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Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea

M. Vazquez-Luis, P. Sanchez-Jerez, J. Bayle-Sempere

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1 **Changes in amphipod (Crustacea) assemblages associated with**
2 **shallow-water algal habitats invaded by *Caulerpa racemosa* var.**
3 ***cylindracea* in the western Mediterranean Sea.**

4
5 Vazquez-Luis¹, M.; Sanchez-Jerez², P. and Bayle-Sempere, J.²

6 (1) Centro de Investigación Marina de Santa Pola (CIMAR), Ayto. de Santa Pola y
7 Univ. de Alicante. Torre d'Enmig s/n, Cabo de Santa Pola, Alicante (Spain).

8 MT.Vazquez@ua.es

9 Tel.: +34 96 5903400x2916

10 Fax: +34 96 590 98 40

11 (2) Departamento de Ciencias del Mar y Biología Aplicada. Edificio Ciencias V.

12 Universidad de Alicante. POB. 99. E-03080 Alicante (Spain).

13
14 **Abstract**

15 The effects of the invasive species *Caulerpa racemosa* var. *cylindracea* (hereafter
16 *C. racemosa*) on amphipod assemblages associated with shallow-water rocky habitats
17 were studied. Two habitats located along the SE Iberian Peninsula were compared;
18 invaded and non-invaded. The results showed that growth of *C. racemosa* affects
19 habitat structure, influencing the species composition and biomass of macroalgae, and
20 detritus accumulation. In turn, such changes in habitat features affected the associated
21 amphipod assemblages with different ecological requirements. However, the species
22 richness of amphipods was relatively high in both habitats, while the species
23 composition of amphipods changed completely. For example, some species such as
24 *Ampithoe ramondi* and *Hyale schmidtii* did not colonize invaded habitats, while others
25 such as *Apocorophium acutum* were favoured by the spread of *C. racemosa*. Habitat

26 invasion by *C. racemosa* can have an important influence on biotic assemblages,
27 modifying both habitat structure and the associated fauna, with unknown effects on the
28 overall ecosystem.

29

30 **Key words:** Amphipoda, *Caulerpa racemosa* var. *cylindracea*, detritus, invasive
31 species, Mediterranean Sea, shallow rocky bottoms.

32

33 **1. Introduction**

34 The green alga *Caulerpa racemosa* (Forsskål) J. Agardh var. *cylindracea* (Sonder)
35 Verlaque, Huisman et Boudouresque (Verlaque et al., 2003) (hereafter *C. racemosa*)
36 was first detected in Tunisia (Mediterranean Sea) in 1926. More recently, during the
37 1990s, *C. racemosa* spread steadily throughout the Mediterranean region (see Piazzini et
38 al., 2005). Recent genetic analyses have shown that the *C. racemosa* population
39 originated from the southwest coast of Western Australia (Verlaque et al., 2003), and is
40 not a Lessepsian migrant as thought originally. A remarkable spread of *C. racemosa*
41 throughout the Mediterranean has been recorded during the last 15 years or so, during
42 which the alga invaded different habitats located at water depths of 0 m to more than 60
43 m. The recorded rate of invasion has been much faster than that for other invasive
44 species such as *Caulerpa taxifolia* (Verlaque et al., 2003). The rapid spread of *C.*
45 *racemosa* can be explained by its very efficient reproductive strategies, both sexual and
46 asexual (via propagules), which is not the case with *Caulerpa taxifolia* (Panayotidis and
47 Žuljević, 2001; Renoncourt and Meisenez, 2002).

48 Several studies have demonstrated that habitat heterogeneity and complexity play an
49 important role in influencing the assemblage structure of epibenthic marine fauna
50 (Johnson, 1970; Stoner, 1980; Dean and Connell, 1987; Edgar, 1992; Taylor and Cole,

51 1994, Ayala and Martín, 2003). The pattern of distribution and species richness and
52 abundance of epifauna on rocky bottoms is affected by changes in the composition of
53 associated macroalgae (Connell, 1972). Therefore, changes in habitat structure of
54 vegetated substrates resulting from the invasion of species such as *C. racemosa* could
55 affect the associated fauna, including amphipods.

56 Amphipods are one of the most important groups of invertebrates associated with
57 vegetated habitats, and they play an important role as trophic resources for fish
58 populations (Sanchez-Jerez et al., 1999; Stål et al., 2006). Amphipods respond to habitat
59 alteration and can therefore be used as an indicator of environmental impacts on
60 vegetated habitats (Bellan-Santini, 1980; Virnstein, 1987; Conradi et al., 1997;
61 Sanchez-Jerez et al., 2000).

62 Since the first records of spread of *C. racemosa* along Mediterranean coastal areas,
63 several studies concerning the ecology of this species have been undertaken (see Ruitton
64 et al., 2005; Cavas et al., 2006). However, information on changes on the associated
65 fauna brought about by the invasive alga is lacking (Argyrou et al., 1999; Piazzini and
66 Balata, 2007). The main aim of this study was to assess the effects of *C. racemosa* on
67 amphipod assemblages associated with a shallow water rocky bottom habitat in the
68 southwestern Mediterranean Sea, by comparing natural rocky algal assemblages and the
69 same habitat type that has been invaded by *C. racemosa*. The hypothesis tested in our
70 study was: invasion by *C. racemosa* should influence the habitat structure of rocky
71 bottom algal assemblages and, consequently, the assemblage structure of associated
72 epifauna such as amphipods may be affected, in terms of species richness and
73 abundance.

74

75 **2. Materials and Methods**

76 2.1. Study area

77 Fieldwork was carried out along the Cape of Santa Pola (Alicante, south-east Spain;
78 Fig. 1) on a shallow rocky platform. In Alicante, *C. racemosa* was first recorded in 2002
79 at a site located around ten kilometres north of our study area, where it colonised soft
80 sediments and dead matte of *Posidonia oceanica*. Following two months, *C. racemosa*
81 was detected on the rocky platform in our study area (Pena-Martin et al., 2003). The
82 alien alga now occurs in extensive areas of ecologically important rocky bottoms, on
83 sandy and muddy substrata, and on dead matte of *Posidonia oceanica*. It also occurs
84 intermixed with *Cymodocea nodosa* in meadows of the seagrass within a wide depth
85 range (0.2 - 1.5 m) and with patchy distribution.

86 2.2. Sampling and experimental design

87 Shallow rocky habitat, located within the 0.2 m - 0.5 m depth range, was sampled.
88 Several sampling sites, separated by hundreds of metres, with *C. racemosa* and without
89 the alien alga, were randomly selected across the study area. All sites presented similar
90 environmental conditions with respect to wave exposure and light (Ferrandis-Ballester
91 and Bartolomé Pina, 1985). Three 'invaded' rocky habitat sites and another three 'non-
92 invaded' rocky habitat sites were sampled in September 2004 (average water
93 temperature = 27.5 °C), which coincides with the period of maximum vegetative growth
94 of the alga (Piazzi and Cinelli, 1999). Other sites were sampled again in March 2005
95 (water temperature = 13 °C) which coincides with the period of minimum vegetative
96 grow. At each site, three random replications were taken using a 20×20 cm quadrat by
97 scraping the whole surface using a trowel (Edgar, 1990). Samples were separated by
98 tens of meters. A 300 µm mesh bag was attached to the quadrat to avoid loss of the
99 motile fauna. Samples were preserved in 4% solution of formaldehyde in seawater.
100 Each replicate was sieved in sea-water through a 500 µm mesh, obtaining the fine

101 fraction of detritus. In the laboratory, the amphipods were separated, identified, and
102 counted. After that, algae were sorted as well as the bigger fragments of detritus.
103 Afterwards the macrophytes and the detritus were dried for 24 h at 80 °C, and weighed.
104 The macrophytes were identified to the species level. Habitat structure was
105 characterised using three attributes: species richness of macrophytes, biomass of each
106 species (g) and quantity of detritus (g).

107

108

109 **2.3. Data analysis**

110 Two different statistical approaches were used to identify potential changes in the
111 amphipod assemblages and habitat features, based on the null hypothesis of no change
112 in amphipod assemblage composition between the two habitat types across different
113 sampling times.

114

115 **2.3.1. Multivariate analysis of assemblage structure**

116 Non-parametric multidimensional scaling (MDS) was used as the ordination method for
117 exploring changes in amphipod and macroalgal assemblages (Clarke and Warwick,
118 1994). The similarity matrix, which was calculated using the Bray-Curtis index and
119 double square transformation of data, was used to construct bivariate MDS plots.
120 Calculation of percentage similarities (SIMPER) was then applied to calculate the
121 contribution of each species to the dissimilarity between sampling times and habitats.
122 (PRIMER software; Clarke, 1993).

