Comparison of epifaunal assemblages between *Cymodocea*nodosa and *Caulerpa prolifera* meadows in Gran Canaria (eastern Atlantic)

Lydia Png González

Máster en Oceanografía

Universidad de Las Palmas de Gran Canaria

Director: Dr. Fernando Tuya Cortés

Tutor: Dr. Santiago Hernández León



Julio 2013

Comparison of epifaunal assemblages between *Cymodocea nodosa* and *Caulerpa prolifera* meadows in Gran Canaria (eastern Atlantic)

Lydia Png-Gonzalez^{1*}, Maite Vázquez-Luis², Fernando Tuya¹

¹Centro en Biodiversidad y Gestión Ambiental, Marine Sciences Faculty, Campus Tafira, Universidad de Las Palmas de Gran Canaria, 35017 Tafira, Las Palmas, Spain ²Instituto Español de Oceanografía, Centro Oceanográfico de Baleares. Muelle de Poniente s/n, 07015 Palma de Mallorca, Spain

ABSTRACT

Epifaunal invertebrates are sensitive to changes in the identity of the dominant host plant, so assessing differences in the diversity, abundance and structure of epifaunal assemblages is particularly pertinent in areas where seagrasses have been replaced by alternative vegetation (e.g. green seaweeds). In this study, we aimed to compare the diversity, abundance and structure of epifaunal assemblages, with particular emphasis on amphipods, between meadows dominated by Cymodocea nodosa and the green algae Caulerpa prolifera on shallow soft bottoms of Gran Canaria Island, determining whether patterns were temporally consistent. The epifaunal assemblage structure (abundance and composition) consistently differed between both plants, being more diverse and abundant epifaunal assemblages associated with C. proliferadominated beds than those inhabiting C. nodosa meadows. Amphipods constituted ca. 70% of crustaceans for the overall study, including 37 species belonging to 16 families. The amphipods abundance recorded was ca. 3 times larger in C. prolifera-dominated beds (1248.13 \pm 136.83 ind. m⁻², mean \pm SE) than in C. nodosa meadows (396.88 \pm 77.36 ind. m⁻²). Multivariate analysis of the community showed significant differences between habitats, with a clear segregation of the species. For instance, Microdeutopus stationis, Dexamine spinosa, Aora spinicornis, Ischyrocerus inexpectatus and Apherusa bispinosa were more abundant in C. prolifera-dominated beds; while the new genus, new species of caprellid, Mantacaprella macaronensis, dominated in C. nodosa meadows. However, some species such as Pseudoprotella phasma and Ampithoe ramondi were found without significant differences in both habitats.

Keywords: Amphipoda, epifauna, assemblage structure, ecosystem services, seagrass, Canary Islands.

1. Introduction

On subtidal soft bottoms, seagrasses form one of the most productive ecosystems worldwide, providing high-value ecosystem services such as delivery of food and habitat for a wide range of organisms (Costanza et al., 1997; Duffy, 2006; Thomsen et al., 2012), support of commercial fisheries, nutrient cycling, sediment stabilization and sequestration of carbon (Duarte et al., 2000; Waycott et al., 2009). Seagrasses, and the services they provide, are, however, threatened by impacts derived from coastal development and growing human population, as well as by impacts caused by climate change (Duarte, 2002; Orth et al., 2006; Waycott et al., 2009). Conservation of these valuable habitats is, therefore, important, particularly since seagrass meadows are declining worldwide, mainly in areas of intense human activities (Hughes et al., 2009).

Cymodocea nodosa (Ucria) Ascherson is a seagrass distributed across the Mediterranean Sea and adjacent areas of the Atlantic Ocean, including the Macaronesian archipelagos of Madeira and the Canaries (Reyes et al., 1995; Tuya et al., 2012). Meadows constituted by *C. nodosa* are the dominant vegetated communities on shallow soft substrates throughout the Canary Islands (Pavón-Salas et al., 2000; Barberá et al., 2005; Monterroso et al., 2012), where they provide food and shelter for diverse invertebrate and fish assemblages, including a 'nursery' habitat for larval and juvenile fish stages (Tuya et al., 2006; Espino et al., 2011a, 2011b). However, *C. nodosa* meadows are severely decreasing at local scales, as a result of a range of human-mediated impacts (Martínez-Samper, 2011; Tuya et al., 2013). In these coastal areas, the decline of *C. nodosa* seagrass meadows often results in the replacement by

opportunistic green algae of the genus *Caulerpa*, *Caulerpa prolifera* (Forsskål) J.V. Lamouroux in particular (Martínez-Samper, 2011; Tuya et al., 2013).

