus defining the  
702 degree of isolation from the sea, and from centimetres to metres in the vertical zonation.  
703 In this way, infralittoral photophilous assemblages and *Posidonia* meadows at Cabo de  
704 Palos showed the highest biomass followed by midlittoral photophilous assemblages in  
705 the same locality, while the latter show the same biomass as the infralittoral  
706 assemblages of the lagoon. Finally, midlittoral lagoon assemblages show the lowest  
707 biomass.

708

709 This parallel effect of confinement and vertical zonation also occurs in species  
710 composition so that, as stated above, some species that are characteristic of the  
711 midlittoral in open coastal zones, are common in the infralittoral in the lagoon. There  
712 are also structural similarities, as shown by the proximity in the ordination diagrams,  
713 between midlittoral photophilous assemblages on rock from Cabo de Palos and the  
714 infralittoral photophilous assemblage in El Ciervo island.

715

716 In addition, many species showed seasonal variations, depending on the locality.  
717 Seasonal changes in algal abundance are common in the Mediterranean where algal  
718 abundance drops off sharply in summer (Coma et al., 2000). However, as with light and  
719 nutrients, the main factors determining the production of algal communities, display  
720 different temporal dynamics. The dynamics of algae from different groups and depths  
721 will be conditioned by the seasonal cycle of the main limiting factor affecting them. In  
722 shallow assemblages that reach a production peak in spring, nutrients are usually the  
723 main limiting factors, while light availability becomes the limiting factor at increasing  
724 depth so that deeper assemblages reach their maximum production in summer  
725 (Ballesteros, 1991). In the study area, light, water temperature and salinity showed  
726 similar seasonal patterns in the three localities, while nutrient concentration in the water  
727 column showed different dynamics. Thus, the difficulty of finding significant seasonal  
728 differences in biomass may be related to the fact that each factor acts in a different way  
729 on the biomass each season. Furthermore, many of the observed changes in vegetation  
730 would be due to the natural seasonal life cycle of the species present. There are  
731 perennial species that are present in a given season in the form of erect thalli and in  
732 other periods as basal parts or encrusting thalli (e.g. *Cystoseira* spp., *Chondrophycus*  
733 *tenerrimus*) and there are annual species which have a life cycle lasting only a restricted  
734 period of the year or species with several generations in a year (*Ulva* spp., *Cladophora*  
735 spp.) (Feldmann, 1951).

736

737 Maximum development of the assemblages on rock was observed in summer and  
738 autumn in Cabo de Palos but in spring at El Ciervo island, a lag that could be related  
739 with the negative effect of extreme summer conditions in the inner lagoon. A spring  
740 maximum in macrophyte biomass has been observed in other Mediterranean lagoons  
741 (De Biasi et al., 2003).

742

743 The pelagic primary productivity cycle shows different patterns in different parts in the  
744 Mar Menor (Pérez-Ruzafa et al., 2005a). In the internal areas of the lagoon, including El

745 Ciervo island, the concentrations of chlorophyll *a* in the water column were also  
746 maximal in spring and minimal in winter. At El Estacio, and in the central part of the  
747 lagoon, under Mediterranean influence, the maximum was reached in summer. This  
748 pattern seems to be similar to that observed in infralittoral photophilous assemblages.

749

750 Of particular note were the differences in biomass observed between the summer of  
751 1995 and 1996, particularly in the Cabo de Palos assemblages, where nearly all the  
752 dominant species decreased substantially during the second year. Only *Haliptilon*  
753 *virgatum*, in the infralittoral photophilous community, showed the inverse pattern.

754

755 Between 1995 and 1996 the total biomass dropped by one third in the midlittoral  
756 photophilous community, by two thirds in the infralittoral photophilous assemblage and  
757 by half in the sciaphilous assemblage. However, the *Posidonia oceanica* assemblage  
758 underwent a much smaller decrease.

759

760 Despite the interannual decrease in biomass observed in the open coast assemblages, the  
761 lagoon assemblages at El Estacio and El Ciervo island did not show the same general  
762 pattern. However, the behaviour of some species, such as *Cladophora albida* and  
763 *Padina pavonica*, whose biomass decreased, or the opposite response shown by  
764 *Chondrophyucus tenerrimus* and *Cystoseira compressa*, whose biomass increased,  
765 suggests that the observed pattern was not a consequence of a local impact but of a  
766 general process affecting the whole area. Such environmental stress would not affect the  
767 species already adapted to extreme environments (*Caulerpa prolifera*, *Chondrophyucus*  
768 *tenerrimus* or *Cystoseira compressa* at El Ciervo island) and would mainly have a  
769 negative effect on the species in more stable environments.

770

771 These differences also suggest that supra-annual temporal scales of variability are  
772 important in macrophyte lagoon assemblage dynamics. In this work, *Caulerpa prolifera*  
773 was present as a frequent and characteristic species on the infralittoral rocky bottoms of  
774 both El Estacio and El Ciervo island. This species is characteristic of muddy substrata  
775 and invaded the Mar Menor lagoon in the early 1970's after widening of El Estacio inlet  
776 (Pérez-Ruzafa et al., 1989, 1991). The colonization of the infralittoral photophilous  
777 assemblages on rock by this invasive algae, which is characteristic of muddy bottoms,  
778 constitutes a progressive process (Pérez-Ruzafa et al., 1991) which is endangering the  
779 biological diversity of the Mar Menor hard substrata lagoon assemblages, in the same  
780 way that it has already affected the communities on sandy bottoms (Pérez-Ruzafa et al.,  
781 2006). Accordingly, long term studies will be necessary to analyze the inter-annual  
782 patterns of variation.

783

784 In conclusion, macrophytic benthic assemblages in the Mar Menor lagoon are not  
785 homogeneous and it is possible to identify distinct assemblages with the same vertical  
786 zonation that can be found in all marine communities, but characterized by well defined  
787 groups of species, according to their isolation from the open sea and the type of

788 substratum. This implies that when applying the EU Water Framework Directive a  
 789 lagoon should not be considered as a homogeneous unit but as a mosaic of assemblages.  
 790  
 791 However, before the structure and composition of the assemblages described for the  
 792 Mar Menor can be generalised and applied to other lagoon communities in the  
 793 Mediterranean, more extensive studies of other lagoons are necessary.  
 794

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1027 Figure captions

1028

1029 Figure 1. Geographical location of the Mar Menor lagoon and the Cabo de Palos marine  
1030 protected area, and location of sampling stations.

