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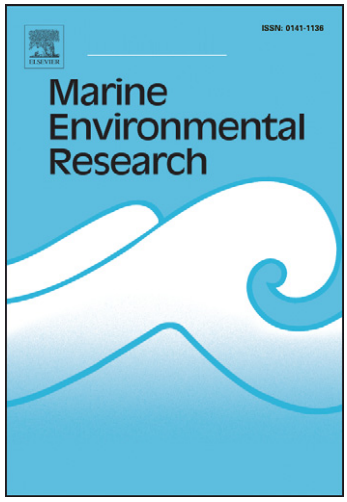

Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea

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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.

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Abstract

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

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

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

1. Introduction

The green alga *Caulerpa racemosa* (Forsskål) J. Agardh var. c*ylindracea* (Sonder) Verlaque, Huisman et Boudouresque (Verlaque et al., 2003) (hereafter *C. racemosa*) was first detected in Tunisia (Mediterranean Sea) in 1926. More recently, during the 1990s, *C. racemosa* spread steadily throughout the Mediterranean region (see Piazzi et al., 2005). Recent genetic analyses have shown that the *C. racemosa* population originated from the southwest coast of Western Australia (Verlaque et al., 2003), and is not a Lessepsian migrant as thought originally. 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 located at water depths of 0 m to more than 60 m. The recorded rate of invasion has been much faster than that for other invasive species such as *Caulerpa taxifolia* (Verlaque et al., 2003). The rapid spread of *C. racemosa* can be explained by its very efficient reproductive strategies, both sexual and asexual (via propagules), which is not the case with *Caulerpa taxifolia* (Panayotidis and Žuljevi´c, 2001; Renoncourt and Meisenez, 2002).

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

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

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

Since the first records of spread of *C. racemosa* 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 on the associated fauna brought about by the invasive alga is lacking (Argyrou et al., 1999; Piazzi and Balata, 2007). The main aim of this study was to assess the effects of *C. racemosa* on amphipod assemblages associated with a shallow water rocky bottom habitat in the southwestern Mediterranean Sea, by comparing natural rocky algal assemblages and the same habitat type that has been invaded by *C. racemosa*. The hypothesis tested in our study was: invasion by *C. racemosa* should influence the habitat structure of rocky bottom algal assemblages and, consequently, the assemblage structure of associated epifauna such as amphipods may be affected, in terms of species richness and abundance.

2. Materials and Methods

2.1. Study area

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

2.2. Sampling and experimental design

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

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

2.3. Data analysis

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

2.3.1. Multivariate analysis of assemblage structure

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

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; Ti=*P* <0.05). During

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

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

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

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

3.2. Amphipod assemblage

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

The two-dimensional MDS plot for the amphipod assemblages showed segregation of sampling sites that was mainly related to the sampling period, while 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.,

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

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

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

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

296 *Ampithoe ramondi* and *Hyale schmidti*), 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 schmidti* 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;