Caulerpa prolifera is a native seaweed in the Canary Islands (Haroun et al., 2003), forming extensive beds on soft bottoms in waters from ca. 5 to 50 m depth. Several Caulerpa species contain caulerpenyne, a major secondary metabolite, which varies depending on the species, locations and seasons (Jung et al., 2002; Box et al., 2010), and appears to possess toxic and feeding deterrent properties against faunal herbivores (Smyrniotopoulos et al., 2003). Caulerpenyne may also act as an antimitotic substance, preventing settlement of most epiphytes (Sánchez-Moyano et al., 2001a). In addition, the high sediment-retention capacity of Caulerpa beds induces organic enrichment (Hendriks et al., 2010), potentially altering the distribution and abundance of associated animal populations (Sánchez-Moyano et al., 2001a).

When seagrasses are replaced by seaweeds, the quantity and quality of habitat for associated faunal assemblages may be altered, as well as flows of energy and matter through the ecosystem (Thomsen et al., 2012). In particular, epifaunal invertebrates are sensitive to changes in plant abundance and structure (e.g. through plant attributes such as plant size, biomass, shoot density, etc.), so differences in the diversity, abundance and structure of invertebrate assemblages are expected between different types (identities) of vegetation within the same geographical and environmental context (Sirota and Hovel, 2006).

The aim of this study was to compare the diversity, abundance and structure of epifaunal assemblages between meadows dominated by *Cymodocea nodosa* and *Caulerpa prolifera* on shallow soft bottoms of Gran Canaria Island, determining whether patterns were temporally consistent. Particular emphasis was concentrated on amphipod assemblages, since amphipods are one of the most quantitatively and

important groups of invertebrates associated with coastal vegetated habitats, while these organisms also play an important role as trophic resources for fish populations (Sánchez-Jerez et al., 1999; Vázquez-Luis et al., 2009). In this sense, amphipods respond to habitat alterations and can, therefore, be used as an indicator of environmental impacts on vegetated habitats (Virnstein, 1987; Conradi et al., 1997; Sánchez-Jerez et al., 2000; Vázquez-Luis et al., 2008, 2009).

2. Material and methods

2.1. Study area and sampling design

The study was carried out in Gran Canaria (Canary Islands, eastern Atlantic), at a range of localities across the island (Table 1) dominated by either subtidal monospecific *Cymodocea nodosa* meadows or beds constituted by *Caulerpa prolifera*.

Table 1. Sampled localities to compare epifaunal assemblages between *Cymodocea nodosa* seagrass meadows and *Caulerpa prolifera*-dominated beds at Gran Canaria Island.

Habitat	Locality	UTM X	UTM Y	Depth (m)	Date
C. nodosa	L1	421440	3080993	11.3	Nov'11
C. nodosa	L2	462235	3082272	10	Nov'11
C. nodosa	L1	461982	3081367	11.3	Oct'12
C. nodosa	L2	462114	3082872	8.8	Oct'12
C. prolifera	L1	463559	3089684	13.7	Nov'11, Oct'12
C. prolifera	L2	463105	3089320	14.6	Nov'11, Oct'12

Each habitat (i.e. *C. nodosa vs. C. prolifera*-dominated beds) was sampled at each of two localities, where n=10, randomly allocated, samples were collected by SCUBA divers, using a 20x20 cm quadrat. Collections were performed cutting the seagrass/seaweed immediately above the sediment surface, keeping the vegetation with

the associated epifauna in unbleached woven cotton bags (Brearley et al., 2008; Gartner et al., 2013). Sampling was repeated twice (November 2011 and October 2012) to merely assess whether patterns in the diversity, abundance and structure of epifaunal assemblages between beds dominated by *C. nodosa* and *C. prolifera* were temporally consistent.