123

124 **2.3.2. Univariate analysis**

125 Algal biomass, *C. racemosa* biomass, species richness of seaweeds, biomass of detritus,
126 total abundance of amphipods, species richness of amphipods and abundance of seven
127 amphipod species (the most important by SIMPER) were analysed using ANOVA. To
128 test whether the abundance of amphipods was similar across habitats and times we used
129 an analysis of variance (ANOVA) which incorporated the following factors: 'Time of
130 sampling', a fixed factor and orthogonal, with two treatments: September-04 and
131 March-05; 'habitat', a fixed factor, with two treatments: macroalgal community with *C.*
132 *racemosa* (invaded habitat) and without *C. racemosa* (non-invaded habitat), and 'Site',
133 a random factor and nested with the both main factors, with three random sampling
134 sites.

135 Prior to ANOVA, heterogeneity of variance was tested with Cochran's *C*-test. Data
136 were $\sqrt{x} + 1$ transformed if variances were significantly different at $p = 0.05$, and $\log(x$
137 $+ 1)$ transformed if variance was still heterogeneous. Where variance remained
138 heterogeneous, untransformed data were analysed, as ANOVA is a robust statistical test
139 and is relatively unaffected by heterogeneity of variances, particularly in balanced
140 experiments (Underwood, 1997), however, in such cases special care was taken in the
141 interpretation of results. Furthermore, in such cases, to reduce type I error, the level of
142 significance was reduced to < 0.01 . When ANOVA indicted a significant difference for
143 a given factor, the source of difference was identified by applying the Student-Newman-
144 Keul (SNK) test (Underwood, 1981; Underwood, 1997).

145

146 **3. Results**

147 **3.1. Habitat features**

148 A total of 24 taxa of macroalgae and one seagrass species were identified (Table 1).

149 Species richness showed significant seasonal differences (Table 2; $T_i = P < 0.05$). During

150 September, the invaded habitat showed a reduced number of macroalgal species: only
151 five together with *C. racemosa*, compared with 11 species recorded from the non-
152 invaded habitat. The most important species in terms of biomass in the non-invaded
153 places were *Jania rubens*, *Halopteris scoparia* and *Cystoseira brachicarpa*, while in the
154 invaded habitat *C. racemosa*, *Jania rubens* and *Padina pavonica* were most important
155 (Table 1). In March, differences between invaded and non-invaded habitats were lower
156 (14 where *C. racemosa* was present and 16 species where it was absent). The most
157 important species in non-invaded sites during March were *Corallina elongata*, *Jania*
158 *rubens* and *Dictyota fasciola*; and *C. racemosa*, *Cladophora* sp. and *Halopteris scoparia*
159 dominated at invaded sites (Table 1). The MDS two-dimensional representation of
160 macrophyte biomass clearly showed segregation of sampling sites mainly related to
161 sampling time and habitat (Fig. 2).

162 In the case of algal biomass, excluding *C. racemosa*, significant differences were
163 noted for the invaded habitat with respect to the non-invaded habitat (Table 2; Fig. 3).
164 Total algal biomass recorded in September was similar between the two different
165 habitats (347.67 ± 117.44 g dw m⁻² for non-invaded habitat compared to 379.55 ± 64.63
166 g dw m⁻² for invaded habitat; Table 1), however, *C. racemosa* contributed a high value
167 (74.6%), and replacing other native species. Non-invaded sites showed the highest mean
168 biomass value, which reached a maximum value of 826.46 ± 203.15 in September (Fig.
169 3). However, total biomass (326.52 ± 79.21 g dw m⁻²) at the invaded sites, without a
170 recovery of the community in spite of the reduction of *C. racemosa* biomass.

171 Differences in accumulated detritus biomass was significant between habitats
172 ($P < 0.05$, Table 2). The highest values were recorded from invaded habitats during both
173 sampling periods (472.48 g dw m⁻² in September and 466.92 g dw m⁻² in March). On
174 the other hand, detritus biomass was relatively low at non-invaded habitats during

175 September (5.87 ± 1.51 g dw m^{-2}), and higher in March (242.22 ± 47.25 g dw m^{-2} ; Fig.
176 3).

177

178 **3.2. Amphipod assemblage**

179 A total of 31 amphipod taxa, belonging to 13 families, were recorded (Table 3).
180 Species richness was significantly different (Ti, $P < 0.05$, Table 4; Fig. 4a) among
181 sampling times but similar between habitats. In September, species richness recorded
182 from the habitat dominated by *C. racemosa* was similar to that recorded from the non-
183 invaded habitat (16 and 14 species respectively; Table 3), while for both habitats, values
184 were higher in March (20 and 24 species, Table 3). Only ten species were present in
185 both habitats and in both months: *Amphilocheirus neapolitanus*, *Ampithoe ramondi*,
186 *Microdeutopus* spp., *Caprella* spp., *Apocorophium acutum*, *Elasmopus* spp., *Lysianassa*
187 *costae*, *Pereionotus testudo*, *Stenothoe monoculodes* and *Hyale schmidtii*. Seven species
188 were found only in the non-invaded habitats: *Amphilocheirus* sp., *Ampelisca*
189 *serraticaudata*, *Ampithoe ferox*, *Lembos* sp., *Leptocheirus guttatus*, *Lysianassa* sp. and
190 *Stenothoe tergestina*; while there seemed to be a relationship between the invaded
191 habitat and the following six amphipods: *Ampelisca diadema*, *Corophium* spp.
192 *Corophium insidiosum*, *Gammarella fucicola*, *Melita palmata* and *Orchomene humilis*.
193 Total abundance was similar between habitats in September, but there were significant
194 differences between the two habitats in March, with a maximum value of 6497.22
195 ind/ m^2 recorded from the non-invaded habitat (Ti x Ha $P < 0.01$, Table 4; Fig. 4b).

196 The two-dimensional MDS plot for the amphipod assemblages showed
197 segregation of sampling sites that was mainly related to the sampling period, while
198 moderate segregation was noted by habitat type during March (Fig. 5). The main

199 species responsible for dissimilarities in amphipod assemblages were *Caprella* spp.,
200 *Ampithoe ramondi*, *Microdeutopus* spp., *Elasmopus* spp., *Apocorophium acutum*, *Hyale*
201 *schmidti* and *Lysianassa costae*, for which an average dissimilarity of 64.73 % was
202 noted between habitats. Together, these species comprised 90 % of the total amphipod
203 abundance.

204 The seven most important amphipod species showed different patterns of
205 abundance values with respect to macroalgal assemblage. Abundance of *Ampithoe*
206 *ramondi* and *Hyale schmidti* were significantly higher in non-invaded habitats (Ha,
207 $P < 0.05$, Table 4; Fig. 6a, b). On the other hand, *Apocorophium acutum* had a
208 significantly higher abundance in the invaded habitat (Ha, $P < 0.05$, Table 4; Fig. 6c).
209 Significant differences were recorded for *Microdeutopus* spp. in terms of sampling
210 times (Ti, $P < 0.05$, Table 4; Fig. 6d), while it was more abundant in September at
211 invaded habitats but without significant differences.

212 With regard to differences between sampling times (Table 3), several species
213 appeared only in September (*Amphilochus* sp., *Melita palmata* and *Orchomene*
214 *humilis*); or in March (*Ampelisca diadema*, *Ampelisca serraticaudata*, *Lembos* sp.,
215 *Leptocheirus guttatus*, *Corophium* spp., *Corophium insidiosum*, *Dexamine spiniventris*,
216 *Gammarella fucicola*, *Melita hergensis*, *Lysianassa* sp. and *Stenothoe tergestina*).
217 Dissimilarity between sampling times within non-invaded sites was not very high
218 (48.09%); the most important species contributing to this dissimilarity were *Caprella*
219 spp. and *Hyale schmidti*. Dissimilarity between sampling times within invaded sites was
220 51.71%, the most important species contributing to this dissimilarity were *Caprella* spp.
221 and *Lysianassa costae*.

222 The abundance of two species (*Caprella* spp. and *Elasmopus* spp.) was not
223 significantly different between the two habitat types, but there was a clear pattern of
224 higher abundances in non-invaded habitat. The abundance of *Caprella* spp. varied
225 significantly with respect to season, being more abundant in March, especially in the
226 non-invaded habitat (Ti, $P < 0.05$, Table 4; Fig. 6e). *Elasmopus* spp. seemed to be more
227 abundant on native seaweeds, especially during September, but not statistical
228 differences were noted (Table 4, Fig. 6f). Finally, the abundance of *Lysianassa costae*,
229 was higher in non-invaded habitats, but this was true only in March (TixHa, $P < 0.01$,
230 Table 4, Fig. 6g); the pattern was opposite during September, but without any
231 significant differences.