1031

1032 Figure 2. Seasonal dynamic of salinity, temperature, nutrient concentration and  
1033 suspended solids in the water column in the three localities studied. CP: Cape of Palos;  
1034 EE: El Estacio; IC: El Ciervo Island.

1035

1036 Figure 3. Hierarchical clustering of presence/absence data performed on a Jaccard  
1037 matrix for macrophyte mean seasonal biomass at each sampling site (assemblage) and  
1038 locality. Sample codes (Locality\_Assemblage\_Season\_Year): CP Cabo de Palos; EE El  
1039 Estacio; IC El Ciervo island\_ MPh: midlittoral photophilous assemblages on rock; IPh:  
1040 infralittoral photophilous assemblages on rock; ISc: infralittoral sciaphilous  
1041 assemblages on rock; PM: *Posidonia oceanica* meadow; CyM: *Cymodocea nodosa*  
1042 meadow; CaM: *Caulerpa prolifera* meadow\_ Sm Summer; A Autumn; W Winter; Sp  
1043 Spring\_5 1995; 6 1996. See text for the description of clusters 1 to 10.

1044

1045 Figure 4. MDS ordination plot based on macrophyte biomass (DW) data.

1046

1047 Figure 5. Ordination of samples (a) and species (b) in the representations of the first  
1048 axes of the redundancy analysis (DCCA) performed on the macrophyte species matrix  
1049 using environmental data as explanatory variables. Key of abbreviations for samples  
1050 and species are showed in Fig. 3 and Tables 3 and 4, respectively.

1051

1052 Figure 6. Environmental variables explaining the species and samples distribution in the  
1053 space defined by the two first axes of the redundancy analysis (DCCA) performed on  
1054 the macrophyte species matrix represented in Fig. 5.

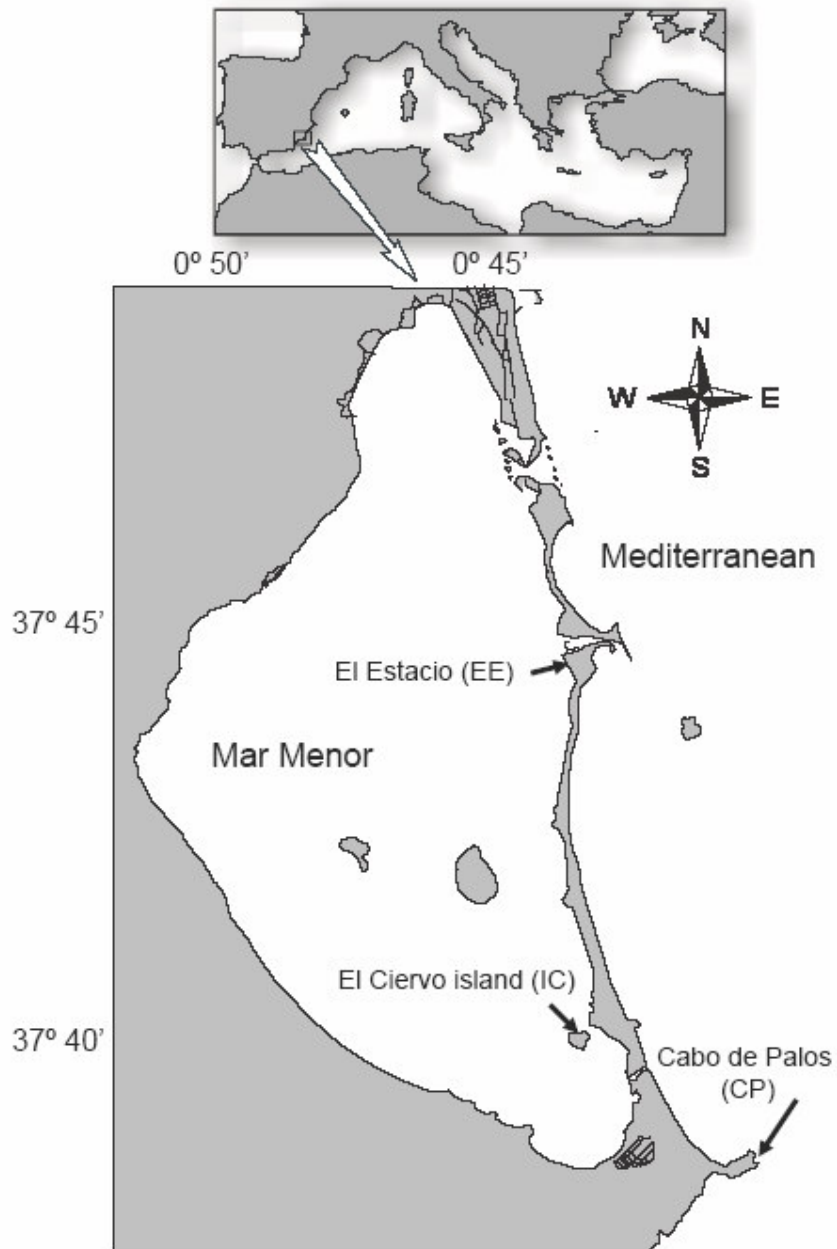
1055

1056 Figure 7. Seasonal variation in biomass (a-d), species richness (e-h) and Shannon  
1057 diversity (i-l) in the macrophyte assemblages of the Mar Menor lagoon and Cabo de  
1058 Palos. Sample codes (locality\_assemblage) correspond to that Fig. 3. Error bars  
1059 correspond to mean standard error.

1060

1061 Figure 8. Seasonal variation in biomass of dominant macrophyte species at the different  
1062 assemblages and localities studied. Sample codes (locality\_assemblage) correspond to  
1063 that Fig. 3. Error bars correspond to mean standard error.