Labelled samples were preserved in a freezer (-20 °C) until processed. In the laboratory, samples collected were initially defrosted and subsequently sieved through a 500 µm mesh to retain macrofaunal organisms. Specimens were sorted and counted into different taxonomic groups under a binocular microscope and preserved in 70% ethanol. Four main functional groups: Crustacea, Mollusca, worms (including Annelida and Sipuncula) and other fauna (Chelicerata, Chordata and Echinodermata) were considered. All organisms were identified to species level, whenever possible. In particular, amphipods were identified to the lower taxonomic resolution (species in most cases), because amphipods was the most abundant taxa and because of their importance as biological indicators of human-induced alterations (Sánchez-Jerez et al., 2000). The amount of vegetated biomass (wet weight) was obtained for each replicate to account for differences in the amount of habitat (vegetation) among samples.

2.2. Statistical analysis

2.2.1. Univariate analysis

Differences in the abundance and species density (the number of species per area) of the dominant groups (here, Crustacea, Mollusca, Amphipoda, worms and other fauna) between habitats, localities within habitats and times were tested using a 3-way ANCOVA, which incorporated the factors: 'Habitat' (fixed with 2 levels: *C. nodosa vs. C. prolifera*), 'Locality' (random and nested within 'Habitat', 2 levels: L1 and L2), and

'Time' (fixed with 2 levels: Nov'11 vs. Oct'12); 'Leaf biomass' was included as a covariate to account for differences in the amount of available habitat for epifauna among samples. Data were square root transformed prior to analyses, and analyses based on Euclidean distances (Anderson, 2001a). For each ANCOVA, we estimated the relative contribution of each factor to explain differences in the response variable through calculation of their corresponding variance components.

2.2.2. Multivariate analysis

Differences in the multivariate structure (what includes the abundance and composition) of assemblages between habitats (*C. nodosa vs. C. prolifera*) were visualized through a non-metric multidimensional scaling (nm-MDS) ordination plot, based on Bray-Curtis similarities. The significance of these multivariate differences were tested by a 3-way PERMANOVA (Anderson, 2001b), using 'Time', 'Habitat' and 'Locality' as factors, following the same design outlined above. The leaf biomass of each replicate was, again, included as a covariate. PERMANOVA data were square root transformed prior to analyses, and analyses were based on Euclidean distances. The individual contribution of each amphipod species to the dissimilarity between habitats (*C. nodosa vs. C. prolifera*) was calculated by the SIMPER routine, based on Bray-Curtis similarities.

All uni- and multivariate procedures were carried out by means of the PRIMER 6.0 & PERMANOVA statistical package.

3. Results

3.1. Epifaunal assemblages

A total of 4655 epifaunal individuals, belonging to 105 taxa (Appendix 1), were counted within the four dominant functional groups: crustaceans (3594 individuals), mollusks (777), worms (138) and other fauna (146). The abundance of crustaceans, which proved to be the dominant group (representing the 77.2 % of the total abundance), was significantly larger in Caulerpa prolifera-dominated beds (1792.5 ± 181.18 ind. m⁻², mean \pm SE) than in *Cymodocea nodosa* meadows (562.5 \pm 81.92 ind. m⁻²) at both sampling times (Fig. 1; 3-way ANCOVA: 'Habitat', P=0.0002, Table 2). The species density of crustaceans was also larger in C. prolifera-dominated beds than in C. nodosa meadows (12.03 \pm 0.52 vs. 5.8 \pm 0.47 sp. 0.04 m⁻², respectively) (Fig. 2; 3-way ANCOVA: 'Habitat', P=0.0002, Table 2). The abundance of mollusks was, again, significantly larger in C. prolifera-dominated beds (415.63 \pm 71.4 ind. m⁻²) than in C. nodosa meadows (70 \pm 15.14 ind. m⁻²) (Fig. 1; 3-way ANCOVA: 'Habitat', P=0.0002, Table 2), as well as the species density of mollusks $(3.45 \pm 0.23 \text{ vs. } 1.6 \pm 0.2 \text{ s.s.})$ sp. 0.04 m⁻², respectively) (Fig. 2; 3-way ANCOVA: 'Habitat', P=0.0002, Table 2). Worms showed a different pattern between sampling times, but abundance and species density were, on average, larger in C. prolifera-dominated beds (80 ± 16.32 ind. m⁻² and 1.33 ± 0.09 sp. 0.04 m⁻², respectively) than in C. nodosa meadows (26.25 ± 6.39 ind. m⁻² ² and 0.65 ± 0.07 sp. 0.04 m^{-2}) (Fig. 1 and 2; 3-way ANCOVA: 'Habitat', P=0.0002, Table 2). Finally, other faunal individuals were more abundant in C. proliferadominated beds (70 ± 20.16 ind. m⁻²) than in *C. nodosa* meadows (70 ± 15.14 ind. m⁻²), but without significant differences (Fig. 1; 3-way ANCOVA: 'Habitat', P=0.6590, Table 2). The species density of other fauna $(0.7 \pm 0.12 \text{ vs. } 0.45 \pm 0.35 \text{ sp. } 0.04 \text{ m}^{-2})$

