

Caprellid assemblages (Crustacea: Amphipoda) in shallow waters invaded by *Caulerpa racemosa* var. *cylindracea* from southeastern Spain

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Abstract Growth of the invasive algae *Caulerpa racemosa* var. *cylindracea* in shallow habitats may influence the faunal assemblage composition. We studied its effects on caprellid assemblages associated with shallow-water habitats of hard and soft bottoms from the SE Iberian Peninsula (native rocky-bottom algae, *C. racemosa* from hard and soft bottoms, and *Caulerpa prolifera*, *Cymodocea nodosa* and *Posidonia oceanica* from soft bottoms). Samples were taken in two different sampling periods (September 2004 and March 2005). A total of seven caprellid species were identified, with important differences in their distribution in different habitats. Total abundance of caprellids was very high in March on native algae on hard bottoms, and on *C. racemosa* on both soft and hard bottoms. On both hard and soft bottoms, abundances of *Caprella hirsuta* recorded from *C. racemosa* were low. On the other hand, a higher abundance of other species, namely *C. acanthifera*, *C. santosrosai*, *Phtisica marina* and *Pseudoprotella phasma*, was recorded from *C. racemosa*. The results indicate that *C. racemosa* may have a positive influence on some caprel-

lid species, while seasonal changes are also evident. It is concluded that introduced *C. racemosa* may serve as a new habitat, promoting and maintaining caprellid populations in shallow Mediterranean habitats.

Keywords Amphipoda · Caprellidae · *Caulerpa racemosa* var. *cylindracea* · Southeastern Spain · Invasive species

Introduction

Caprellids are marine crustaceans, which inhabit algae, hydroids, ascidians, anthozoans, bryozoans, sponges and seagrasses (McCain 1968; Guerra-García 2001). They feed on suspended materials, prey on other organisms or graze on epibiotic fauna and flora (Guerra-García et al. 2002b; Thiel et al. 2003), and they are important prey for many coastal fish species (Caine 1991). Recently, caprellids have also been found to be useful bioindicators of marine pollution and environmental stress (Guerra-García and García-Gómez 2001; Ohji et al. 2002; Takeuchi et al. 2004).

During the last decade, an effort has been undertaken to contribute to the knowledge of the Caprellidea from the Iberian Peninsula and nearby areas, especially in the Strait of Gibraltar (Guerra-García 2001; Guerra-García and García-Gómez 2001; Guerra-García and Takeuchi 2002; Guerra-García et al. 2000, 2001, 2002a, b). A recent contribution has dealt with the community structure of caprellids on seagrasses from southern Spain (González et al. 2008), but the ecological distribution of caprellids clinging to *Caulerpa* beds has been little studied. The only available studies, which report caprellids associated with *Caulerpa* species in Iberian Peninsula waters, consist of descriptions of the macrofaunal community associated with *Caulerpa*

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prolifera from Algeciras Bay, southern Spain (Sánchez-Moyano et al. 2001, 2007) and the taxonomic description of the new species *Caprella caulerpensis* from this bay (Guerra-García et al. 2002a). Because of the lack of information about caprellids inhabiting *Caulerpa* beds, we conducted an ecological study to characterise the caprellid distribution in shallow habitats of southeastern Spain colonised by the invasive *Caulerpa racemosa* (Forsskål) J. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque (Verlaque et al., 2003) (hereafter *C. racemosa*).

The presence of vegetation allows a greater species diversity and abundance of individuals than those found in unvegetated habitats (Heck and Orth 1980; Peterson et al. 1984; Irlandi 1994), which is usually correlated with an increase in habitat complexity (Johnson 1970; Stoner 1980; Dean and Connell 1987; Edgar 1992; Taylor and Cole 1994; Ayala and Martín 2003). Therefore, changes in habitat structure of vegetated substrata resulting from the invasion of species such as *C. racemosa* could affect the associated fauna, including caprellids. Along the Mediterranean coast, two seagrass species, *Posidonia oceanica* and *Cymodocea nodosa*, develop meadows on shallow sandy bottoms (Buia and Mazzella 1991). Like seagrasses, the alga *Caulerpa prolifera* usually forms dense beds on soft bottoms from 1 to 20 m depth, especially in sheltered areas, with low flow, little water renewal and considerable input of organic matter (Sánchez-Moyano et al. 2001). A remarkable spread of *C. racemosa* throughout the Mediterranean has been recorded during the last 15 years or so, during which the alga invaded different habitats and most types of substrata located at water depths of 0 m to more than 60 m. The recorded rate of invasion has been much faster than that of other invasive species such as *Caulerpa taxifolia* (Verlaque et al. 2003). Since the first records of *C. racemosa* spreading along Mediterranean coastal areas, several studies concerning the ecology of this species have been undertaken (see Ruitton et al. 2005; Cavas et al. 2006). However, information on changes in the associated fauna brought about by the invasive alga is

lacking (but see Argyrou et al. 1999; Piazzini and Balata 2008; Vázquez-Luis et al. 2008).