232

233 4. Discussion

234 Our results show that the presence and abundance of *C. racemosa* had a marked
235 effect on the macroalgal assemblage structure of Mediterranean shallow rocky
236 communities, affecting the species composition of vegetation and increasing the detritus
237 stock. This causes important changes in the associated amphipod assemblage, in terms
238 of both abundance and species composition. The effects of the invasive species on
239 habitat structure were more important in September because the alga was dominant at
240 that time. The seasonal variation in abundance values for *C. racemosa* recorded from
241 our study area was similar to that described in other localities, i.e. with maximum
242 development in the warm season, while biomass values were similar or even greater
243 than those recorded from other Mediterranean localities (Piazzi and Cinelli, 1999). The
244 peculiar growth of *C. racemosa*, with stolons that spread rapidly in all directions, and its
245 colonisation pattern that results from sexual reproduction (Panayotidis and Žuljevič,
246 2001), together with dispersal of fragments detached from the plant (Ceccherelli et al.,

247 2001; Ceccherelli and Piazzì, 2001) and propagules (Renoncourt and Meinesz, 2002)
248 permit *C. racemosa* to colonize a habitat very efficiently. This results in strong
249 modification of habitat structure, particularly that of macroalgal assemblages. On the SE
250 coast of Spain and other locations (e.g. Nervi, Italy; Modena et al., 2000), colonisation
251 by *C. racemosa* has been mostly recorded from rocky bottom habitats located in
252 shallow waters (0.5 m), however, on a wider scale across the Mediterranean region (e.g.
253 France, Italy and Cyprus) more extensive spread of the alga have been recorded on soft
254 bottom habitats in deeper waters (15-20 m) (Argyrou et al., 1999; Verlaque et al., 2004),
255 and on dead mat of *Posidonia oceanica*. Therefore, one would expect that the spread
256 of *C. racemosa* will extend to both rocky and soft bottom habitats, as well as to
257 degraded *P. oceanica* meadows.

258 With respect to changes in vegetation resulting from the presence of *C. racemosa*,
259 an important reduction in species richness was recorded in September. On the other
260 hand, contrary to results from other studies (Piazzì et al., 2001), species richness was
261 similar between invaded and non-invaded habitats in March (the colder month), which
262 implies that some native species colonized the habitat irrespective of the different
263 species composition and biomass of benthic vegetation. Some authors have shown that
264 several years are necessary for the development of dense and continuous *C. racemosa*
265 stands (Ruitton et al., 2005); possibly during the forthcoming years the effects will
266 persist also during the coldest period at the study area, reducing the possibility of algae
267 colonization. However, the total biomass of *C. racemosa* recorded from our study (259
268 g dw m⁻²) is comparable or higher than that recorded from studies carried out on French
269 and Italian coasts, and is also higher than values obtained for *C. taxifolia* and *C.*
270 *prolifera* meadows at some localities (see a review in Capiomont et al., 2005).

271 One of the remarkable impacts of *C. racemosa* is the accumulation of detritus,
272 which persists throughout the year. In spite of the important seasonal variability of *C.*
273 *racemosa* biomass, detritus accumulation persist in winter. The mesh generated by the
274 stolons of this species ensure that detritus is retained, while the multilayered structure
275 formed by the thallus traps the sediment (Piazzi et al., 2001). Detritus values recorded
276 during both seasons were 2 to 6 times higher than those recorded from native seaweeds.
277 This accumulation of detritus causes import changes in the structure of the sediment and
278 in the granulometric composition (Walker et al., 1991), leading to anoxic conditions in
279 which toxic substances can be possibly accumulated. On the other hand, detritus plays a
280 very important role as a trophic resource for marine invertebrates, being one of the main
281 trophic pathways of the marine ecosystem (Valiella, 1995) and is one of the most
282 important features of habitat structure in vegetated habitats (Allesina et al., 2005).
283 Therefore, any modification of the detritus compartment can affect the overall trophic
284 web, because it could lead to a change in the faunal assemblage structure resulting from
285 modification of trophic guilds due to different trophic requirements.

286 With respect to the epifauna, various studies have demonstrated that modification
287 of habitat complexity affects crustacean assemblages (Hicks, 1977, 1982; Stoner, 1980;
288 Virnstein, 1987; Virnstein and Howard, 1987; Edgar, 1983, 1992; Sanchez-Jerez et al.,
289 1999; Ayala and Martín, 2003). In our study, the amphipod assemblages were affected
290 by changes in habitat structure due to colonisation by *C. racemosa*. The total abundance
291 of amphipods was greater on native seaweeds, mainly in March. However, the species
292 richness of the amphipod assemblage did not decrease because of the spread of *C.*
293 *racemosa* but because of an indirect effect; namely the increase in detritus biomass in
294 invaded habitat resulted in an increase in the abundance of detritivores species (e.g.
295 *Apocorophium acutum*), and increase in the abundance of herbivorous species (e.g.

296 *Ampithoe ramondi* and *Hyale schmidtii*), hence resulting in a large overall modification
297 of the assemblage species composition.

298 The main modification in amphipod assemblage structure was manifested as an
299 increase in abundance of *Apocorophium acutum* in habitat invaded by *C. racemosa*,
300 which was four times higher than that of other Corophiidae species in eutrophic habitats
301 (Guerra-García and García-Gómez, 2005). Species belonging to the genus
302 *Apocorophium* are tube-dwelling amphipods that inhabit small U-shaped tubes and are
303 selective deposit feeders (Ciarelli et al., 1997), and feed on bacteria, algae, and diatoms
304 adsorbed onto the surface of sediment particles (Meadows and Reid, 1966). Several
305 species of this genus are continuously exposed to toxicants in the sediment, which they
306 ingest while feeding (Bat and Raffaelli, 1998), hence they have been used for sediment
307 toxicity tests. The accumulation of detritus in habitats invaded by *C. racemosa* seems to
308 favour colonization by *Corophium* spp., resulting in a dramatic increase in abundance
309 and establishment of a large population in an altered habitat. *Microdeutopus* spp. also
310 showed a small increase in abundance in habitat invaded by *C. racemosa*, but the effect
311 was only recorded in September. This genus is generally associated with *Posidonia*
312 *oceanica* and fine sand habitats (Ruffo, 1982), but in experiments carried out recently
313 by Roberts and Poore (2005), the family Aoridae were noted to prefer bare rock with a
314 thin cover of sediment than an algal substratum. Furthermore, other taxonomic groups,
315 such as the polychaetes, are favoured by accumulation of detritus amongst the *C.*
316 *racemosa* stolons, as shown by Argyrou et al. (1999) from their study carried out in
317 Cyprus.

318 On the other hand, the abundance of some species, such as *Ampithoe ramondi*,
319 *Hyale schmidtii* or *Caprella* spp., was reduced in habitat invaded by *C. racemosa*, since
320 these species have a preference for native seaweeds (Kocatas, 1976; Russo, 1997;

321 Guerra-Garcia and García-Gómez, 2001; Roberts and Poore, 2005). Other studies have
322 also shown displacement of *Ampithoe ramondi* resulting from the presence of other
323 *Caulerpa* species, e.g. *Caulerpa prolifera* (Sánchez-Moyano et al., 2001). The displaced
324 species have a close relationship with seaweeds, as has been demonstrated by Viejo
325 (1999). In the case of other species, such as *Lysianassa costae*, the effects of *C.*
326 *racemosa* seem to be seasonal, inhabiting habitats that have a large algal biomass,
327 irrespective of the species composition.

328 Comparing the results of the present study with ones on the effects of *C. taxifolia*
329 on amphipod assemblages, the species richness recorded from the latter appears to be
330 lower (Bellan-Santini et al., 1995). Furthermore, the effects of *C. taxifolia* on the
331 abundance of amphipods also seem to be more critical (Bellan-Santini et al, 1995). Such
332 differences could be due to several factors, such as the species composition of *Caulerpa*
333 beds. Stands of *C. taxifolia* are monospecific, while in our case; the *C. racemosa* grew
334 intermixed with other macroalgal species during both sampling periods. Consequently,
335 during the initial stages of invasion of a host habitat by an invasive seaweed, an
336 increment in habitat complexity will occur if the initial cover is low, hence a new and
337 additional habitat for the local epifauna becomes available (Viejo, 1999). However, if
338 growth of the invasive species continues, leading to a monospecific and dense meadow,
339 it could lead to impoverishment of the amphipod assemblage as has been noted for *C.*
340 *taxifolia* elsewhere.