respectively) (Fig. 2) was not significant either (3-way ANCOVA: 'Habitat', P=1.0000, Table 2).

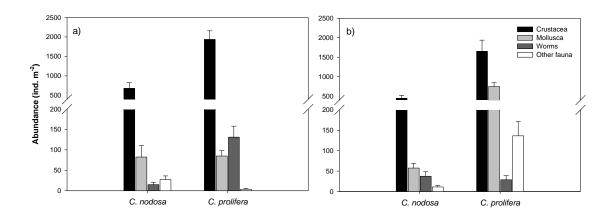


Figure 1. Mean abundance (ind. $m^{-2} \pm SE$) of the 4 functional groups at each habitat in (a) November 2011 and (b) October 2012.

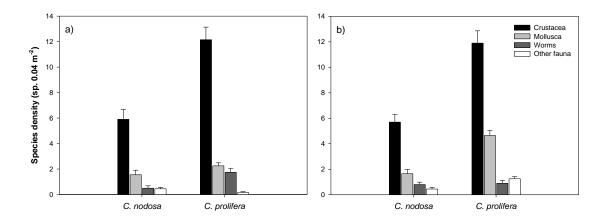


Figure 2. Mean species density (number of species \pm SE) of the 4 functional groups at each habitat in (a) November 2011 and (b) October 2012.

Table 2. Results of 3-way ANCOVAs testing for differences between habitats, times and localities within habitats, for the abundance and species density of each functional group. *Significant difference at P<0.05. The amount of variance (%CV) explained by each factor is included.