The aim of the present study was to compare the caprellid assemblages among the most important shallow water environments (rocky and sandy bottoms) in Mediterranean coastal areas and to explore the effect of the invasive alga *C. racemosa* on the caprellid community in comparison with natural habitats (algae, seagrasses and sand).

Methods

Study area

Fieldwork was carried out along the Cape of Santa Pola (Alicante, southeastern Spain; Fig. 1a). *C. racemosa* was first recorded from Alicante in 2002, at a site located approximately 10 km north of our study area, where it colonised soft sediments and dead matte of *Posidonia oceanica*. Two months after its appearance in Alicante, *C. racemosa* was detected on a rocky platform in our study area (Pena-Martín et al. 2003). During the study period, *C. racemosa* occurred in extensive areas of ecologically important rocky bottom habitat, on sandy and muddy substrata and on dead matte of *Posidonia oceanica*. It was also found mixed patchily with *Cymodocea nodosa* in meadows of the seagrass (0.2–1.5 m). Depth in the study area varied between 0 and 5 m. The seabed present in the shallower parts (0–0.5 m) of the study area is characterised by a rocky platform that supports native seaweeds, namely *Halopteris scoparia*, *Jania rubens*, *Padina pavonica*, *Dictyota fasciola*, *Cystoseira brachicarpa* and *C. racemosa*. The seabed within the 0.5–5 m depth range comprised a sandy bottom that is colonised by *C. racemosa* and native macrophytes, namely *Cymodocea nodosa*, *C. prolifera* and *P. oceanica*. The two seabed types (rocky and soft bottom) are separated by a small rocky step (Fig. 1b).

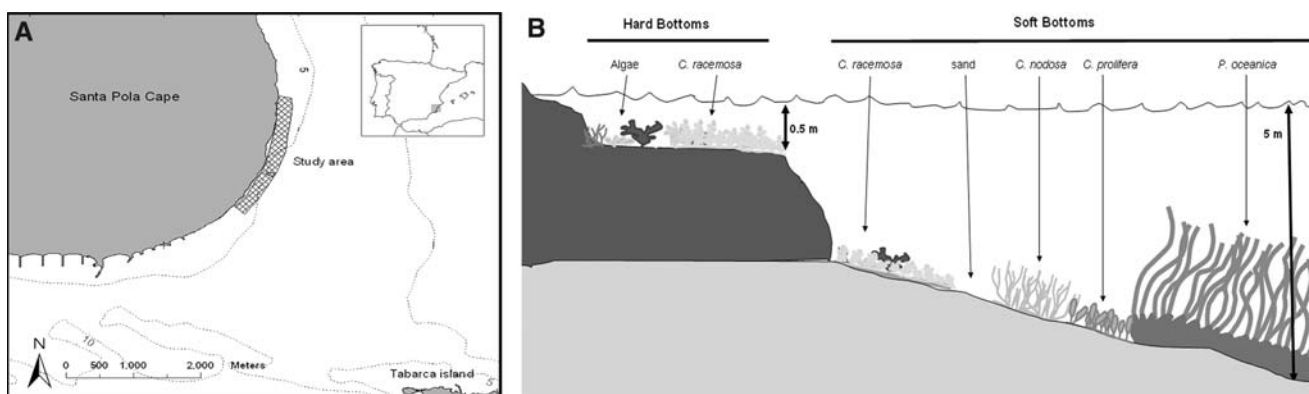


Fig. 1 Map showing the study area in Santa Pola Cape, southeastern Spain (a) and transverse profile of biotopes present in the study area (b)

Sampling design

Seven different shallow habitats were selected for the present study. Two habitats were studied on hard bottoms (0.2–0.5 m depth): natural habitats of native seaweeds (A) and similar habitats invaded by *C. racemosa* (CrHB). On soft bottoms, five habitats were studied (2–5 m depth): soft bottoms colonised by *C. racemosa* (CrSB), *Caulerpa prolifera* beds (Cp), *Cymodocea nodosa* meadows (Cym), *Posidonia oceanica* meadows (Po) and unvegetated substratum (Sand). *C. racemosa* was distributed across the study area in patches of around 100 m².

The two species of *Caulerpa* distributed in the study area, *C. racemosa* and *C. prolifera*, are algae of tropical and subtropical affinity, and both are strongly affected by natural seasonal disturbances in the Mediterranean Sea. Their growth and reproductive cycles are dependent on water temperature, with considerable decrease in spatial extension during winter and notable growth when temperature rises (Meinesz 1980; Piazzì and Cinelli 1999). Therefore, the seven habitats were sampled in September 2004 (summer conditions with an average water temperature of 27.5°C), which coincides with the period of maximum vegetative growth of *C. racemosa* (Piazzì and Cinelli 1999), and again in March 2005 (winter conditions with an average water temperature of 13°C), which is the period of minimum growth of *C. racemosa*.