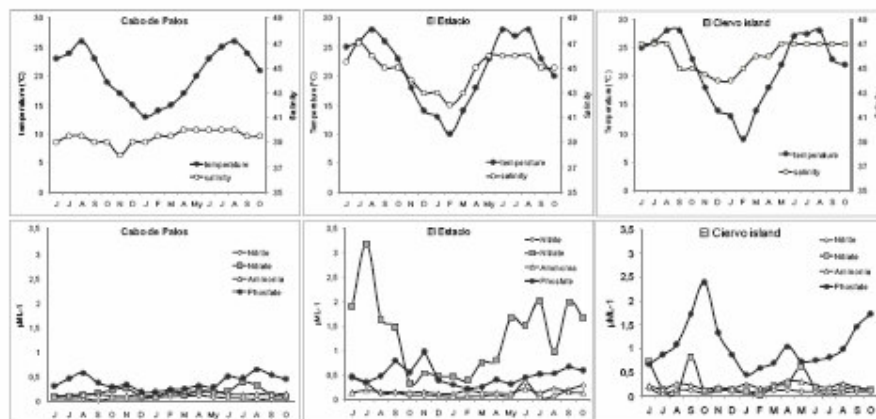
1064 Figure 1



1065

AC

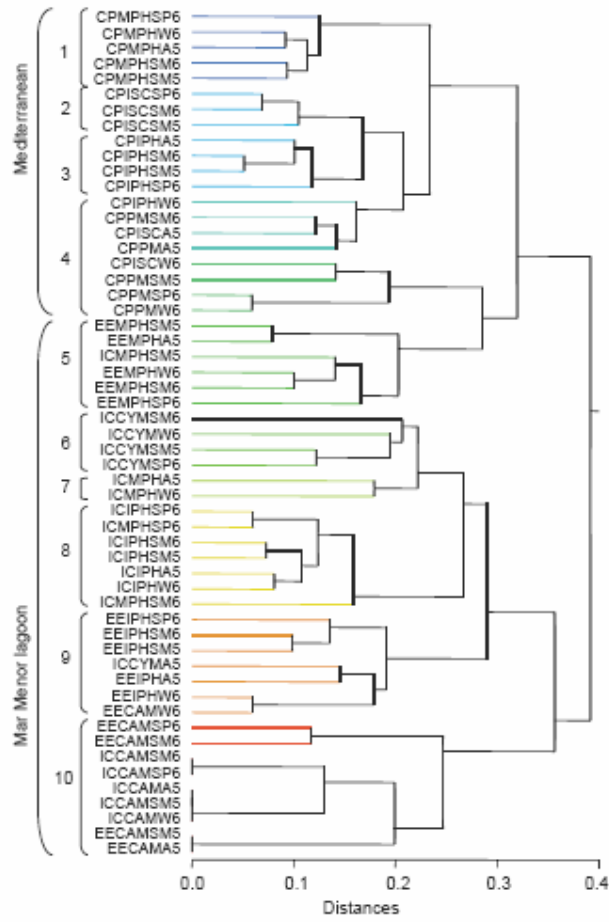
1066 Figure 2



1067

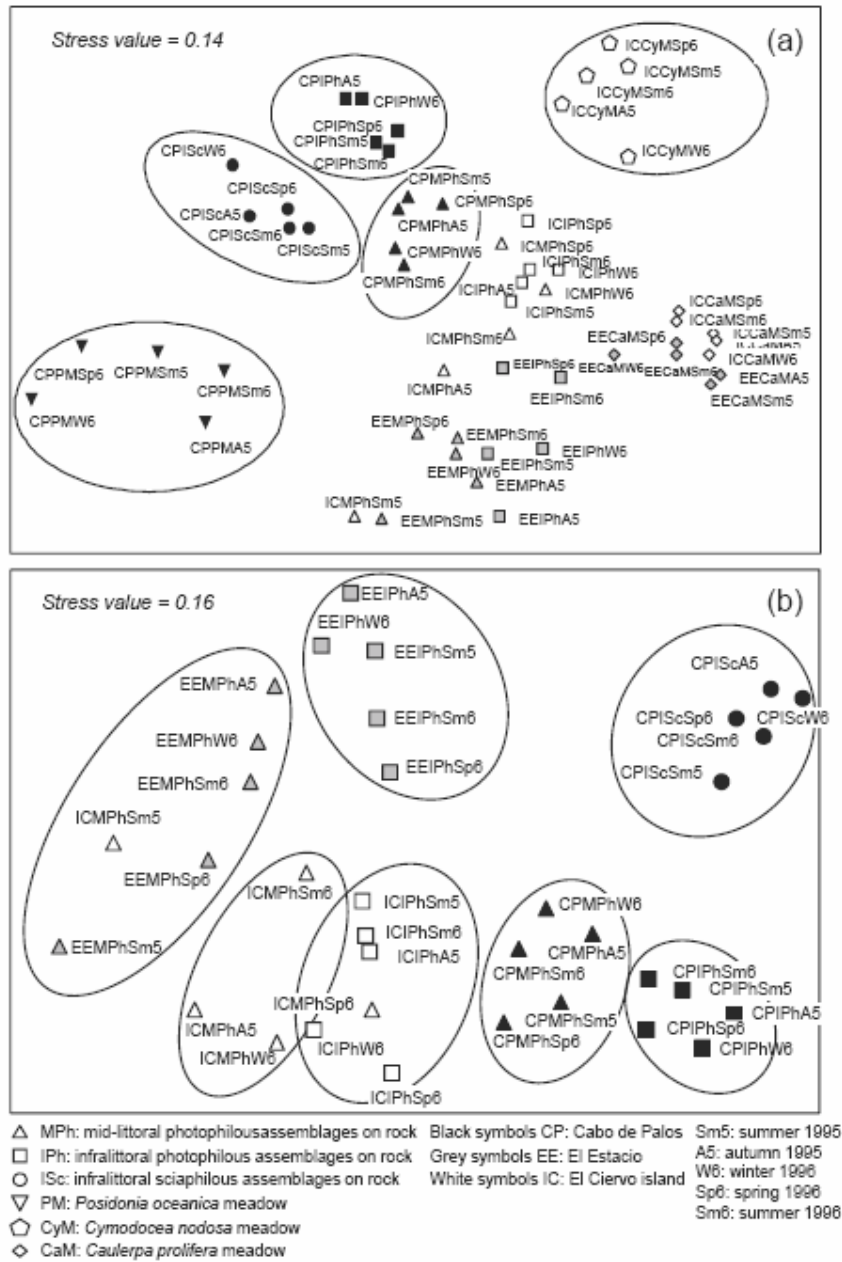
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1068 Figure 3