CRUSTACEA		Abunda	nce		Species density				
	df	MS	F	P	%CV	MS	F	P	%CV
Covariate = Leaf biomass	1	903.86	2.1887	0.1462	5.35%	1.74	1.0657	0.3052	1.52%
Time	1	75.89	0.0460	0.8266	0%	0.13	0.0357	0.8410	0%
Habitat	1	7085.30	5.9660	0.0002*	30.42%	23.86	4.8950	0.0002*	33.16%
Locality(Ha)	2	1574.70	24.2620	0.0002	18.76%	6.49	38.1210	0.0002	23.33%
TixHa	1	80.91	0.0617	0.8100	0%	0.60	0.2138	0.6791	0%
TixLo(Ha)	2	1642.10	25.3000	0.0002	28.09%	3.52	20.6610	0.0002	24.87%
Residual	71	64.90			17.39%	0.17			17.12%
Total	79								
MOLLUSCA		Abunda	nce	_,		Species	density	_,	
	df	MS	F	P	%CV	MS	F	P	%CV
Covariate = Leaf biomass	1	386.81	3.3939	0.0762	4.7916	0.97	0.7060	0.3910	0.0000
Time	1	2262.20	7.8276	0.1048	19.3216	4.94	4.4910	0.1550	14.5368
Habitat	1	1292.50	3.9539	0.0002*	14.7938	8.75	2.1964	0.0002*	17.7108
Locality(Ha)	2	433.26	23.6670	0.0002	11.8233	5.29	26.3780	0.0002	22.3086
TixHa	1	1472.90	6.7506	0.1099	24.6531	2.03	2.6053	0.2347	13.2611
TixLo(Ha)	2	271.08	14.8070	0.0002	13.5152	0.93	4.6486	0.0108	12.3886
Residual	71	18.31			11.1013	0.20			19.7949
Total	79								
				Species de					
WORMS		Abunda	nce	-		Species	density	-	
WORMS	df	Abundar	nce F	Р	%CV	Species MS	density F	Р	%CV
WORMS Covariate = Leaf biomass	df			P 0.5430	%CV 0%		-	P 0.7252	% CV
		MS	F			MS	F		
Covariate = Leaf biomass	1	MS 8.46	F 0.3701	0.5430	0%	MS 0.04	F 0.1204	0.7252	0%
Covariate = Leaf biomass Time	1	MS 8.46 53.98	F 0.3701 0.3520	0.5430 0.5856	0% 0%	MS 0.04 0.09	F 0.1204 0.0520	0.7252 0.8190	0% 0%
Covariate = Leaf biomass Time Habitat	1 1 1	MS 8.46 53.98 310.50	F 0.3701 0.3520 8.6372	0.5430 0.5856 0.0002*	0% 0% 20.06%	MS 0.04 0.09 3.74	F 0.1204 0.0520 9.7138	0.7252 0.8190 0.0002*	0% 0% 24.00%
Covariate = Leaf biomass Time Habitat Locality(Ha)	1 1 1 2	MS 8.46 53.98 310.50 42.50	F 0.3701 0.3520 8.6372 2.5050	0.5430 0.5856 0.0002* 0.0854	0% 0% 20.06% 7.46%	MS 0.04 0.09 3.74 0.39	F 0.1204 0.0520 9.7138 1.1012	0.7252 0.8190 0.0002* 0.3414	0% 0% 24.00% 3.04%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa	1 1 1 2 1	MS 8.46 53.98 310.50 42.50 254.03	F 0.3701 0.3520 8.6372 2.5050 2.0613	0.5430 0.5856 0.0002* 0.0854 0.2672	0% 0% 20.06% 7.46% 20.24%	MS 0.04 0.09 3.74 0.39 1.66	F 0.1204 0.0520 9.7138 1.1012 0.9854	0.7252 0.8190 0.0002* 0.3414 0.4229	0% 0% 24.00% 3.04% 0%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha)	1 1 2 1 2	MS 8.46 53.98 310.50 42.50 254.03 151.36	F 0.3701 0.3520 8.6372 2.5050 2.0613	0.5430 0.5856 0.0002* 0.0854 0.2672	0% 0% 20.06% 7.46% 20.24% 25.06%	MS 0.04 0.09 3.74 0.39 1.66 2.03	F 0.1204 0.0520 9.7138 1.1012 0.9854	0.7252 0.8190 0.0002* 0.3414 0.4229	0% 0% 24.00% 3.04% 0% 30.23%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual	1 1 2 1 2 71	MS 8.46 53.98 310.50 42.50 254.03 151.36	F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221	0.5430 0.5856 0.0002* 0.0854 0.2672	0% 0% 20.06% 7.46% 20.24% 25.06%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36	F 0.1204 0.0520 9.7138 1.1012 0.9854	0.7252 0.8190 0.0002* 0.3414 0.4229	0% 0% 24.00% 3.04% 0% 30.23%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total	1 1 2 1 2 71	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96	F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221	0.5430 0.5856 0.0002* 0.0854 0.2672	0% 0% 20.06% 7.46% 20.24% 25.06%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634	0.7252 0.8190 0.0002* 0.3414 0.4229	0% 0% 24.00% 3.04% 0% 30.23%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total	1 1 2 1 2 71 79	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96	F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042	0% 0% 24.00% 3.04% 0% 30.23% 42.73%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA	1 1 2 1 2 71 79	