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

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

Several studies have demonstrated that consequences of *C. racemosa* in host systems are very important, particularly since it appears that this introduced species most invasive in the Mediterranean Sea (Verlaque et al., 2003). The presence of *C. racemosa* in the southeastern coast of Spain is an incipient problem. It was recorded 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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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	*Acetabularia acetabulum* (Linnaeus) P.C. Silva	-	-	-	0.08 ± 0.06
	Caulerpa prolifera (Forsskål) J.V. Lamouroux	2.23 ± 1.02	19.4 ± 10.57	-	0.01 ± 0.01
	Caulerpa racemosa (Forsskål) J. Agardh	-	259.49 ± 65.99	-	68.91 ± 18.71
	Cladophora sp. Kützing, 1843	0.30 ± 0.30	-	54.38 ±14.60	98.19 ± 28.9
	Codium (cf) F.S. Collins & Hervey, 1917	-	-	17.43 ± 16.87	-
	Dasycladus vermicularis (Scopoli) Krasser	4.27 ± 1.55	0.78 ± 0.36	-	0.99 ± 0.63
	Flabellia petiolata (Turra) Nizamuddin	-	-	0.13 ± 0.11	-
	Halimeda tuna (J. Ellis & Solander) J.V. Lamouroux	0.09 ± 0.09	-	0.64 ± 0.64	-
	Ulva sp. Linnaeus	-	-	5.46 ± 1.64	15.15 ± 5.78
Phaeophyta	*Cladostephus spongiosus* (Hudson) C. Agardh	-	-	0.15 ± 0.15	-
	Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	-	-	6.97 ± 4.99	3.94 ± 3.93
	Cystoseira brachicarpa J. Agardh	34.75 ± 23.07	-	-	-
	Cystoseira compressa (Esper) Gerloff & Nizamuddin	-	-	63.92 ± 63.92	0.71 ± 0.71
	Dictyota fasciola (Roth) J. V. Lamouroux	1.51 ± 0.97	-	134.78 ± 53.99	20.72 ± 17.44
	Halopteris scoparia (Linnaeus) Sauvageau	35.81 ± 34.45	-	104.82 ± 57.53	68.04 ± 48.43
	Padina pavonica (Linnaeus) Thivy	20.31 ± 6.86	26.87 ± 14.99	44.14 ± 34.64	37.16 ± 19.51
	Sargassum vulgare C.Agardh	2.13 ± 2.13	-	32.83 ± 32.56	-
Rodophyta	*Ceramium* spp. (Hudson) C.A. Agardh	0.11 ± 0.11	-	10.72 ± 8.78	-
	Corallina ellongata Ellis et Solander	-	-	186.77 ± 175.87	0.59 ± 0.59
	Halopitys incurvus (Hudson) Batters	-	5.13 ± 4.19	-	-
	Jania rubens (Linnaeus) J.V. Lamouroux	246.16 ± 83.17	67.87 ± 29.74	163.12 ± 113.76	-
	Laurencia pinnatifida (Hudson) Lamouroux	-	-	1.24 ± 1.24	-
	Peyssonnelia sp. (S.G. Gmelin) Decaisne	-	-	-	9.88 ± 9.88
	Alsidium corallinum (cf) C. Agardh	-	-	-	0.29 ± 0.29
Seagrasses	*Cymodocea nodosa* (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 *C. racemosa*		Detritus		*F* versus
		MS	*P*	MS	*P*	MS	*P*	MS	*P*	
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 m^2 ± 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
Amphilochidae	*Amphilochus* sp. Bate, 1862	5.56 ± 5.56	-	-	-
	Amphilochus neapolitanus Della Valle, 1893	2.78 ± 2.78	5.56 ± 5.56	50 ± 25.0	5.56 ± 3.68
Ampeliscidae	*Ampelisca diadema* (A. Costa, 1853)	-	-	-	2.78 ± 2.78
	Ampelisca serraticaudata Chevreux, 1888	-		2.78 ± 2.78	-
Amphithoidae	*Ampithoe ferox* (Chevreux, 1902)	2.78 ± 2.78	-	2.78 ± 2.78	-
	Ampithoe ramondi Audouin, 1826	1619.44 ± 426.08	977.78 ± 425.11	830.56 ± 262.69	108.33 ± 33.07
Aoridae	*Lembos* spp. Bate, 1856	-	-	2.78 ± 2.78	-
	Leptocheirus guttatus (Grube, 1864)	-	-	5.56 ± 3.68	-
	Microdeutopus spp. A. Costa, 1853	1130.56 ± 286.47	1433.33 ± 401.11	230.56 ± 87.28	230.56 ± 35.3
Caprellidae	*Caprella* spp. Lamarck, 1801	116.67 ± 84.68	2.78 ± 2.78	3744.44 ± 1022.81	1236.11 ± 596.05
Corophiidae	*Corophium* spp. Latreille, 1806	-	-	-	5.56 ± 5.56
	Apocorophium acutum (Chevreux, 1908)	58.33 ± 35.11	402.78 ± 108.29	27.78 ± 17.4	172.22 ± 108.45
	Corophium insidiosum Crawford, 1937	-	-	-	2.78 ± 2.78
	Ericthonius brasiliensis (Dana, 1855)	-	2.78 ± 2.78	22.22 ± 15.28	8.33 ± 5.89
Dexaminidae	*Atylus massiliensis* Bella-Santini, 1975	-	2.78 ± 2.78	105.56 ± 35.79	-
	Atylus guttatus (A. Costa, 1851)	2.78 ± 2.78	-	100 ± 60.42	5.56 ± 3.67
	Dexamine spiniventris (A. Costa, 1853)	-	-	75 ± 50.69	44.44 ± 36.03
	Guernea coalita (Norman, 1868)	-	8.33 ± 5.89	41.67 ± 21.25	-
Gammaridae	*Elasmopus* spp. A. Costa, 1853	586.11 ± 241.35	272.22 ± 87.35	202.78 ± 63.25	97.22 ± 40.7
	Gammarella fucicola (Leach, 1814)	-	-	-	2.78 ± 2.78
	Maera inaequipes (A. Costa, 1857)	-	2.78 ± 2.78	11.11 ± 8.45	2.78 ± 2.78
	Melita hergensis Reid, 1939	-	-	16.67 ± 13.82	50 ± 44.1
	Melita palmata Montagu, 1804	-	2.78 ± 2.78	-	-
Lysianassidae	*Lysianassa* sp.	-	-	13.89 ± 9.42	-
	Lysianassa costae Milne Edwards, 1830	127.78 ± 45.54	230.56 ± 51.67	258.33 ± 64.28	33.33 ± 27.32
	Orchomene humilis (A. Costa, 1853)	-	25 ± 17.68	-	-
Oedicerotidae	*Periculodes aequimanus* (Kossman, 1880)	5.56 ± 3.68	-	2.78 ± 2.78	8.33 ± 5.89
Phliantidae	*Pereionotus testudo* (Montagu, 1808)	2.78 ± 2.78	2.78 ± 2.78	19.44 ± 16.55	13.89 ± 11.11
Stenothoidae	*Stenothoe monoculoides* (Montagu, 1813)	63.89 ± 30.08	5.56 ± 5.56	77.78 ± 27.15	36.11 ± 26.06
	Stenothoe tergestina (Nebeski, 1880)	-	-	5.56 ± 5.56	-
Talitridae	*Hyale schmidti* (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**