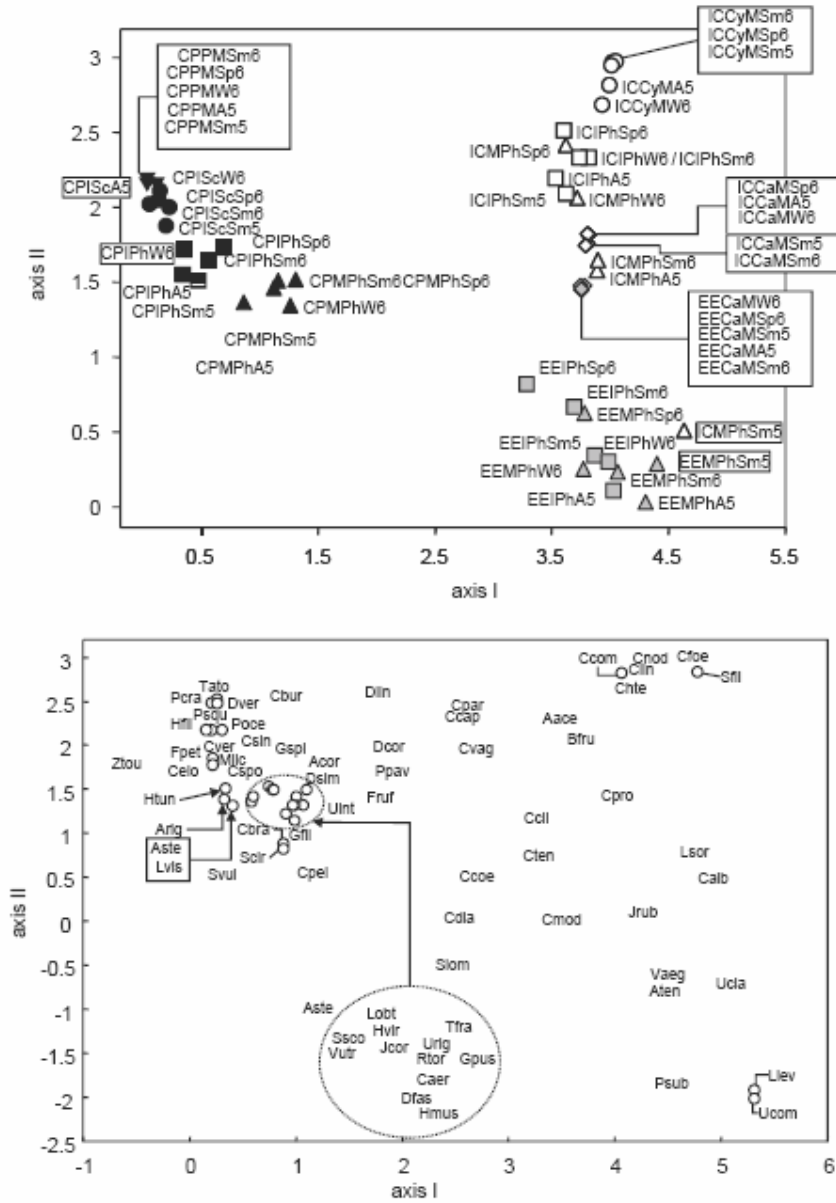
1069

1070 Figure 4



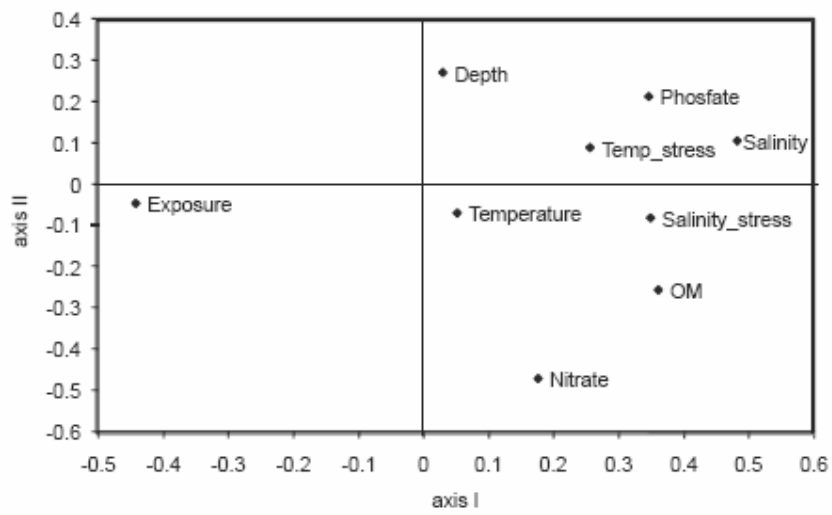
1071

1072 Figure 5



1073

1074 Figure 6

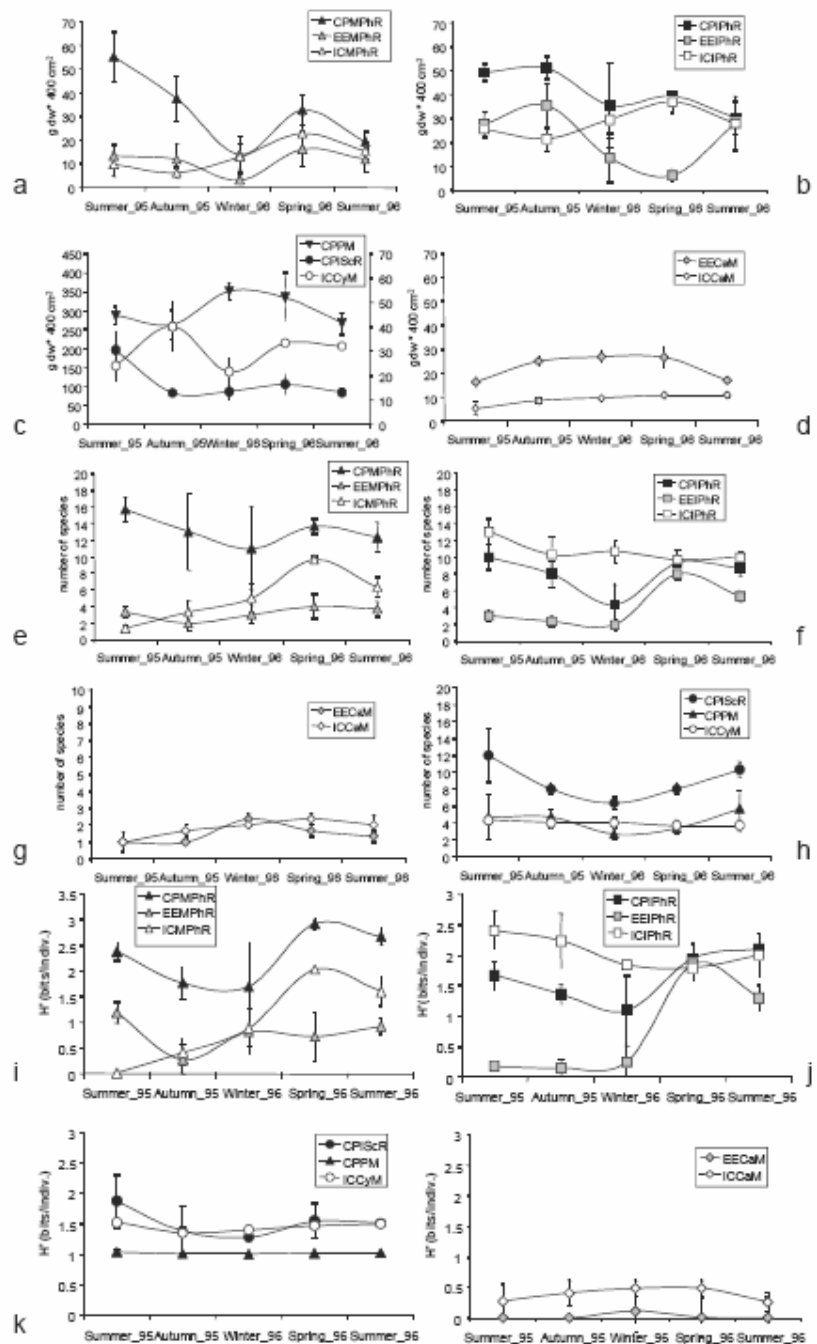


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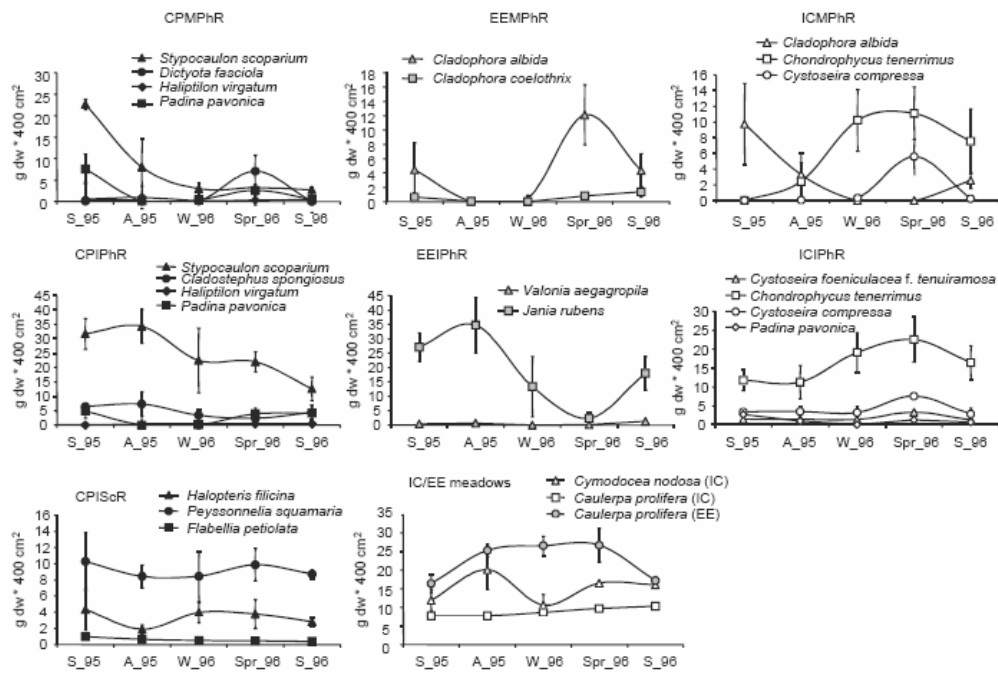


1076 Figure 7



1077

1078 Figure 8



1079

Table 1. Mean values ( $\pm$  standard error of the mean, SEM) of environmental variables at the three localities studied. Salinity stress and Temperature stress are the difference between maximum and minimum values of these variables through the studied period.

	Cabo de Palos		El Ciervo island		El Estacio	
	mean	$\pm$ SEM	mean	$\pm$ SEM	mean	$\pm$ SEM
Wave exposure	76518.58	$\pm$ 8212.63	1411.17	$\pm$ 139.51	3568.90	$\pm$ 442.81
<b>water column</b>						
Nitrite ( $\mu$ M)	0.071	$\pm$ 0.007	0.100	$\pm$ 0.008	0.126	$\pm$ 0.025
Nitrate ( $\mu$ M)	0.196	$\pm$ 0.022	0.214	$\pm$ 0.056	1.216	$\pm$ 0.208
Ammonia ( $\mu$ M)	0.152	$\pm$ 0.008	0.217	$\pm$ 0.015	0.165	$\pm$ 0.009
Phosphate ( $\mu$ M)	0.383	$\pm$ 0.038	1.055	$\pm$ 0.129	0.488	$\pm$ 0.054
Salinity	39.43	$\pm$ 0.14	45.90	$\pm$ 0.31	44.80	$\pm$ 0.38
Temperature ( $^{\circ}$ C)	20.07	$\pm$ 1.20	21.23	$\pm$ 1.66	21.27	$\pm$ 1.61
pH	8.10	$\pm$ 0.04	8.22	$\pm$ 0.06	8.12	$\pm$ 0.04