341 Several studies have demonstrated that consequences of *C. racemosa* in host
342 systems are very important, particularly since it appears that this introduced species
343 most invasive in the Mediterranean Sea (Verlaque et al., 2003). The presence of *C.*
344 *racemosa* in the southeastern coast of Spain is an incipient problem. It was recorded
345 from Alicante in 2002 and, in less than three years, important changes in the structure of

346 shallow rocky habitat assemblages occurred, although to date the distribution of *C.*
347 *racemosa* has been rather patchy, hence its effects are not very widespread locally.
348 Several years may be necessary for development of a dense and continuous *C. racemosa*
349 meadow (Ruitton et al., 2005); therefore in the near future, one can expect dramatic
350 changes in rocky bottom habitats, leading to a direct impact on marine benthic
351 communities along the western Mediterranean coast. It is therefore very important to
352 increase our research effort to establish the ecological implications of the spread of *C.*
353 *racemosa* in the Mediterranean Sea, as this will provide the necessary information and
354 tools to develop new mitigation and eradication programs.

355

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364

6. References

- 365 Allesina, S., Bondavalli, C., Scharler, U.M., 2005. The consequences of the
366 aggregation of detritus pools in ecological networks. *Ecological Modelling* 189,
367 221-232.
- 368 Argyrou, M., Demetropoulos, A., Hadjichristophorou, M., 1999. Expansion of the
369 macroalga *Caulerpa racemosa* and changes in soft bottom macrofaunal
370 assemblages in Moni Bay, Cyprus. *Oceanologica Acta* 22, 517-528.
- 371 Ayala, Y., Martín, A., 2003. Relaciones entre la comunidad de anfípodos y las
372 macroalgas a las que están asociados, en una plataforma rocosa del litoral central
373 de Venezuela. *Boletín Instituto Español Oceanografía* 19 (1-4), 171-183.
- 374 Bat, L., Raffaelli, D., 1998. Sediment toxicity testing: a bioassay approach using the
375 amphipod *Corophium volutator* and the polychaete *Arenicola marina*. *Journal of*
376 *Experimental Marine Biology and Ecology* 226, 217-239.
- 377 Bellan-Santini, D., 1980. Relationship Between Populations of Amphipods and
378 Pollution. *Marine Pollution Bulletin* 11, 224-227.
- 379 Bellan-Santini, D., 1995. Faune d'invertébrés du peuplement à *Caulerpa taxifolia*.
380 Données préliminaires pour les côtes de provence (Méditerranée nord-occidentale)
381 *Biologia Marina Mediterranea* Vol 2, fasc 2 « Atti XXV Congresso »
- 382 Capiomont, A., Breugnot, E., den Haan, M., Meinesz, A., 2005. Phenology of a
383 deep-water population of *Caulerpa racemosa* var. *cylindracea* in the northwestern
384 Mediterranean Sea. Short communication. *Botanica Marina* 48, 80-83.
- 385 Cavas, L., Baskin, Y., Yurdakoc, K., Olgun, N., 2006. Antiproliferative and newly
386 attributed apoptotic activities from an invasive marine alga: *Caulerpa racemosa*
387 var. *cylindracea*. *Journal of Experimental Marine Biology and Ecology* 339, 111-
388 119.
- 389 Ceccherelli, G., Piazzzi, L., Cinelli, F., 2001. The role of vegetative fragments in the
390 recruitment process of *Caulerpa taxifolia* and *Caulerpa racemosa*. In: Gravez V,
391 Ruitton S, Boudouresque CF, Le Direac'h L, Meinesz A, Scabbia G, Verlaque M
392 (eds) Fourth International Workshop on *Caulerpa taxifolia*. GIS Posidonie Publ,
393 Marseilles, France, pp 111-117.
- 394 Ceccherelli, G., Piazzzi, L., 2001. *Caulerpa racemosa* e *Caulerpa taxifolia* in
395 Mediterraneo: effetto della complessità dei popolamenti macroalgali autoctoni e
396 dei loro rapporti competitivi. 328 Congresso SIBM, p 45.
- 397 Ciarelli, S., Vonck, WAPMA., van Straalen, N.M., 1997. Reproducibility of spiked-
398 sediment bioassays using the marine benthic amphipod, *Corophium volutator*.
399 *Marine Environmental Research* 4, 329-343.
- 400 Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community
401 structure. *Australian Journal of Ecology* 18, 117-143.

- 402 Clarke, K.R., Warwick, R.M., 1994. Changes in Marine Communities: an approach
403 to statistical analysis and interpretation. Natural Environment Research Council
404 UK, 144 pp.
- 405 Connell, J.H., 1972. Community interactions on marine rocky intertidal shores.
406 Annual Review of Ecology and Systematics 3, 169-192.
- 407 Conradi, M.; López-González, P.J.; García-Gómez, J.C., 1997. The Amphipod
408 Community as a Bioindicator in Algeciras Bay (Southern Iberian Peninsula)
409 Based on a Spatio-Temporal Distribution. Marine Ecology 18 (2), 97-111.
- 410 Dean, R.L., Connell, J.H., 1987. Marine invertebrates in algal succession. II. Test of
411 hypotheses to explain changes in diversity with succession. Journal of
412 Experimental Marine Biology and Ecology 109, 217-247.
- 413 Edgar, G.J., 1983. The ecology of South-East Tasmanian phytal animal
414 communities. IV. Factors affecting the distribution of amphipod amphipods
415 among algae. Journal of Experimental Marine Biology and Ecology 70, 205-225.
- 416 Edgar, G.J., 1990. The influence of plant structure on the species richness, biomass
417 and secondary production of macrofaunal assemblages associated with Western
418 Australian seagrass beds. Journal of Experimental Marine Biology and Ecology
419 137, 215-240.
- 420 Edgar, G.J., 1992. Patterns of colonization of mobile epifauna in Western Australian
421 seagrass bed. Journal of Experimental Marine Biology and Ecology 157, 225-246.
- 422 Ferrandis-Ballester, E., and Bartolomé-Pina, F., 1985. Dulces bárbaros del este y del
423 oeste (Análisis estadísticos de los vientos en la bahía de Alicante). In: Ramos, A.
424 A. (Ed.). La reserva marina de la Isla Plana o Nueva Tabarca (Alicante), 51-93 pp.
- 425 Guerra-García, J.M., García-Gómez, J.C., 2001. The spatial Distribution of
426 Caprellidea (Crustacea: Amphipoda): A Stress Bioindicator in Ceuta (North
427 Africa, Gibraltar Area). Marine Ecology 22, 357-367.
- 428 Guerra-García, J.M., García-Gómez, J.C., 2005. Oxygen levels versus chemical
429 pollutants: do they have similar influence on macrofaunal assemblages? A case
430 study in a harbour with two opposing entrances. Environmental Pollution 135,
431 281-291.
- 432 Hicks, G.R.F., 1997. Observations of substrate preference of marine phytal
433 harpacticoids (Copepoda). Hydrobiology 56, 7-9.
- 434 Hicks, G.R.F., 1982. Habitat structure, disturbance, and equilibrium in crustacean
435 communities. Marine Ecology 3, 41-45.
- 436 Johnson, M., 1970. Variations in diversity within benthic marine communities.
437 American Naturalist 104, 285-308.
- 438 Kocatas, A., 1976. Note préliminaire sur les amphipodes recueillis dans les horizons
439 supérieurs de l'étage infralitoral rocheux du Golfe d'Izmir (Turquie). Tethys 7 (2-
440 3), 235-240.