538

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		*Ampithoe ramondi*		*F* versus
		MS	*P*	MS	*P*	MS	*P*	
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	*Hyale schmidtii*		*Apocorophium acutum*		*Microdeutopus* spp.		*F* versus
		MS	*P*	MS	*P*	MS	*P*	
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	*Caprella* spp.		*Elasmopus* spp.		*Lysianassa costae*		*F* versus
		MS	*P*	MS	*P*	MS	*P*	
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		

543
544

Fig. 1. Map showing the location of Alicante on the southeastern coast of Spain, and the study area.

Fig. 2. Two-dimensional MDS plot for algal biomass; S: September-04; M: March-05; I: Invaded habitat; NI: Non-invaded habitat, for each of the six sampling sites.

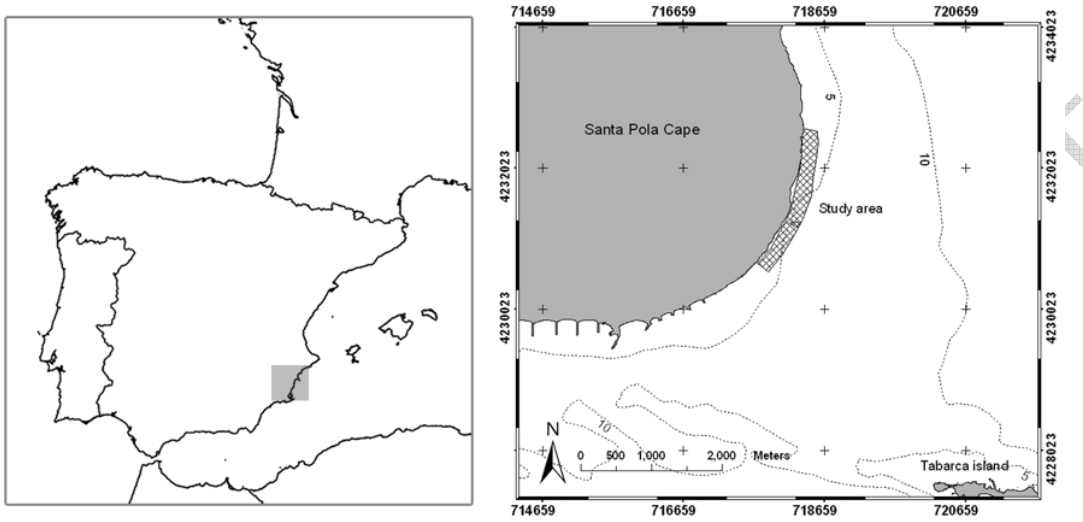
Fig. 3. Mean seaweed biomass (± SE) recorded from the two different sampling periods and habitats. Seaweed = biomass of seaweeds (without *C. racemosa*); *C. racemosa* = biomass of *C. racemosa;* and Detritus = biomass of detritus.