Suspended solids ( $\text{gL}^{-1}$ )	0.074	$\pm$ 0.010	0.087	$\pm$ 0.007	0.080	$\pm$ 0.010
Salinity stress	2		3		5	
Temperature stress ( $^{\circ}$ C)	13		19		18	
<b>sediment</b>						
Organic carbon (%)	0.61	$\pm$ 0.02	1.49	$\pm$ 0.24	3.19	$\pm$ 0.34
Clay (%)(<2 $\mu$ )	7.28	$\pm$ 0.11	10.32	$\pm$ 1.04	17.55	$\pm$ 0.71
Fine Silt (%) (2-20 $\mu$ )	1.46	$\pm$ 0.18	2.52	$\pm$ 0.76	8.59	$\pm$ 1.96
Coarse Silt (%) (20-50 $\mu$ )	0.58	$\pm$ 0.07	1.00	$\pm$ 0.30	3.42	$\pm$ 0.78
Fine Sand (%) (50 $\mu$ -0.2mm)	4.06	$\pm$ 0.34	17.84	$\pm$ 1.70	39.74	$\pm$ 2.98
Coarse Sand (%) (0.2-2mm)	86.62	$\pm$ 0.41	68.31	$\pm$ 3.49	30.69	$\pm$ 3.34



Table 3. Mean values of biomass (DW) per 400 cm<sup>2</sup>, relative dominance (% D) and class (F) of frequency of occurrence of the macrophyte species sampled in this study at Cabo de Palos (CP). Abbreviations of species names used in Fig. 4b, total species richness (Sr), mean total biomass (B) and Shannon diversity (H', in bits\*indiv<sup>-1</sup>) at each assemblage, are also indicated (F frequent; S seasonal; O occasional). MPhR: Midlittoral Photophilous assemblage on Rock; IPhR: Infralittoral Photophilous assemblage on Rock; IScR: Infralittoral Sciaphilous assemblage on Rock; PM: *Posidonia oceanica* meadow.