- 441 Meadows, P.S., Reid, A., 1966. The behaviour of *Corophium volutator*. Journal of
442 Zoology London 150, 387–399.
- 443 Modena, M., Matricardi, G., Vacchi, M., Guidetti, P., 2000. Spreading of *Caulerpa*
444 *racemosa* (Forsskål) J. Agardh (Bryopsidaceae, Chlorophyta) along the coasts of
445 the Ligurian Sea. Cryptogamie Algologie 21, 301-304.
- 446 Panayotidis, P., Žuljevič, A., 2001. Sexual reproduction of the invasive green alga
447 *Caulerpa racemosa* var. *occidentalis* in the Mediterranean Sea. Oceanologica Acta
448 24, 199-203.
- 449 Pena-Martín, C., Cristóbal-Fernanz, J.C., Crespo, M.B., 2003. *Caulerpa racemosa*
450 (Forssk.) J Agardh (Caulerpaeae, Chlorophyceae), nueva para la flora de
451 Alicante. Anales Jardín Botánico de Madrid 60 (2), 448-449.
- 452 Piazzzi, L., Balata, D., Ceccherelli, G., Cinelli, F., 2001. Comparative study of the
453 growth of two co-occurring introduced green algae *Caulerpa taxifolia* and
454 *Caulerpa racemosa* along the Tuscan coast (Italy, western Mediterranean).
455 Cryptogamie Algologie 22, 459-466.
- 456 Piazzzi, L., Balata, D., 2007. The spread of *Caulerpa racemosa* var. *cylindracea* in in
457 the Mediterranean Sea: an example of how biological invasions can influence beta
458 diversity. Marine Environmental Research (2007),
459 doi:10.1016/j.marenvres.2007.07.002
- 460 Piazzzi, L., Cinelli, F., 1999. Développement et dynamique saisonnière d'un
461 peuplement méditerranéen de l'algue tropicale *Caulerpa racemosa* (Forsskål) J.
462 Agardh. Cryptogamie Algologie 20 (4), 295-300.
- 463 Piazzzi, L., Meinesz, A., Verlaque, M., Akçali, B., Antolić, B., Argyrou, M., Balata,
464 D., Ballesteros, E., Calvo, S., Cinelli, F., Cirik, S., Cossu, A., D'Archino, R.,
465 Djellouli, A.S., Javel, F., Lanfranco, E., Mifsud, C., Pala, D., Panayotidis, P.,
466 Peirano, A., Pergent, G., Petrocelli, A., Ruitton, S., Žuljevič, A., Ceccherelli, G.
467 2005. Invasion of *Caulerpa racemosa* var. *cylindracea* (Caulerpales, Chlorophyta)
468 in the Mediterranean Sea: an assessment of the spread. Cryptogamie Algologie 26
469 (2), 189-202.
- 470 Renoncourt, L., Meinesz, A., 2002. Formation of propagules on a invasive strain of
471 *Caulerpa racemosa* (Chlorophyta) in the Mediterranean Sea. Phycologia 5, 533-
472 535.
- 473 Roberts, D.A., and Poore, A.G.B., 2005. Habitat configuration affects colonisation
474 of epifauna in marine alga bed. Biological Conservation 127, 18-26.
- 475 Ruffo, S., (ed) 1982. The Amphipoda of the Mediterranean. Part 1, Gammaridea.
476 Mémoires de l'Institut Océanographique, Monaco 13 :364 pp.
- 477 Ruitton, S., Verlaque, M., Boudouresque, C.F., 2005. Seasonal changes of the
478 introduced *Caulerpa racemosa* var. *cylindracea* (Caulerpales, Chlorophyta) at th e
479 northwest limit of its Mediterranean range. Aquatic Botany 82, 55-70.

- 480 Russo, A.R., 1997. Epifauna living on sublittoral seaweeds around Cyprus.
481 *Hidrobiología* 344, 169-179.
- 482 Sanchez-Jerez, P., Barberá-Cebrián, C., Ramos-Esplá, A.A., 1999. Comparison of
483 the epifauna spatial distribution in *Posidonia oceanica*, *Cymodocea nodosa* and
484 unvegetated bottoms: Importance of meadow edges. *Acta Oecologica* 20, 391-405.
- 485 Sanchez-Jerez, P., Barberá-Cebrián, C., Ramos-Esplá, A.A., 2000. Influence of the
486 structure of *Posidonia oceanica* meadows modified by bottom trawling on
487 crustacean assemblages: comparison of amphipods and decapods. *Scientia Marina*
488 64, 319-326.
- 489 Sánchez-Moyano, J.E., Estacio, J.F., García-Adiego, E.M., García-Gómez, J.C.,
490 2001. Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal
491 variation of invertebrate macrofauna. *Aquatic Botany* 70, 163-174.
- 492 Stål, J., Pihl, L., Wennhage, H., 2006. Food utilisation by coastal fish assemblages
493 in rocky and soft bottoms on the Swedish west coast: Inference for identification
494 of essential fish habitats. *Estuarine Coastal and Shelf Science* doi:
495 10.1016/j.ecss.2006.09.008
- 496 Stoner, A.W., 1980. Perception and choice of substratum by epifaunal amphipods
497 associated with seagrasses. *Marine Ecology Progress Series* 3, 105-111.
- 498 Taylor, R.B., Cole, R.G., 1994. Mobile epifauna on subtidal brown seaweeds in
499 northeastern New Zealand. *Marine Ecology Progress Series* 115, 271-282.
- 500 Underwood, A.J., 1981. Techniques of analysis of variance in experimental biology
501 and ecology. *Oceanography and Marine Biology. An Annual Review* 19, 513-605.
- 502 Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and*
503 *Interpretation Using Analysis of Variance*, Cambridge University Press, 504 p.
- 504 Valiela, I., 1995. *Marine Ecological Processes*. Springer, Verlag New York.
- 505 Verlaque, M., Alfonso-Carrillo, J., Gil-Rodriguez, M.C., Durand, C., Boudouresque,
506 C.F., and Le Parco, Y., 2004. Blitzkrieg in a marine invasion: *Caulerpa racemosa*
507 var. *cylindracea* (Bryopsidales, Chlorophyta) reaches the Canary Islands (north-
508 est Atlantic). *Biological Invasions* 6, 269-281.
- 509 Verlaque, M., Durand, C., Huisman, J.M., Boudouresque, C.F., Le Parco, Y., 2003.
510 On the identity and origin of the Mediterranean invasive *Caulerpa racemosa*
511 (Caulerpales, Chlorophyta). *European Journal of Phycology* 38, 325-339.
- 512 Viejo, R.M., 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and
513 two local seaweeds in northern Spain. *Aquatic Botany* 64, 131-149.
- 514 Virnstein, R.W., 1987. Seagrass-associated invertebrate communities of the
515 Southeastern U S A: a review. *Florida Marine Research Publication* 42, 89-116.

- 516 Virnstein, R.W., Howard, R.K., 1987. Motile epifauna of marine macrophytes in the
517 Indian River Lagoon, Florida. I. Comparisons among three species of seagrasses
518 from adjacent beds. *Bulletin of Marine Sciences* 41, 1-12.
- 519 Walker, D.I., Hutchings, P.A., Wells, F.E., 1991. Seagrass, sediment and infauna: a
520 comparison of *Posidonia australis*, *Posidonia sinuosa* and *Amphibolis antarctica*
521 in Princess Royal Harbour, south-western Australia. I. Seagrass biomass,
522 productivity and contribution to sediments. In: Wells, F.E., Walker, D.I., Kirkman,
523 H., Lethbridge, R., (eds), *The Marine Flora and Fauna of Albany, W Australia*,
524 Vol 2 W Australian Museum, Perth, pp 597–610.

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525 **Table 1** Mean biomass (g dw m⁻²) values ± SE for the different species, together with total biomass, total
 526 species richness and detritus weight for the two sampling periods and habitats.
 527
 528