Within each habitat (Ha) and sampling time (Ti), three sites (Si) were randomly selected. Each site corresponded to a different patch of habitat with similar conditions that were separated by hundreds of meters. At each site (patch), three random samples separated by tens of meters were taken using a 20 × 20 cm² quadrat by scraping the whole surface using a trowel (Edgar 1990). In soft bottom areas, samples were taken by SCUBA diving. A 300-µm mesh bag was attached to the quadrat to avoid loss of the motile fauna. Samples were preserved in a 4% solution of formaldehyde in seawater. Each replicate was sieved in sea-water through a 500-µm mesh, retaining the fine fraction of detritus. In the laboratory, the caprellids were separated, identified and counted. Algae were sorted and identified to species level, and detritus was also separated. The macrophytes and the detritus were dried for 24 h at 80°C and weighed. Habitat structure was characterised using three attributes: species richness of macrophytes, biomass of each species (g) and quantity of detritus (g).

Data analysis

The affinities among sampling habitats based on vegetal species biomass, and among caprellids based on their abun-

dance in the different habitats, were established by cluster analysis using UPGMA method and the Bray Curtis similarity index. Data were fourth root transformed. Multivariate analyses were carried out using the PRIMER package (Clarke and Gorley 2001).

Total abundance, species richness and abundance of each caprellid species were analysed using ANOVA. To test whether the abundance of caprellids was similar across habitats and times, we used an analysis of variance (ANOVA), which incorporated the following factors: ‘Time of sampling’, a fixed factor and orthogonal, with two treatments: September 2004 and March 2005; ‘habitat’, a fixed factor, with seven treatments: native seaweeds on hard bottoms (A), *C. racemosa* on hard bottoms (CrHB), *C. racemosa* on soft bottoms (CrSB), *Caulerpa prolifera* beds (Cp), *Cymodocea nodosa* meadows (Cym), *Posidonia oceanica* meadows (Po) and unvegetated sandy bottoms (Sand); ‘Site’, a random factor and nested within both main factors, with three random sampling sites.

Prior to ANOVA, heterogeneity of variance was tested with Cochran’s *C* test. Data were $\sqrt{x + 1}$ -transformed if variances were significantly different at $P = 0.05$. Where variances remained heterogeneous, untransformed data were analysed, as ANOVA is a robust statistical test and is relatively unaffected by heterogeneity of variances, particularly in a balanced design (Underwood 1997). In such cases, special care was taken in the interpretation of results, and to reduce type I errors, the level of significance was reduced to <0.01. When ANOVA indicated a significant difference for a given factor, the source of difference was identified by applying the Student–Newman–Keul (SNK) test (Underwood 1981, 1997).

Results

Habitat description

A total of 25 taxa of macroalgae and two seagrass species were identified (Table 1). Vegetal biomass on natural hard bottoms was higher in March than in September, mainly due to the proliferation of *Corallina elongata*, *Jania rubens*, *Dyctiota fasciola*, *Halopteris scoparia* and *Cystoseira compressa* (these species represented 79% of total biomass). *Jania rubens* was the dominant species, together with *Corallina elongata*, which was the species with highest biomass in March. During September, hard bottom habitats invaded by *C. racemosa* were characterised by a low species richness of associated algae (five species plus *C. racemosa*), whereas species richness increased in March (14 species plus *C. racemosa*). In the case of soft bottoms, the different

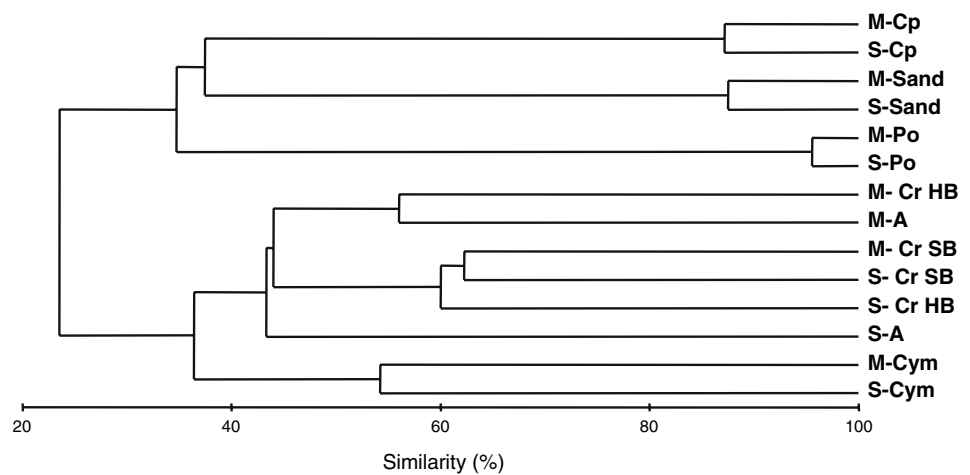
Table 1 Mean biomass (g dw m⁻²) values ($n = 9$) for the different macrophyte species, together with total biomass, total species richness and detritus weight for the two sampling periods and habitats