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundan	F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042	0% 0% 24.00% 3.04% 0% 30.23% 42.73%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA Covariate = Leaf biomass	1 1 2 1 2 71 79 df 1	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundar MS 180.77	© F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221 mce F 6.1752	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18% %CV 8.46%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS 0.0024	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F 0.0045	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042	0% 0% 24.00% 3.04% 0% 30.23% 42.73%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA Covariate = Leaf biomass Time	1 1 2 1 2 71 79 df 1	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundan MS 180.77 474.15	© F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221 mce F 6.1752 11.0950	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004 P 0.0182 0.0758	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18% %CV 8.46% 21.43%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS 0.0024 3.73	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F 0.0045 3.1454	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042 P 0.9442 0.2040	0% 0% 24.00% 3.04% 0% 30.23% 42.73% *CV 0% 15.22%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA Covariate = Leaf biomass Time Habitat	1 1 2 1 2 71 79 df 1 1 1	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundar MS 180.77 474.15 0.63	R 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221 mce F 6.1752 11.0950 0.0114	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004 P 0.0182 0.0758 0.6590	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18% *CV 8.46% 21.43% 0%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS 0.0024 3.73 0.08	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F 0.0045 3.1454 0.0603	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042 P 0.9442 0.2040 1.0000	0% 0% 24.00% 3.04% 0% 30.23% 42.73% *CV 0% 15.22% 0%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA Covariate = Leaf biomass Time Habitat Locality(Ha)	1 1 2 1 2 71 79 df 1 1 1 2	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundan MS 180.77 474.15 0.63 68.69	F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221 mce F 6.1752 11.0950 0.0114 3.9334	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004 P 0.0182 0.0758 0.6590 0.0182	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18% **CV 8.46% 21.43% 0% 9.85%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS 0.0024 3.73 0.08 1.75	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F 0.0045 3.1454 0.0603 10.1600	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042 P 0.9442 0.2040 1.0000 0.0006	0% 0% 24.00% 3.04% 0% 30.23% 42.73% **CV 0% 15.22% 0% 15.99%
Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa TixLo(Ha) Residual Total OTHER FAUNA Covariate = Leaf biomass Time Habitat Locality(Ha) TixHa	1 1 2 1 2 71 79 df 1 1 1 2 1	MS 8.46 53.98 310.50 42.50 254.03 151.36 16.96 Abundar MS 180.77 474.15 0.63 68.69 264.64	© F 0.3701 0.3520 8.6372 2.5050 2.0613 8.9221 mce F 6.1752 11.0950 0.0114 3.9334 7.4973	0.5430 0.5856 0.0002* 0.0854 0.2672 0.0004 P 0.0182 0.0758 0.6590 0.0182 0.1146	0% 0% 20.06% 7.46% 20.24% 25.06% 27.18% *CV 8.46% 21.43% 0% 9.85% 24.99%	MS 0.04 0.09 3.74 0.39 1.66 2.03 0.36 Species MS 0.0024 3.73 0.08 1.75 4.07	F 0.1204 0.0520 9.7138 1.1012 0.9854 5.6634 density F 0.0045 3.1454 0.0603 10.1600 4.4363	0.7252 0.8190 0.0002* 0.3414 0.4229 0.0042 P 0.9442 0.2040 1.0000 0.0006 0.1566	0% 0% 24.00% 3.04% 0% 30.23% 42.73% *CV 0% 15.22% 0% 15.99% 27.08%