Abbrev.	CP		IPhR		IScR		PM			
	MPhR	%D	f	%D	f	%D	f	%D	f	
<b>Cyanophyta</b>										
<i>Lyngbia sordida</i> Gomont	Lsor	0.005	0.0	O						
<b>Chlorophyta</b>										
<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva	Aace	0.007	0.0	O	0.002	0.0	O	0.009	0.1	S
<i>Anadyomene stellata</i> (Wulfen) C. Agardh	Aste	0.037	0.1	S	0.021	0.0	S	0.035	0.2	O
<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	Caer	0.007	0.0	O						
<i>Cladophora coelothrix</i> Kützing	Ccoe	0.644	2.1	S						
<i>Cladophora pellucida</i> (Hudson) Kützing	Cpel	0.001	0.0	O						
<i>Cladophora vagabunda</i> (Linnaeus) Hoek	Cvag	0.007	0.0	O			0.006	0.0	O	0.004
<i>Cladophoropsis modonensis</i> (Kützing) Reinbold	Cmod	0.039	0.1	O						O
<i>Codium bursa</i> (Linnaeus) C. Agardh	Cbur				0.034	0.1	O			
<i>Codium vermicularis</i> (Olivier) Delle Chiaje	Cver				0.449	1.1	S	0.288	1.7	S
<i>Dasycladus vermicularis</i> (Scopoli) Krasser	Dver	0.127	0.4	O	0.336	0.8	O			O
<i>Flabellia petiolata</i> (Turra) Nizamuddin	Fpet	0.002	0.0	O	0.017	0.0	O	0.520	3.1	F
<i>Halimeda tuna</i> (J. Ellis & Solander) J.V. Lamouroux	Htun	0.238	0.8	F	0.081	0.2	S	0.360	2.1	F
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	Pcra						0.024	0.1	O	
<i>Ulva intestinalis</i> Linnaeus	Uint	1.310	4.2	F						
<i>Ulva rigida</i> C. Agardh	Urig	0.018	0.1	O						
<i>Valonia utricularis</i> (Roth) C. Agardh	Vutr	0.052	0.2	F			0.042	0.3	O	
<b>Magnoliophyta</b>										
<i>Posidonia oceanica</i> (L.) Delile	Poce								143.0	99.5
<b>Ochrophyta</b>										
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	Cspo	0.131	0.4	S	4.835	11.7	F	0.131	0.8	F
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	Csin	0.047	0.1	O	0.122	0.3	O	0.011	0.1	O
<i>Cystoseira brachycarpa</i> var. <i>balearica</i> (Sauvageau) Giaccone	Cbra	1.119	3.6	F	0.038	0.1	O			
<i>Cystoseira compressa</i> (Esper) Gerloff & Nizamuddin	Ccom	0.391	1.2	S						
<i>Dictyota fasciola</i> (Roth) J.V. Lamouroux	Dfas	1.781	5.7	F			0.012	0.1	O	
<i>Dictyota linearis</i> (C. Agardh) Greville	Dlin				0.620	1.5	S	0.151	0.9	F
<i>Halopteris filicina</i> (Grateloup) Kützing	Hfil						3.342	19.8	F	0.371
<i>Padina pavonica</i> (Linnaeus) Thivy	Ppav	2.616	8.3	F	2.475	6.0	F	0.296	1.8	S
<i>Sargassum vulgare</i> C. Agardh	Svul				0.093	0.2	O			O
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Slom	0.071	0.2	O						
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	Scir	0.009	0.0	S						
<i>Stypocaulon scoparium</i> (Linnaeus) Kützing	Ssco	8.022	25.5	F	25.27	60.9	F			
<i>Taonia atomaria</i> (Woodward) J. Agardh	Tato				0.007	0.0	O			
<i>Zonaria tournefortii</i> (J.V. Lamouroux) Montagne	Ztou								0.114	0.1
<b>Rhodophyta</b>										
<i>Alsidium corallinum</i> C. Agardh	Acor	0.089	0.3	O	0.002	0.0	O			
<i>Amphiroa rigida</i> J.V. Lamouroux	Arig	0.105	0.3	S	0.405	1.0	S	0.267	1.6	F