Fig. 4. (a) Mean number of amphipod species (individuals m^{-2} ± SE) and **(b)** total abundance (individuals m^{-2} ± SE), recorded from the two different sampling periods and habitats.

Fig. 5. Two-dimensional MDS plot amphipod species abundance. S = September-04; M = March-05; I = Invaded habitat; NI = Non-invaded habitat for each of the six sampling sites.

Fig. 6. Mean abundance (number of individuals ±SE) of the seven most abundant amphipods: *Ampithoe ramondi* (**a**); *Hyale schmidti* (**b**); *Apocorophium acutum* (**c**); *Microdeutopus* spp. (**d**); *Caprella* spp. (**e**); *Elasmopus* spp. (**f**) and *Lysianassa costae* **(g)**

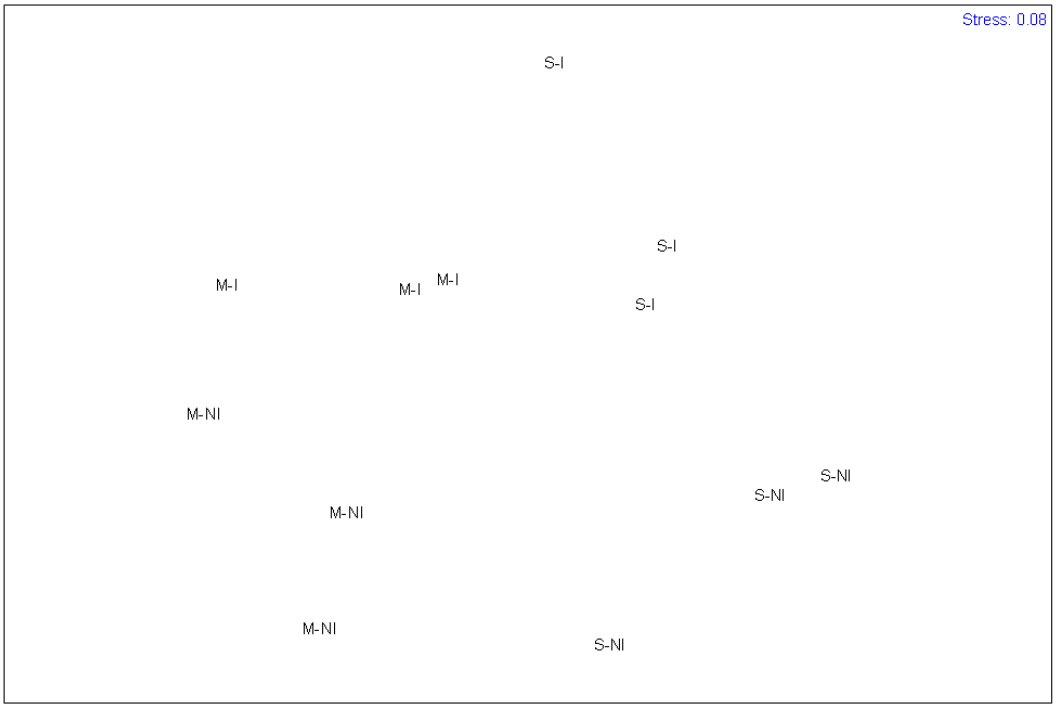