Species	SEPTEMBER - 04		MARCH - 05	
	Non-invaded habitat	Invaded habitat	Non-invaded habitat	Invaded habitat
Chlorophyta <i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva	-	-	-	0.08 ± 0.06
<i>Caulerpa prolifera</i> (Forsskål) J.V. Lamouroux	2.23 ± 1.02	19.4 ± 10.57	-	0.01 ± 0.01
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh	-	259.49 ± 65.99	-	68.91 ± 18.71
<i>Cladophora</i> sp. Kützting, 1843	0.30 ± 0.30	-	54.38 ± 14.60	98.19 ± 28.9
<i>Codium</i> (cf) F.S. Collins & Hervey, 1917	-	-	17.43 ± 16.87	-
<i>Dasycladus vermicularis</i> (Scopoli) Krasser	4.27 ± 1.55	0.78 ± 0.36	-	0.99 ± 0.63
<i>Flabellia petiolata</i> (Turra) Nizamuddin	-	-	0.13 ± 0.11	-
<i>Halimeda tuna</i> (J. Ellis & Solander) J.V. Lamouroux	0.09 ± 0.09	-	0.64 ± 0.64	-
<i>Ulva</i> sp. Linnaeus	-	-	5.46 ± 1.64	15.15 ± 5.78
Phaeophyta <i>Cladostephus spongiosus</i> (Hudson) C. Agardh	-	-	0.15 ± 0.15	-
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	-	-	6.97 ± 4.99	3.94 ± 3.93
<i>Cystoseira brachicarpa</i> J. Agardh	34.75 ± 23.07	-	-	-
<i>Cystoseira compressa</i> (Esper) Gerloff & Nizamuddin	-	-	63.92 ± 63.92	0.71 ± 0.71
<i>Dictyota fasciola</i> (Roth) J. V. Lamouroux	1.51 ± 0.97	-	134.78 ± 53.99	20.72 ± 17.44
<i>Halopteris scoparia</i> (Linnaeus) Sauvageau	35.81 ± 34.45	-	104.82 ± 57.53	68.04 ± 48.43
<i>Padina pavonica</i> (Linnaeus) Thivy	20.31 ± 6.86	26.87 ± 14.99	44.14 ± 34.64	37.16 ± 19.51
<i>Sargassum vulgare</i> C. Agardh	2.13 ± 2.13	-	32.83 ± 32.56	-
Rodophyta <i>Ceramium</i> spp. (Hudson) C.A. Agardh	0.11 ± 0.11	-	10.72 ± 8.78	-
<i>Corallina ellongata</i> Ellis et Solander	-	-	186.77 ± 175.87	0.59 ± 0.59
<i>Halopitys incurvus</i> (Hudson) Batters	-	5.13 ± 4.19	-	-
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	246.16 ± 83.17	67.87 ± 29.74	163.12 ± 113.76	-
<i>Laurencia pinnatifida</i> (Hudson) Lamouroux	-	-	1.24 ± 1.24	-
<i>Peyssonnelia</i> sp. (S.G. Gmelin) Decaisne	-	-	-	9.88 ± 9.88
<i>Alsidium corallinum</i> (cf) C. Agardh	-	-	-	0.29 ± 0.29
Seagrasses <i>Cymodocea nodosa</i> (Ucria) Ascherson	-	-	-	1.81 ± 1.81
Total biomass	347.67 ± 117.44	379.55 ± 64.63	826.49 ± 203.15	326.52 ± 79.21
Species richness	11	6	16	15
Detritus	5.87 ± 1.51	472.48 ± 123.05	242.22 ± 47.25	466.92 ± 68.91

529

530 **Table 2** Result of ANOVA (three-factor) for the different habitat attributes: macrophyte species richness,
 531 macrophyte biomass, macrophyte biomass without *C. racemosa*, and detritus. MS = mean square; *P* =
 532 level of probability; df = degrees of freedom; Si= site; ns = non-significant; * significant at $p < 0.05$

533

Source of variation	df	Species richness		Macrophyte biomass		Macrophyte biomass without <i>C. racemosa</i>		Detritus		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Sampling time=Ti	1	53.78	0.0158*	6.59	0.2154	6.05	0.1066	191.75	0.3812	Si(TixHa)
Habitat=Ha	1	2.78	0.5077	5.88	0.2395	10.04	0.0472*	1720.49	0.0241*	Si(TixHa)
TixHa	1	11.11	0.2029	12.34	0.1030	0.27	0.7110	210.67	0.3599	Si(TixHa)
Si (TixHa)	8	5.78	0.0043*	3.64	0.0821	1.83	0.0002*	223.34	0.0001*	Res
Residual	24	1.47		1.77		0.29		31.75		
Cochran's C-test		C=0.3585 ns		C=0.3917 ns		C=0.2616 ns		C=0.3368 ns		
Transformation		None		Sqrt(X+1)		Ln(X+1)		None		

534 **Table 3** Abundance of amphipod species (number of individuals per m² ± SE) recorded from the different
 535 habitats for each of the two different sampling periods, together with total abundance and species richness
 536 for the two sampling periods and habitats.
 537

Family	Species	SEPTEMBER - 04		MARCH - 05	
		Non-invaded habitat	Invaded habitat	Non-invaded habitat	Invaded habitat
Amphilochoidea	<i>Amphilocheus</i> sp. Bate, 1862	5.56 ± 5.56	-	-	-
	<i>Amphilocheus neapolitanus</i> Della Valle, 1893	2.78 ± 2.78	5.56 ± 5.56	50 ± 25.0	5.56 ± 3.68
Ampeliscaidae	<i>Ampelisca diadema</i> (A. Costa, 1853)	-	-	-	2.78 ± 2.78
	<i>Ampelisca serraticaudata</i> Chevreux, 1888	-	-	2.78 ± 2.78	-
Amphithoidea	<i>Amphithoe ferox</i> (Chevreux, 1902)	2.78 ± 2.78	-	2.78 ± 2.78	-
	<i>Amphithoe ramondi</i> Audouin, 1826	1619.44 ± 426.08	977.78 ± 425.11	830.56 ± 262.69	108.33 ± 33.07
Aoridae	<i>Lembos</i> spp. Bate, 1856	-	-	2.78 ± 2.78	-
	<i>Leptocheirus guttatus</i> (Grube, 1864)	-	-	5.56 ± 3.68	-
	<i>Microdeutopus</i> spp. A. Costa, 1853	1130.56 ± 286.47	1433.33 ± 401.11	230.56 ± 87.28	230.56 ± 35.3
Caprellidae	<i>Caprella</i> spp. Lamarck, 1801	116.67 ± 84.68	2.78 ± 2.78	3744.44 ± 1022.81	1236.11 ± 596.05
Corophiidae	<i>Corophium</i> spp. Latreille, 1806	-	-	-	5.56 ± 5.56
	<i>Apocorophium acutum</i> (Chevreux, 1908)	58.33 ± 35.11	402.78 ± 108.29	27.78 ± 17.4	172.22 ± 108.45
	<i>Corophium insidiosum</i> Crawford, 1937	-	-	-	2.78 ± 2.78
	<i>Erichthonius brasiliensis</i> (Dana, 1855)	-	2.78 ± 2.78	22.22 ± 15.28	8.33 ± 5.89
Dexaminidae	<i>Atylus massiliensis</i> Bella-Santini, 1975	-	2.78 ± 2.78	105.56 ± 35.79	-
	<i>Atylus guttatus</i> (A. Costa, 1851)	2.78 ± 2.78	-	100 ± 60.42	5.56 ± 3.67
	<i>Dexamine spiniventris</i> (A. Costa, 1853)	-	-	75 ± 50.69	44.44 ± 36.03
	<i>Guerneia coalita</i> (Norman, 1868)	-	8.33 ± 5.89	41.67 ± 21.25	-
Gammaridae	<i>Elasmopus</i> spp. A. Costa, 1853	586.11 ± 241.35	272.22 ± 87.35	202.78 ± 63.25	97.22 ± 40.7
	<i>Gammarella fucicola</i> (Leach, 1814)	-	-	-	2.78 ± 2.78
	<i>Maera inaequipis</i> (A. Costa, 1857)	-	2.78 ± 2.78	11.11 ± 8.45	2.78 ± 2.78
	<i>Melita hergensis</i> Reid, 1939	-	-	16.67 ± 13.82	50 ± 44.1
	<i>Melita palmata</i> Montagu, 1804	-	2.78 ± 2.78	-	-
Lysianassidae	<i>Lysianassa</i> sp.	-	-	13.89 ± 9.42	-
	<i>Lysianassa costae</i> Milne Edwards, 1830	127.78 ± 45.54	230.56 ± 51.67	258.33 ± 64.28	33.33 ± 27.32
	<i>Orchomene humilis</i> (A. Costa, 1853)	-	25 ± 17.68	-	-
Oedicerotidae	<i>Periculodes aequimanus</i> (Kossmann, 1880)	5.56 ± 3.68	-	2.78 ± 2.78	8.33 ± 5.89
Phliantidae	<i>Pereionotus testudo</i> (Montagu, 1808)	2.78 ± 2.78	2.78 ± 2.78	19.44 ± 16.55	13.89 ± 11.11
Stenothoidae	<i>Stenothoe monoculoides</i> (Montagu, 1813)	63.89 ± 30.08	5.56 ± 5.56	77.78 ± 27.15	36.11 ± 26.06
	<i>Stenothoe tergestina</i> (Nebeski, 1880)	-	-	5.56 ± 5.56	-
Talitridae	<i>Hyale schmidti</i> (Heller, 1866)	52.78 ± 38.74	2.78 ± 2.78	605.56 ± 198.55	25 ± 13.82
Unidentified		5.56 ± 5.56	-	41.67 ± 25.68	38.89 ± 30.65
Total abundance		3861.11 ± 925.18	3383.33 ± 844.11	6497.22 ± 1586.08	2130.56 ± 793.68
Species richness		14	16	24	20

539 **Table 4** Results of ANOVA (three-factor) for amphipod species richness, total abundance, and
 540 abundance of the seven most abundant species. MS = mean square; *P* = level of probability; df = degrees
 541 of freedom; Si= site, ns = non-significant; * significant at $p < 0.05$