<i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau	Ccil	0.351	1.1	O																
<i>Ceramium diaphanum</i> (Lightfoot) Roth	Cdia	0.016	0.1	O																
<i>Ceramium tenerrimum</i> (G. Martens) Okamura	Cten	0.064	0.2	O																
<i>Champia parvula</i> (C. Agardh) Harvey	Cpar	0.003	0.0	O																
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	Ccap	0.141	0.4	F								0.011	0.1	O						
<i>Chondrophyucus tenerrimus</i> (Cremades) G. Furnari, Boisset, Cormaci et Serio	Chten	0.555	1.8	F																
<i>Corallina elongata</i> J. Ellis & Solander	Celo	0.141	0.4	O	0.177	0.4	O	1.391	<b>8.2</b>	O										
<i>Dasya corymbifera</i> J. Agardh	Dcor				0.010	0.0	O	0.032	0.2	O										
<i>Digenea simplex</i> (Wulfen) C. Agardh	Dsim	0.188	0.6	O																
<i>Falkenbergia rufolanosa</i> Stadium	Fruf	0.009	0.0	O								0.004	0.0	O						
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	Gpus	0.037	0.1	O																
<i>Gelidium spinosum</i> (S.G. Gmelin) P.C. Silva	Gspi	0.047	0.2	O							0.009	0.1	O							
<i>Grateloupia filicina</i> (J.V. Lamouroux) C. Agardh	Gfil	0.005	0.0	O																
<i>Haliptilon virgatum</i> (Zanardini) Garbary & H.W. Johansen	Hvir	9.254	<b>29.4</b>	F	4.384	<b>10.6</b>	F	0.638	3.8	F	0.027	0.0	O							
<i>Hypnea musciformis</i> (Wulfen) J.V. Lamouroux	Hmus	0.065	0.2	S																
<i>Jania Rubens</i> (Linnaeus) J.V. Lamouroux	Jrub	0.617	2.0	F	0.292	0.7	F	0.043	0.3	F	0.002	0.0	O							
<i>Jania rubens var corniculata</i> (Linnaeus) Yendo	Jcor	2.468	<b>7.9</b>	F	1.169	2.8	F	0.170	1.0	F	0.007	0.0	O							
<i>Laurencia obtusa</i> (Hudson) J.V. Lamouroux	Lobt				0.001	0.0	O	0.020	0.1	S										
<i>Liagora viscida</i> (Forsskål) C. Agardh	Lvis	0.174	0.6	O	0.625	1.5	S													
<i>Mesophyllum lichenoides</i> (J. Ellis) M. Lemoine	Mlic							0.378	2.2	S										
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne	Psqu							8.716	<b>51.6</b>	F	0.103	0.1	S							
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman & Townsend	Tfra	0.415	1.3	S				0.002	0.0	O										
	Sr	43			24			26			15									
	B	31.42			41.47			16.90			143.8									
	H'(log <sub>2</sub> )	3.26			2.08			2.45			0.06									

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Table 4. Mean values of biomass (DW) per 400 cm<sup>2</sup>, relative dominance (% D) and class (F) of frequency of occurrence of the macrophyte species sampled in this study at the Mar Menor localities. Abbreviations of species names used in Fig. 4b, total species richness (Sr), mean total biomass (B) and Shannon diversity (H', in bits\*indiv<sup>-1</sup>) at each assemblage, are also indicated (F frequent; S seasonal; O occasional). EE: El Estacio; IC: El Ciervo Island. MPhR: Midlittoral Photophilous assemblage on Rock; IPhR: Infralittoral Photophilous assemblage on Rock; CaM: *Caulerpa prolifera* meadow; CyM: *Cymodocea nodosa* meadow. + indicate species observed in the assemblage but not collected in the sample.

	EE						IC																
	Abrev	MPhR mean	%D	f	IPhR mean	%D	f	CaM mean	%D	f	MPhR mean	%D	f	IPhR mean	%D	f	CyM mean	%D	f	CaM mean	%D	f	
<b>Cyanophyta</b>																							
<i>Lyngbia sordida</i> Gomont	Lsor	0.994	<b>9.6</b>	S							0.217	1.7	O	0.215	0.8	O	0.006	0.0	O				
<b>Chlorophyta</b>																							
<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva	Aace	0.062	0.6	O	0.057	0.3	S	0.001	0.0	O	0.038	0.3	O	0.099	0.4	F	0.006	0.0	O	0.001	0.0	O	
<i>Acetabularia calyculus</i> J.V. Lamouroux	Acal													+			+						
<i>Caulerpa prolifera</i> (Forsskål) J.V. Lamouroux	Cpro				1.378	<b>6.8</b>	F	22.22	<b>99.6</b>	F	0.088	0.7	S	0.859	3.3	F	0.033	0.2	O	11.63	<b>97.2</b>	F	
<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	Caer	+																					
<i>Chaetomorpha linum</i> (O.F. Müller) Kützing	Clin										0.004	0.0	O	0.246	0.9	F	0.006	0.0	O	0.315	2.6	S	
<i>Cladophora albida</i> (Nees) Kützing	Calb	3.860	<b>37.2</b>	F							2.984	<b>23.5</b>	F	0.035	0.1	O							
<i>Cladophora coelothrix</i> Kützing	Ccoe	0.543	<b>5.2</b>	F							0.093	0.7	O	0.096	0.4	S							
<i>Cladophora vagabunda</i> (Linnaeus) Hoek	Cvag				0.008	0.0	O				0.022	0.2	O	0.005	0.0	O							
<i>Cladophoropsis modonensis</i> (Kützing) Reinbold	Cmod				0.319	1.6	O				0.009	0.1	O										
<i>Ulva clathrata</i> (Roth) C. Agardh	Ucla	1.257	<b>12.1</b>	S																			
<i>Ulva compressa</i> Linnaeus	Ucom	0.285	2.7	S																			
<i>Ulva intestinalis</i> Linnaeus	Uint										0.040	0.3	O	0.016	0.1	O							
<i>Ulva rigida</i> C. Agardh	Urig																						
<i>Valonia aegagropila</i> C. Agardh	Vaeg				0.510	2.5	F							0.011	0.0	O							
<i>Valonia utricularis</i> (Roth) C. Agardh	Vutr																						
<b>Magnoliophyta</b>																							
<i>Cymodocea nodosa</i> (Ucria) Asch.	Cnod										0.321	2.5	S	0.811	3.1	F	14.60	<b>98.9</b>	F	0.024	0.2	O	
<b>Ochrophyta</b>																							
<i>Cystoseira compressa</i> (Esper) Gerloff & Nizamuddin	Ccom										1.097	<b>8.6</b>	S	4.095	<b>15.6</b>	F	0.063	0.4	O				
<i>Cystoseira foeniculacea f. tenuiramosa</i> (Ercegovic) A. Gómez Garreta, M.C. Barceló, M.A. Ribera & J. Rull Lluch	Cfoe										0.466	3.7	S	1.755	<b>6.7</b>	F	0.016	0.1	O				
<i>Dictyota linearis</i> (C. Agardh) Greville	Dlin										0.054	0.4	O	0.063	0.2	S							
<i>Liebmannia leveillei</i> J. Agardh	Llev	0.022	0.2	O										+									
<i>Padina pavonica</i> (Linnaeus) Thivy	Ppav				0.166	0.8	S				0.201	1.6	O	1.048	4.0	F							
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Slom	0.132	1.3	O										+									
<i>Sphacelaria tribuloides</i> Meneghini	Stri				+																		
<b>Rhodophyta</b>																							
<i>Aspidium corallinum</i> C. Agardh	Acor													+			+						
<i>Anotrichium tenue</i> (C. Agardh) Nägeli	Aten	0.007	0.1	O	0.014	0.1	O																
<i>Boergesenella fruticulosa</i> (Wulfen) Kylin	Bfru													0.031	0.1	O							
<i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau	Ccil	0.376	3.6	O	0.435	2.1	O				0.271	2.1	O	0.063	0.2	O							
<i>Ceramium diaphanum</i> (Lightfoot) Roth	Cdia	0.022	0.2	O	0.008	0.0	O																
<i>Ceramium tenerrimum</i> (G. Martens) Okamura	Cten	0.082	0.8	O	0.110	0.5	O				0.005	0.0	O	0.025	0.1	O							