563 Figure 1



564

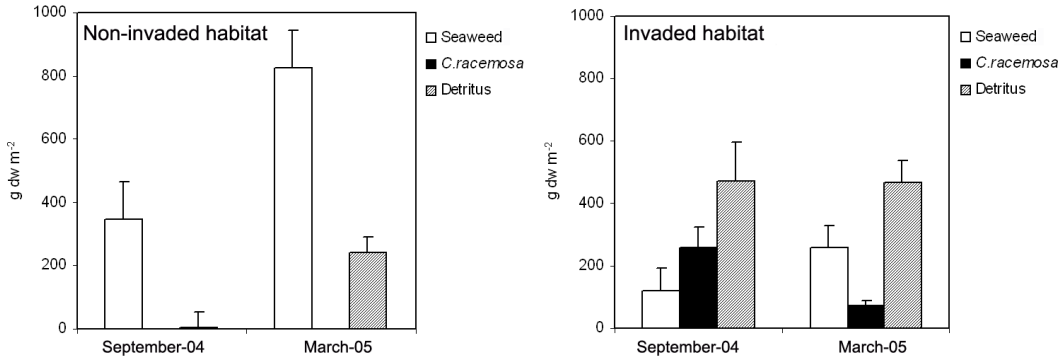
565

566 Figure 2



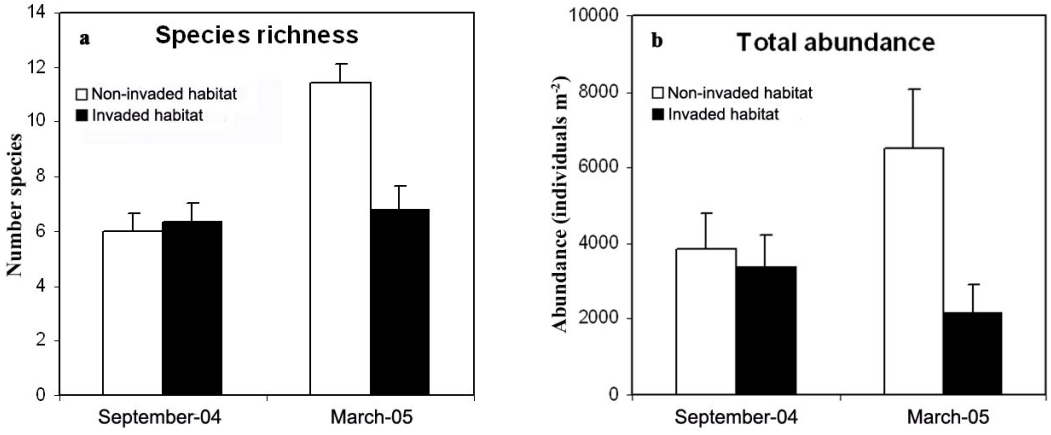
567

568 Figure 3



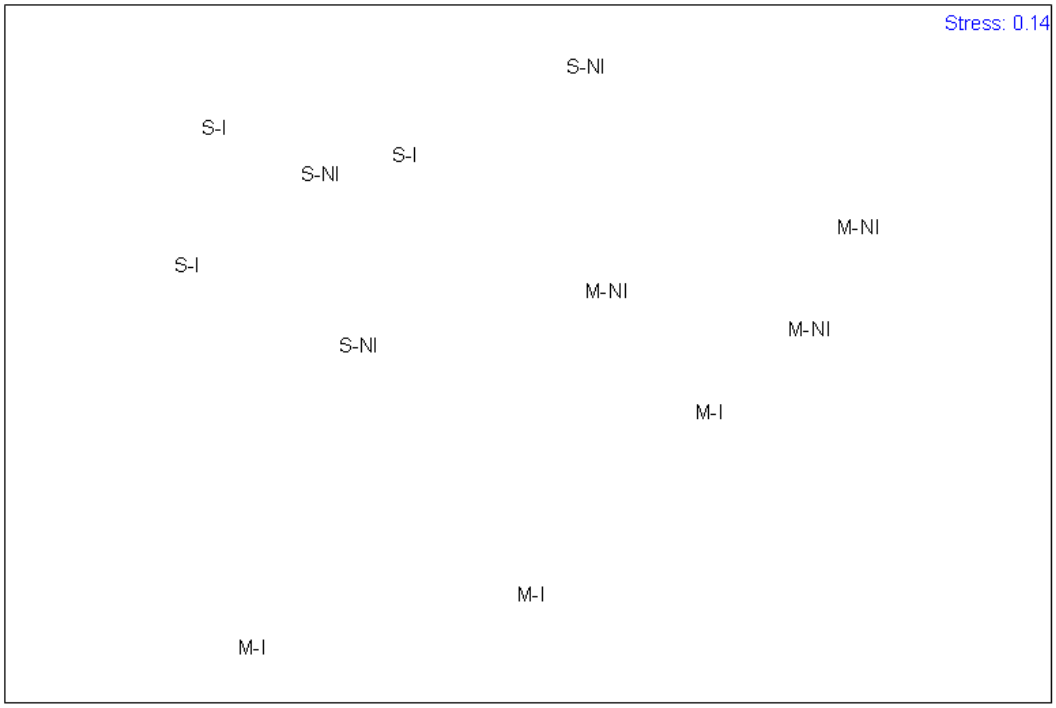
569

570 Figure 4



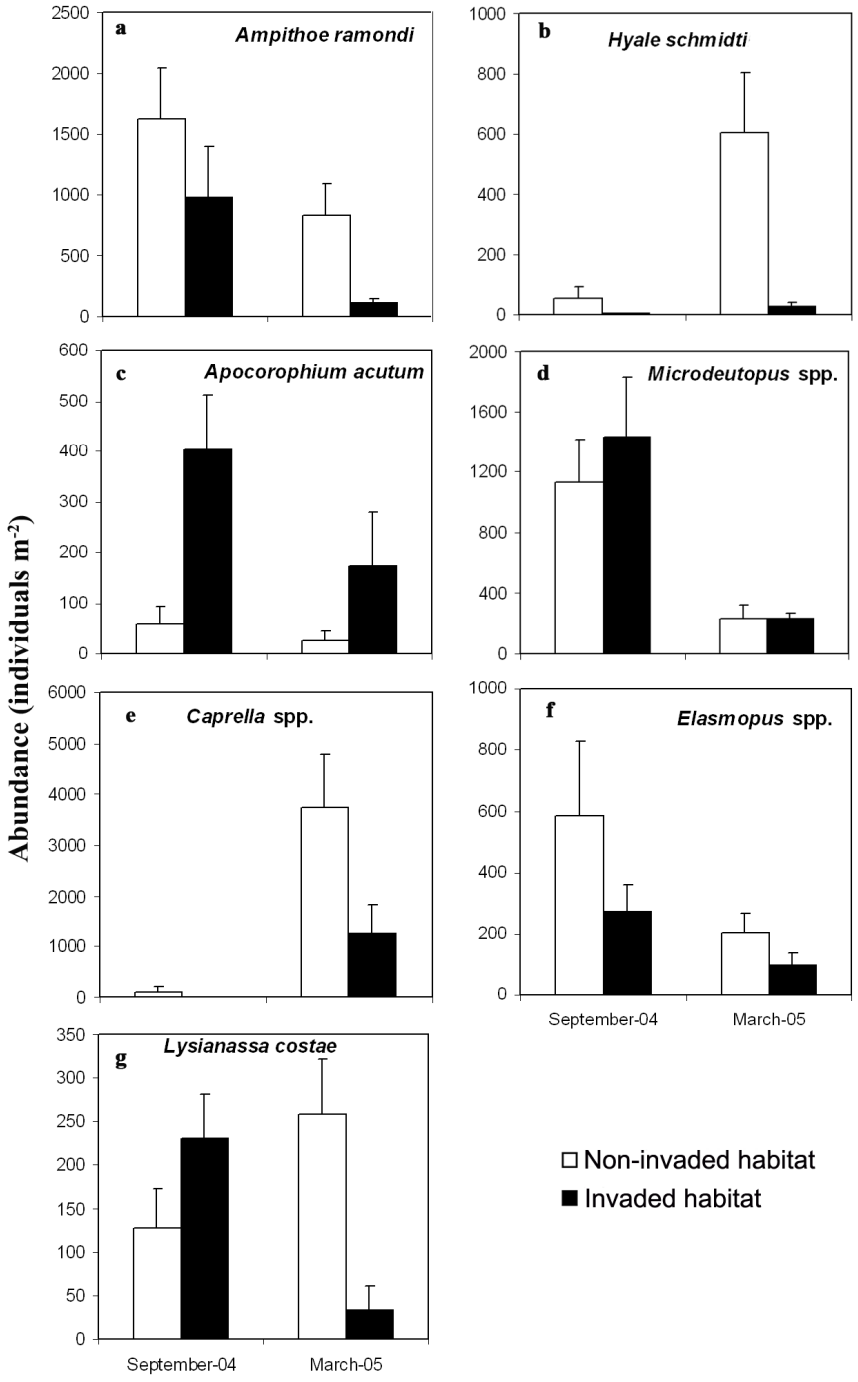
571

572 Figure 5



573

574 Figure 6



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