542

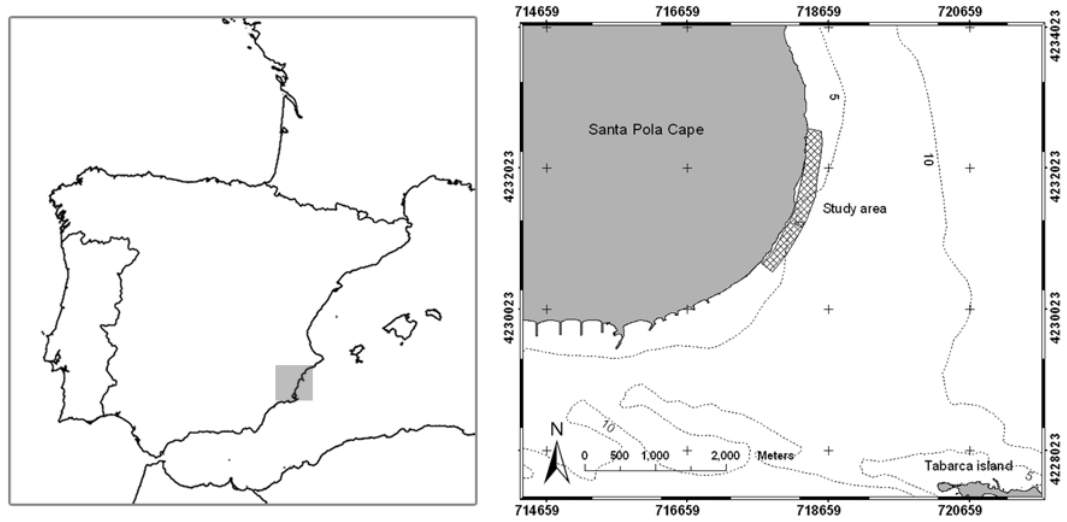
Source of variation	df	Species richness		Total abundance		<i>Ampithoe ramondi</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Sampling time=Ti	1	78.03	0.0158*	6889.00	0.6864	13.28	0.0348*	Si(TixHa)
Habitat=Ha	1	42.25	0.0551	84487.11	0.1807	12.04	0.0420*	Si(TixHa)
TixHa	1	56.25	0.0321*	54444.44	0.0033*	2.47	0.3054	Si(TixHa)
Si (TixHa)	8	8.39	0.0481*	39278.50	0.0033 *	2.06	0.0028*	Res
Residual	24	3.53		9534.44		0.48		
Cochran's C-test		C=0.1654 ns		C=0.2210 ns		C=0.2488 ns		
Transformation		None		None		Ln(X+1)		
Source of variation	df	<i>Hyale schmidtii</i>		<i>Apocorophium acutum</i>		<i>Microdeutopus spp.</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Sampling time=Ti	1	14.69	0.0104*	230.02	0.0980	23.49	0.0008*	Si(TixHa)
Habitat=Ha	1	16.63	0.0076*	890.02	0.0062*	0.82	0.3590	Si(TixHa)
TixHa	1	6.96	0.0511	132.25	0.1934	0.0003	0.9853	Si(TixHa)
Si (TixHa)	8	1.32	0.0508	65.58	0.7064	0.87	0.0943	Res
Residual	24	0.56		96.77		0.44		
Cochran's C-test		C=0.3841 ns		C=0.3720 ns		C=0.2565 ns		
Transformation		Ln(X+1)		None		None		
Source of variation	df	<i>Caprella spp.</i>		<i>Elasmopus spp.</i>		<i>Lysianassa costae</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Sampling time=Ti	1	85069.44	0.0166*	15.39	0.1746	16.00	0.5058	Si(TixHa)
Habitat=Ha	1	24753.77	0.1420	8.57	0.2986	53.77	0.2374	Si(TixHa)
TixHa	1	20640.11	0.1753	0.21	0.8648	386.77	0.0090*	Si(TixHa)
Si (TixHa)	8	9331.33	0.0359*	6.93	0.0033*	32.97	0.5053	Res
Residual	24	3650.83		1.68		35.19		
Cochran's C-test		C=0.3862 ns		C=0.2690 ns		C=0.3228 ns		
Transformation		None		Sqrt(X+1)		None		

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544

- 545 **Fig. 1.** Map showing the location of Alicante on the southeastern coast of Spain, and the study area.
546
- 547 **Fig. 2.** Two-dimensional MDS plot for algal biomass; S: September-04; M: March-05; I: Invaded habitat;
548 NI: Non-invaded habitat, for each of the six sampling sites.
549
- 550 **Fig. 3.** Mean seaweed biomass (\pm SE) recorded from the two different sampling periods and habitats.
551 Seaweed = biomass of seaweeds (without *C. racemosa*); *C. racemosa* = biomass of *C. racemosa*; and
552 Detritus = biomass of detritus.
553
- 554 **Fig. 4. (a)** Mean number of amphipod species (individuals $m^{-2} \pm$ SE) and **(b)** total abundance (individuals
555 $m^{-2} \pm$ SE), recorded from the two different sampling periods and habitats.
556
- 557 **Fig. 5.** Two-dimensional MDS plot amphipod species abundance. S = September-04; M = March-05; I =
558 Invaded habitat; NI = Non-invaded habitat for each of the six sampling sites.
559
- 560 **Fig. 6.** Mean abundance (number of individuals \pm SE) of the seven most abundant amphipods: *Ampithoe*
561 *ramondi* **(a)**; *Hyale schmidti* **(b)**; *Apocorophium acutum* **(c)**; *Microdeutopus* spp. **(d)**; *Caprella* spp. **(e)**;
562 *Elasmopus* spp. **(f)** and *Lysianassa costae* **(g)**

563 Figure 1

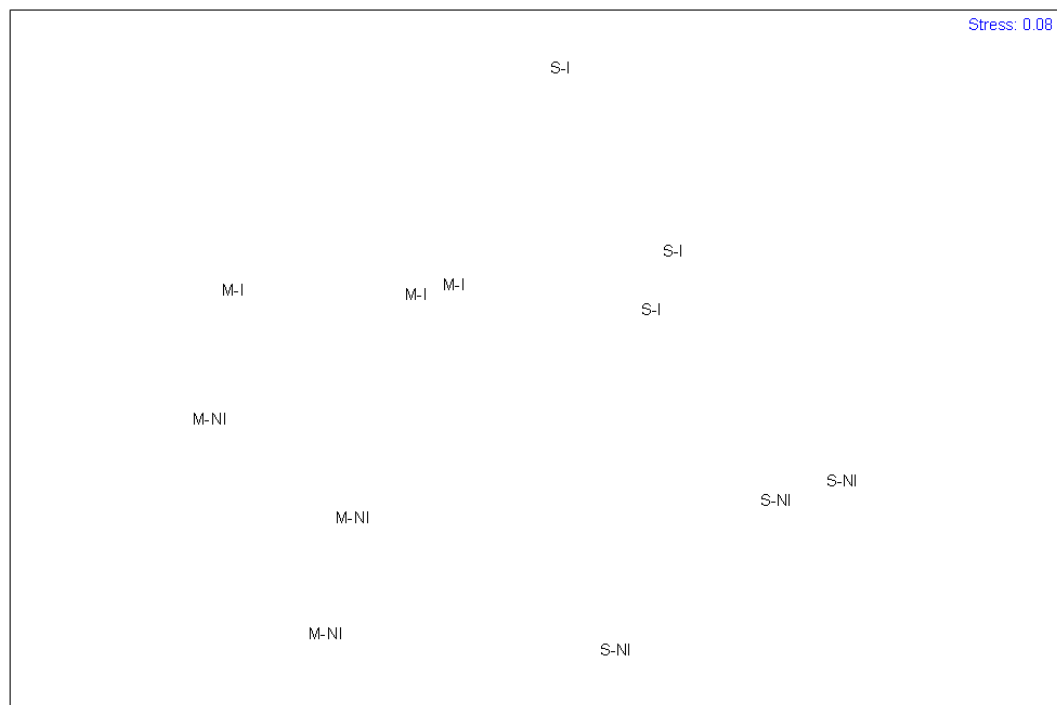


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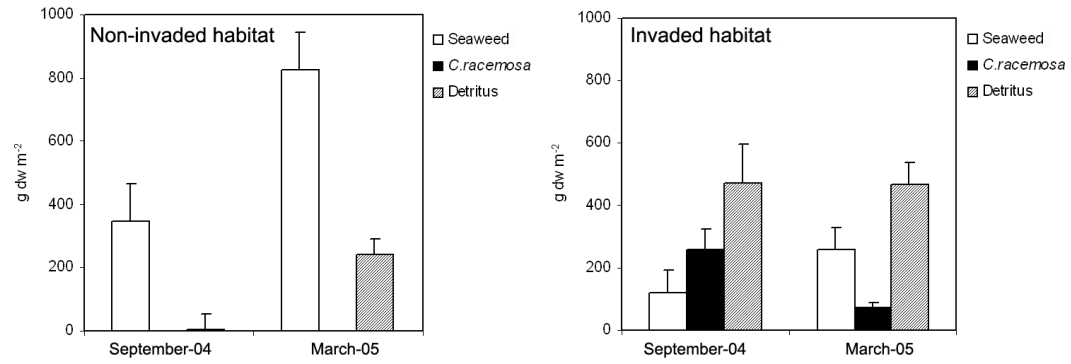
566 Figure 2