Species	September 2004				March 2005							
	Hard bottoms		Soft bottoms		Hard bottoms		Soft bottoms					
	Algae	<i>C. racemosa</i>	<i>C. racemosa</i>	<i>C. prolifera</i>	<i>C. nodosa</i>	Algae	<i>C. racemosa</i>	<i>C. racemosa</i>	<i>C. prolifera</i>	<i>C. nodosa</i>	<i>P. oceanica</i>	Sand
Algae	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva	-	-	-	-	-	-	0.08	0.06	-	-	-	-
<i>Aspidium corallinum</i> (cf) C. Agardh	-	-	-	-	-	-	0.29	-	-	-	-	-
<i>Caulerpa prolifera</i> (Forsskål) J.V. Lamouroux	2.23	19.4	10.07	335.47	0.82	-	0.01	4.34	250.07	3.01	-	-
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh	-	259.49	122.24	-	0.69	-	68.91	42.49	-	-	-	-
<i>Ceramium</i> spp. (Hudson) C.A. Agardh	0.11	-	-	-	-	-	10.72	-	-	-	-	-
<i>Cladophora</i> sp. Kützing, 1843	0.3	-	1.02	-	0.11	-	54.38	98.19	0.54	-	-	-
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	-	-	-	-	-	-	0.15	-	-	-	-	-
<i>Codium</i> (cf) F.S. Collins & Hervey, 1917	-	-	-	-	-	-	17.43	0.19	-	-	-	-
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	-	-	-	-	-	-	6.97	3.94	-	0.39	-	-
<i>Corallina elongata</i> Ellis et Solander	-	-	0.37	-	-	-	186.77	0.59	0.09	2.35	-	-
<i>Cystoseira brachicarpa</i> J. Agardh	34.75	-	-	-	-	-	-	-	-	-	-	-
<i>Cystoseira compressa</i> (Esper) Gerloff & Nizamuddin	-	-	-	-	-	-	63.92	0.71	4.26	-	-	-
<i>Dasycladus vermicularis</i> (Scopoli) Krasser	4.27	0.78	0.08	16.95	-	-	0.99	0.15	-	0.79	-	-
<i>Dicyopteris membranacea</i> (Stackhouse) Batters	-	-	-	-	-	-	-	0.21	-	-	-	-
<i>Dicryota fasciola</i> (Roth) J. V. Lamouroux	1.51	-	-	-	-	-	134.78	20.72	0.91	0.63	-	-
<i>Flabellia petiolata</i> (Turra) Nizamuddin	-	-	0.344	-	-	-	0.13	0.24	-	-	-	-
<i>Halimeda tuna</i> (J. Ellis & Solander) J.V. Lamouroux	0.09	-	0.17	-	-	-	0.64	-	-	-	-	-

Table 1 continued

Species	September 2004				March 2005										
	Hard bottoms		Soft bottoms		Hard bottoms		Soft bottoms								
	Algae	<i>C. racemosa</i>	<i>C. racemosa</i>	<i>C. prolifera</i>	<i>C. nodosa</i>	<i>P. oceanica</i>	Sand	Algae	<i>C. racemosa</i>	<i>C. racemosa</i>	<i>C. prolifera</i>	<i>C. nodosa</i>	<i>P. oceanica</i>	Sand	
<i>Halophytis incurvus</i> (Hudson) Batters	-	5.13	-	-	0.19	-	-	-	-	-	-	-	-	1.18	-
<i>Halopteris scoparia</i> (Linnaeus) Sauvageau	35.81	-	3.35	-	3.18	-	-	104.82	68.04	-	-	-	-	1.43	-
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	246.16	67.87	14.21	-	-	-	-	163.12	-	-	-	-	-	26.67	0.63
<i>Laurencia pinnatifida</i> (Hudson) Lamouroux	-	-	-	-	-	-	-	1.24	-	-	-	-	-	-	-
<i>Padina pavonica</i> (Linnaeus) Thivy	20.31	26.87	-	-	-	-	-	44.14	37.16	-	-	-	-	5.4	-
<i>Peyssonnelia</i> sp. (S.G. Gmelin) Decaisne	-	-	-	-	-	-	-	-	9.88	-	-	-	-	-	-
<i>Sargassum vulgare</i> C.Agardh	2.13	-	-	-	-	-	-	32.83	-	-	-	-	-	-	-
<i>Ulva</i> sp. Linnaeus	-	-	-	-	-	-	-	5.46	15.15	-	-	-	-	0.83	-
Seagrasses	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodocea nodosa</i> (Ucria) Ascherson	-	-	44.31	-	79.76	-	-	-	1.81	-	-	-	-	4.21	97.05
<i>P. oceanica</i> (Linnaeus) Delile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4222.45
<i>P. oceanica</i> (dead matre)	-	-	-	-	-	-	-	-	-	-	-	-	-	464.41	-
Vegetal biomass	347.67	379.55	196.18	352.43	84.76	3395.83	0	826.49	326.52	557.73	250.07	104.86	4222.45	0	0
Species richness	11	6	10	2	6	1	0	16	15	17	1	7	1	0	0
Detritus	5.87	472.48	127.21	830.02	7.66	169.96	21.4	242.22	466.92	453.86	1123.85	31.55	322.28	58.63	58.63