<i>Champia parvula</i> (C. Agardh) Harvey	Cpar								0.005	0.0	O								
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	Ccap								0.048	0.4	O	0.178	0.7	F	0.004	0.0	O		
<i>Chondrophyucus tenerrimus</i> (Cremades) G. Furnari, Boisset, Cormaci et Serio	Chten	0.051	0.5	O	0.093	0.5	F	0.056	0.3	O	5.749	<b>45.3</b>	F	15.31	<b>58.2</b>	F	0.014	0.1	O
<i>Dasya corymbifera</i> J. Agardh	Dcor				0.007	0.0	O										0.006	0.0	O
<i>Falkenbergia rufolanosa</i> Stadium	Fruf												0.013	0.1	O				
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	Hsec				+														
<i>Hypnea musciformis</i> (Wulfen) J.V. Lamouroux	Hmus																		
<i>Jania Rubens</i> (Linnaeus) J.V. Lamouroux	Jrub	2.690	<b>25.9</b>	S	17.20	<b>84.7</b>	F	0.025	0.1	O	0.851	<b>6.7</b>	S	1.042	4.0	F	0.012	0.1	O
<i>Polysiphonia subulata</i> (Ducluzeau) P.L. Crouan & H.M. Crouan	Psub				0.001	0.0	O												
<i>Spyridia filamentosa</i> (Wulfen) Harvey	Sfil										0.137	1.1	O	0.287	1.1	S			
	Sr	14			14			4			21			22			11		4
	B	10.38			20.31			22.30			12.70			26.31			14.76		11.97
	H'	2.53			0.99			0.04			2.52			2.21			0.12		0.20

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Table 8. Results of mixed analysis of variance showing the effects of the factors season, local\_assemblage and their interaction (Season\*Local\_Assemblage) on the biomass, of frequent species, indicating  $F_{-}va$  lues and significance levels. \* $p<0.05$ ; \*\* $p<0.01$ ; \*\*\* $p<0.005$ ; \*\*\*\* $p<0.001$ ; ns: not significant.

Species	Abrev.	SEASON	LOCAL_ASSEMBLAGE	SEASON*LOCAL_ASSEMBLAGE
<i>Acetabularia acetabulum</i>	Aace	6.365 ****	3.621 ***	3.302 ****
<i>Caulerpa prolifera</i>	Cpro	2.745 *	114.808 ****	2.933 *
<i>Ceramium ciliatum</i>	Ccil	2.863 *	0.274 ns	0.86 ns
<i>Ceramium diaphanum</i>	Cdia	1.202 ns	0.234 ns	0.949 ns
<i>Ceramium tenerrimum</i>	Cten	5.432 ***	0.345 ns	0.345 ns
<i>Champia parvula</i>	Cpar	0.79 ns	0.162 ns	1.21 ns
<i>Chondria capillaris</i>	Ccap	0.613 ns	4.402 ***	2.063 *
<i>Chondrophycus tenerrimus</i>	Chte	2.78 *	41.414 ****	1.271 ns
<i>Cladophora albida</i>	Calb	2.373 ns	4.977 *	2.935 *
<i>Cladophora coelothrix</i>	Ccoe	1.008 ns	1.066 ns	0.973 ns
<i>Cladophora vagabunda</i>	Cvag	0.794 ns	0.408 ns	1.041 ns
<i>Cladophoropsis modonensis</i>	Cmod	2.023 ns	1.197 ns	1.291 ns
<i>Cladostephus spongiosus</i>	Cspo	0.679 ns	15.886 ****	0.643 ns
<i>Corallina elongata</i>	Celo	0.878 ns	0.774 ns	1.057 ns
<i>Cymodocea nodosa</i>	Cnod	1.48 ns	119.785 ****	1.713 ns
<i>Cystoseira compressa</i>	Ccom	9.488 ****	21.087 ****	1.438 ns
<i>Cystoseira foeniculacea f. tenuiramosa</i>	Cfoe	7.77 ****	24.82 ****	1.804 ns
<i>Dasya corymbifera</i>	Dcor	1.144 ns	0.798 ns	0.9 ns
<i>Dictyota fasciola</i>	Dfas	3.496 *	3.779 ns	3.531 *
<i>Dictyota linearis</i>	Dlin	3.781 **	2.537 ns	2.28 *
<i>Falkenbergia rufolanosa</i>	Fruf	2.042 ns	0.605 ns	2.298 *
<i>Haliptilon virgatum</i>	Hvir	2.896 *	29.688 ****	2.896 **
<i>Halopteris filicina</i>	Hfil	0.593 ns	18.794 ****	0.272 ns
<i>Jania rubens</i>	Jrub	3.438 *	24.07 ****	2.241 ***
<i>Jania rubens var. corniculata</i>	Jcor	2.896 *	29.688 ****	2.896 **
<i>Laurencia obtusa</i>	Lobt	0.996 ns	1.16 ns	1.099 ns
<i>Liagora viscida</i>	Lvis	1.926 ns	1.03 ns	0.628 ns
<i>Lyngbia sordida</i>	Lsor	1.162 ns	1.671 ns	1.318 ns
<i>Padina pavonica</i>	Ppav	5.77 ****	6.865 ****	2.112 **
<i>Peyssonnelia squamaria</i>	Psqu	0.142 ns	70.693 ****	0.119 ns
<i>Posidonia oceanica</i>	Poce	1.088 ns	-	-
<i>Scytosiphon lomentaria</i>	Slom	1.927 ns	-	-
<i>Stypocaulon scoparium</i>	Ssco	4.545 ***	26.023 ****	0.979 ns
<i>Ulva clathrata</i>	Ucla	1.762 ns	-	-
<i>Ulva intestinalis</i>	Uint	4.219 **	10.083 ****	4.511 ***
<i>Valonia aegagropila</i>	Vaeg	1.651 ns	0.182 ns	0.311 ns