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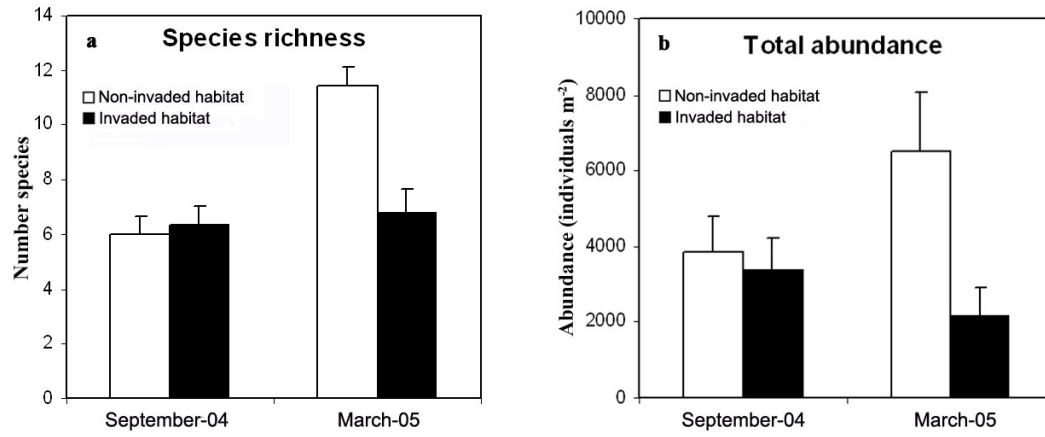
568 Figure 3



569

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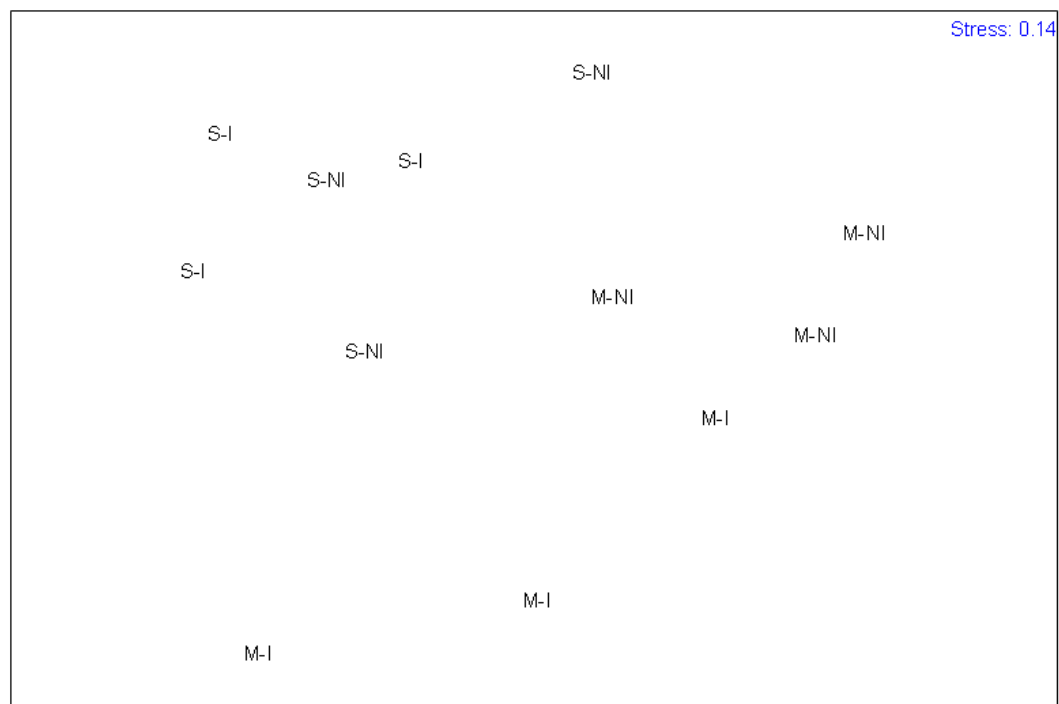
570 Figure 4



571

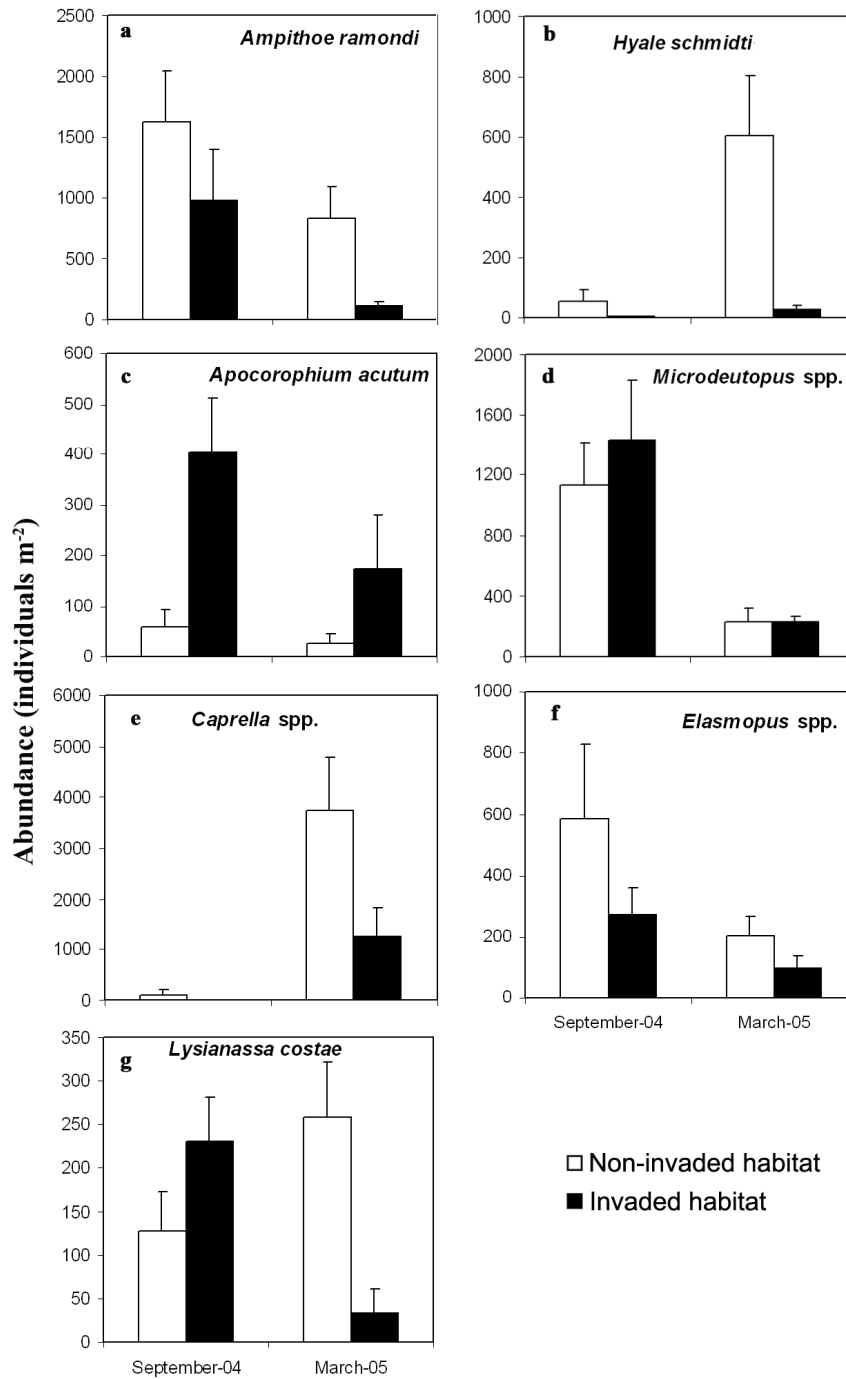
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572 Figure 5



573

574 Figure 6



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