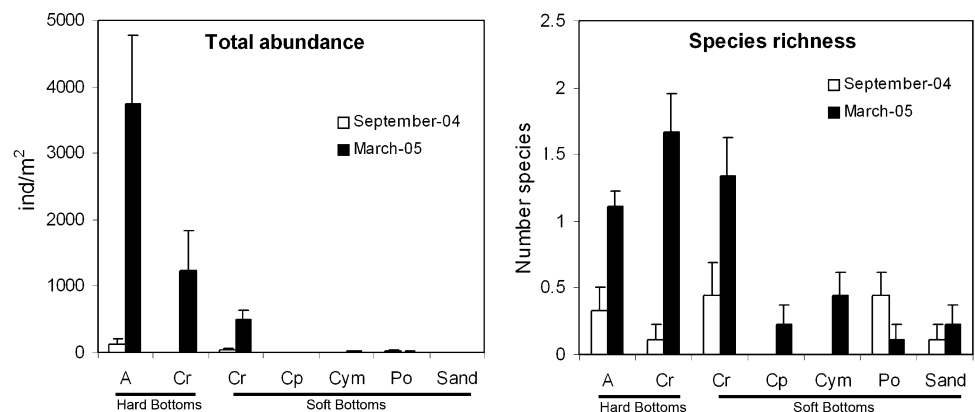
Fig. 2 Cluster analysis conducted using the mean values of macrophyte biomass within each habitat and sampling time. A, native algae; CrHB, *Caulerpa racemosa* hard bottoms; CrSB, *Caulerpa racemosa* soft bottoms; Cp, *Caulerpa prolifera*; Cym, *Cymodocea nodosa*; Po, *Posidonia oceanica*; Sand, unvegetated substrate; M, March; S, September



habitats showed less variability between September and March (see Table 1), except for *Caulerpa racemosa*, which decreased in biomass in March, allowing other algae to colonise the substrata. In general, the amount of detritus was higher in March than in September, and the highest amounts were found with significant differences at *C. prolifera* and *C. racemosa* patches on hard bottoms (Ha, $P < 0.01$). The most diverse habitats in terms of algal composition were the native hard bottoms and those invaded by *C. racemosa*, both on hard and soft bottoms.

The classification analysis showed segregation of sampling sites according to the habitat, regardless of the season (Fig. 2). Bottoms dominated by *Caulerpa prolifera* and *Posidonia oceanica* clustered together with the sand habitat. These three ecosystems were the poorest in terms of macrophyte species richness. Natural hard bottoms and invaded habitats of *C. racemosa* formed a second group, characterised by high species richness of associated algae (the highest species richness was found on soft bottoms with *C. racemosa*; 17 species in March). A third group including the habitats of *Cymodocea nodosa* could be observed, with an intermediate number of vegetal species associated (five species in September and six in March plus *C. nodosa*).

Fig. 3 Total caprellid abundance (number of individuals/ $\text{m}^2 \pm \text{SE}$) and species richness (number of species per replicates $\pm \text{SE}$) recorded from the seven habitats and the two sampling times



Caprellid assemblages

The native algae on hard bottoms and *C. racemosa* on both soft and hard bottoms had the highest abundance and species richness of caprellids, with a peak in March, reaching a maximum value of $3,747 \pm 1,022$ individuals/ m^2 in native seaweeds. These differences were significant ($\text{Ti} \times \text{Ha}$, $P < 0.01$; Table 2, Fig. 3). In *C. prolifera*, *C. nodosa*, *P. oceanica* and on sand, abundances were very low at both sampling times (Fig. 3). Although abundances were very high on hard bottoms, the number of caprellid species was low in all habitats. Natural hard bottoms and habitats invaded by *C. racemosa* had significantly more caprellid species than the rest of the habitats in March but not in September ($\text{Ti} \times \text{Ha}$, $P < 0.05$, Table 2, Fig. 3).

Seven caprellid species were found during the present study: *Caprella acanthifera* (Leach, 1814), *Caprella grandimana* (Mayer, 1882), *Caprella hirsuta* Mayer, 1890, *Caprella santosrosai* Sanchez-Moyano, Jimenez Martín and García-Gómez, 1995, *Deutella schieckei* Cavedini, 1982, *Phthisica marina* Slabber, 1769 and *Pseudoprotella phasma* (Montagu, 1804) (Fig. 4). *C. grandimana* and *C. hirsuta* were the dominant species in terms of abundance. The abundance of *C. hirsuta* on algae was significantly higher in March ($\text{Ti} \times \text{Ha}$, $P < 0.01$, Table 2,

Table 2 Results of ANOVA (three-factor) for caprellid total abundance, species richness and abundance of the seven species

Source of variation	df	Total abundance			Species richness			<i>Caprella acanthifera</i>			F versus
		MS	F	P	MS	F	P	MS	F	P	
Sampling time = Ti	1	29384.64	10.93	0.0026**	1.2419	15.05	0.0006**	16.79	1.00	0.3259	Si(Ti × Ha)
Habitat = Ha	6	14525.08	5.41	0.0008**	0.3064	3.71	0.0077**	16.79	1.00	0.4448	Si(Ti × Ha)
Ti × Ha	6	13038.35	4.86	0.0016**	0.2338	2.83	0.0277*	16.79	1.00	0.4448	Si(Ti × Ha)
Si (Ti × Ha)	28	2683.97	2.54	0.0006	0.0825	3.84	0.0000	16.79	1.00	0.4794	Res
Residual	84	1058.45			0.0215			16.79			
Cochran's C test		C = 0.3806 (P < 0.01)			C = 0.1493 (ns)			C = 1.0000 (P < 0.01)			
Transformation		None			Sqrt(x + 1)			None			

Source of variation	df	<i>Caprella grandimana</i>			<i>Caprella hirsuta</i>			<i>Caprella santosrosai</i>			F versus
		MS	F	P	MS	F	P	MS	F	P	
Sampling time = Ti	1	1843.84	5.30	0.0290	15533.34	15.31	0.0005**	0.0079	0.50	0.4853	Si(Ti × Ha)
Habitat = Ha	6	437.59	1.26	0.3081	11476.53	11.31	0.0000**	0.0714	4.50	0.0026**	Si(Ti × Ha)
Ti × Ha	6	398.43	1.15	0.3628	9979.60	9.84	0.0000**	0.0079	0.50	0.8029	Si(Ti × Ha)
Si (Ti × Ha)	28	347.88	1.17	0.2897	1014.31	1.60	0.0521	0.0159	0.67	0.8869	Res
Residual	84	298.23			633.50			0.0238			
Cochran's C test		C = 0.7873 (P < 0.01)			C = 0.5620 (P < 0.01)			C = 0.3333 (P < 0.01)			
Transformation		None			None			None			

Source of variation	df	<i>Deutella schieckei</i>			<i>Phthisica marina</i>			<i>Pseudoprotella phasma</i>			F versus
		MS	F	P	MS	F	P	MS	F	P	
Sampling time = Ti	1	0.6429	1.53	0.2266	0.1270	2.00	0.1683	0.0317	1.00	0.3259	Si(Ti × Ha)
Habitat = Ha	6	1.3413	3.19	0.0164	0.0529	0.83	0.5545	0.0317	1.00	0.4448	Si(Ti × Ha)
Ti × Ha	6	0.6429	1.53	0.2055	0.0529	0.83	0.5545	0.0317	1.00	0.4448	Si(Ti × Ha)
Si (Ti × Ha)	28	0.4206	2.04	0.0068**	0.0635	4.00	0.0000**	0.0317	1.00	0.4749	Res
Residual	84	0.2063			0.0159			0.0317			
Cochran's C test		C = 0.5000 (P < 0.01)			C = 0.5000 (P < 0.01)			C = 1.0000 (P < 0.01)			
Transformation		None			None			None			

MS mean square, F F value, P level of probability, df degrees of freedom, ns non-significant

* Significant at P < 0.05; ** significant at P < 0.01

Fig. 4). The abundance of *C. grandimana* was higher in March on hard bottoms (both habitat types) and *C. racemosa* on soft bottoms, although no statistical differences were found (Table 2, Fig. 4). *Caprella grandimana*, *C. hirsuta* and *C. acanthifera* were mainly associated to hard bottoms, whereas the remaining species were only found in soft bottom habitats. *Deutella schieckei* were exclusively found associated with *Posidonia* beds, while *C. santosrosai* (Ha, P < 0.01, Table 2, Fig. 4), *P. marina* and *P. phasma* were associated to *Caulerpa* beds, as shown by the cluster analysis based on the caprellid assemblage (Fig. 5).

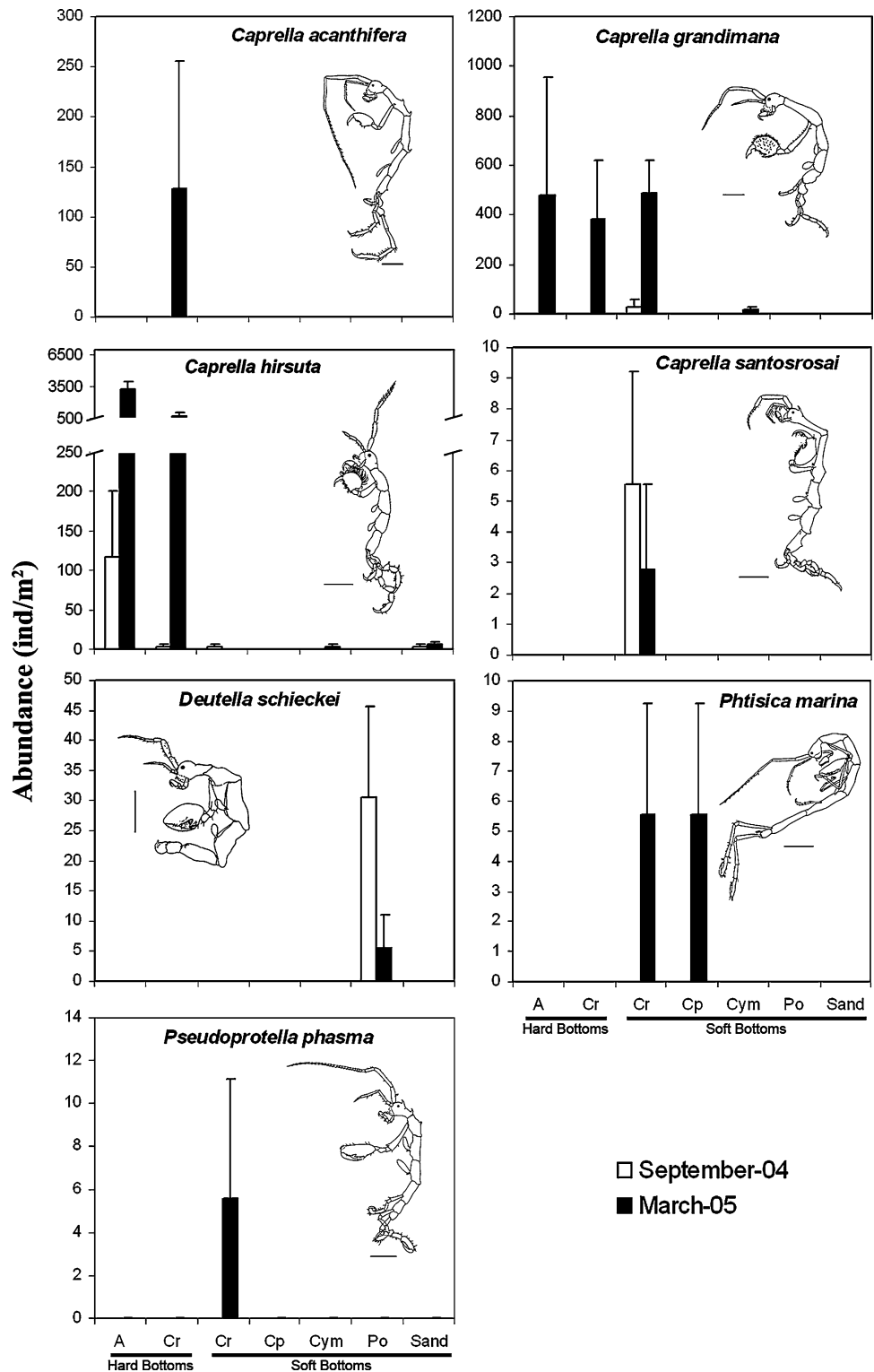
Discussion

This study shows that caprellid assemblages differ markedly among habitats, with considerable seasonal variation.

The presence of *Caulerpa racemosa* influences the spatial distribution of caprellid assemblages on both hard and soft bottoms, probably due to changes in the composition of vegetation and the increase in detritus levels. *C. racemosa* held reduced abundances of *Caprella hirsuta*, but other species such as *C. acanthifera*, *C. santosrosai*, *P. marina* and *P. phasma* were more abundant in this alga. The ‘positive effect’ of *C. racemosa* on the caprellid community has also been found in habitats of the Balearic Islands, where the presence of *C. racemosa* significantly favoured *C. acanthifera* and also enabled other caprellid species to colonise (Box et al. 2006).

Some caprellid species found in the present study, such as *P. marina*, *P. phasma* or *C. acanthifera*, have been reported as common species on many different substrata (see Guerra-García 2001) and can tolerate stressed habitats of low flow and high rates of sedimentation and

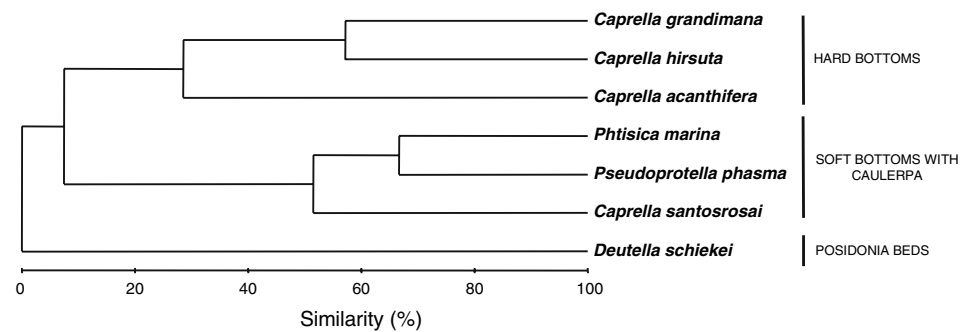
Fig. 4 Mean abundance (number of individuals per square meter \pm SE) of the seven caprellid species found during the study. A, native algae; Cr, *Caulerpa racemosa*; Cp, *Caulerpa prolifera*; Cym, *Cymodocea nodosa*; Po, *Posidonia oceanica*; Sand, unvegetated substrate. Vertical scale differs among species. Figures are redrawn from Krapp-Schickel (1993) and Guerra-García (2001)



organic matter (Guerra-García and García-Gómez 2001). *Deutella schieckei* is a Mediterranean endemic described as interstitial (Krapp-Schickel 1993), and along the Spanish coast, this species has been only reported from algae in shallow waters (Jimeno and Turón 1995; Box et al. 2006). *Caprella santosrosai* was described from bryozoans

at Algeiras Bay, Cádiz (Sánchez-Moyano et al. 1995), and later it was collected from hydroids, anthozoans and sponges in North Africa (Guerra-García 2001; Guerra-García and Takeuchi 2002) and the present study represents the third locality in which this species has been found, after Algeiras Bay and Ceuta, enlarging its

Fig. 5 Cluster analysis based on caprellid abundances estimated within each habitat and sampling time



distribution from the Strait of Gibraltar to the Mediterranean side of the Iberian Peninsula.

Several studies include data related to caprellids associated to different species of *Caulerpa*, demonstrating that some species seem to be associated to the habitat. In a study on the effect of wave exposure on the amphipod fauna of *Caulerpa brownie* in New Zealand, Fenwick (1976) reported the caprellid *Caprellina longicollis* as one of the dominant amphipod species. In Cyprus, Argyrou et al. (1999) concluded that the expansion of *C. racemosa* imposed successional changes on macrofaunal communities: gastropods and crustaceans decreased while polychaetes increased and became the dominant group. However, no caprellids were reported in their study and gammarids had surprisingly low abundances. Most studies dealing with the effect of *Caulerpa* on macrofaunal communities from the Iberian Peninsula have dealt with *C. prolifera* beds. Sánchez-Moyano et al. (2001, 2007) studied the invertebrate macrofauna from a *C. prolifera* bed in Algeciras Bay and reported the presence of the caprellids *Phtisica marina* and *Pariambus typicus* in low abundances. These authors concluded that *C. prolifera* allowed establishment of important crustacean assemblages and, in some cases, showed richer communities than more structured habitats, such as sea-grass beds. However, Bellan-Santini (1995) found a decrease in the amphipod community in a *Caulerpa taxifolia* bed located on the Mediterranean French coast compared with a reference station. These observations suggest that changes in the epifaunal community due to the expansion of *Caulerpa* species differ greatly from one location to another.

Caprellids showed considerable seasonal variation in abundance, with a peak during the cold season, reaching maximum values of thousands of individuals per square meter in native seaweeds. The high abundances of caprellids in the shallow habitats on the rocky terrace is possibly due to limited access of fish predators to these habitats, compared to the habitats on the deeper sandy substrata. Seasonal variation of invertebrate abundance is common in many vegetated systems (Edgar 1990) and the influence of biomass (Ansari et al. 1991), surface area (Lewis 1984) and

epiphyte biomass (Schneider and Mann 1991) on epifauna have been demonstrated. This reduction of abundance during summer is related to the increase of fish abundance due to the recruitment of juvenile fish and movement of adults into *P. oceanica* meadows, which increases the predation pressure on epifauna (Bell and Harmelin-Vivien 1982, 1983). It is necessary to consider the effects of predators on epifaunal abundance to explain changes in the assemblage composition of fauna between habitats. The abundance of potential prey results from a balance between refuge against predation and the availability of favourable space for living (Orth 1992). Our results showed different abundances of caprellids between the two sampling periods, which could be explained by natural population dynamics or by the different feeding intensities of predators over a 1-year period (Page et al. 2007). At low temperatures, fish may cease to feed, but as the temperature increases, the rate of consumption also increases up to a maximum. Wootton (1990) detected an immediate disappearance of epibenthic caprellid amphipods in field surveys as a result of the appearance of demersal fish species (Caine 1991). However, Edgar and Robertson (1992) reported that while predators should not be the main cause for reduction of the epifauna in substrata with vegetation, they might play an important role in determining the spatial distribution of epifauna.

In conclusion, our study shows that *C. racemosa* stands promote changes in caprellid assemblages, namely by playing an important role as a new benthic habitat. The observed abundances of caprellids were relatively high, but the species richness was generally low. This may have resulted from the close relationship of certain caprellid species with particular habitats. For example, *C. hirsuta* and *C. grandimana* were present in high densities, while *P. marina* and *P. phasma* had low abundances. The results of the present study also detected an important effect of the time of sampling, probably due the synergistic effect of seasonal changes in algal composition and predation pressure. Further studies should be conducted to determine top-down and bottom-up ecological regulations of caprellid populations in habitats invaded by *C. racemosa*.

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