The two-dimensional MDS plot showed a separation of epifaunal assemblages by habitats and times: epifauna associated with *Cymodocea nodosa* meadows are in the left-hand side of the ordination space, while epifauna inhabiting *Caulerpa prolifera*-dominated beds are in the right-hand side of the plot. In addition, samples corresponding to November 2011 are in the top side, whereas those corresponding to October 2012 are in the bottom side of the plot (Fig. 3). This multivariate response, however, was only statistically significant between habitats (3-way PERMANOVA: 'Habitat', P=0.0002; Table 3).

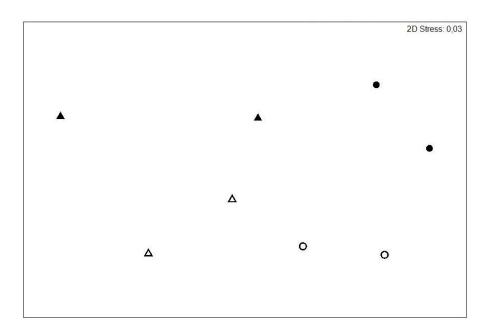


Figure 3. Two-dimensional MDS plot showing similarities in the epifaunal assemblage structure between habitats and times. Each symbol corresponds to a sampling locality within each habitat. Triangles: *C. nodosa*, circles: *C. prolifera*. Filled symbols: Nov'11, unfilled symbols: Oct'12.

Table 3. Results of 3-way PERMANOVA testing for differences between habitats, times and localities within habitats, for the epifaunal assemblage structure. *Significant differences for P<0.05. The amount of variance (%CV) explained by each factor is included.

	df	MS	F	P	%CV
Covariate = Leaf biomass	1	5212.7	3.0345	0.001	5.97%
Time	1	13002	2.6701	0.1278	13.67%
Habitat	1	11108	2.4333	0.0002*	13.41%
Locality(Ha)	2	5987.8	13.656	0.0002	15.05%
TixHa	1	7014.8	1.8769	0.2272	13.87%
TixLo(Ha)	2	4610.3	10.515	0.0002	19.12%
Residual	71	438.47			18.92%
Total	79				

3.2. Amphipod assemblages

A total of 37 amphipod species, belonging to 16 families, were recorded (Appendix 1). The abundance of amphipods constituted ca. 70% of crustaceans for the overall study and was significantly larger in *Caulerpa prolifera*-dominated beds (1248.13 \pm 136.83 ind. m⁻², mean \pm SE) than in *Cymodocea nodosa* meadows (396.88 \pm 77.36 ind. m⁻²) at both sampling times (Fig. 4*a*; 3-way ANCOVA: 'Habitat', P=0.0002, Table 4). A similar pattern was found for amphipod species density (7.05 \pm 0.47 *vs.* 4.25 \pm 0.38 sp. 0.04 m⁻², respectively; Fig. 4*b*), but differences were not statistically significant (3-way ANCOVA: 'Habitat', P=0.3406, Table 4).

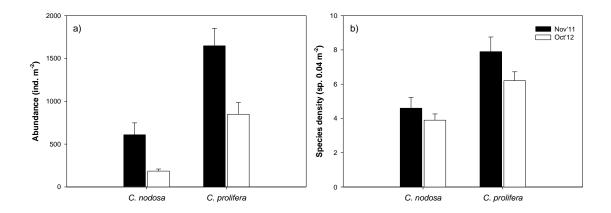


Figure 4. (a) Mean abundance (ind. $m^{-2} \pm SE$) and (b) mean species density (number of species $\pm SE$) of amphipods at each habitat and time.

Table 4. Results of 3-way ANCOVA testing for differences between habitats, times and localities within habitats, for the total abundance and species density of amphipods. *Significant difference at P<0.05. The amount of variance (%CV) explained by each factor is included.

		Total abundance			Total species density					
	df	MS	F	P	%CV	MS	F	P	%CV	
Covariate = Leaf biomass	1	1550.8	4.5936	0.0396	9.42%	14.06	0.3522	0.5544	0%	
Time	1	994.15	0.7567	0.4326	0%	5.54	0.0705	0.8078	0%	
Habitat	1	4804.3	4.8642	0.0002*	27.43%	196.15	1.6149	0.3406	17.65%	
Locality(Ha)	2	1312.5	28.8590	0.0002	19.27%	162.20	49.5220	0.0002	31.39%	
TixHa	1	12.32	0.0123	0.9186	0%	0.02	0.0004	0.9896	0%	
TixLo(Ha)	2	1253.2	27.5540	0.0002	27.55%	74.69	22.8030	0.0002	30.82%	
Residual	71	45.48			16.32%	3.28			20.14%	
Total	79									

The two-dimensional MDS plot showed a clear segregation of amphipod assemblages mainly by habitat: amphipods associated with *Cymodocea nodosa* meadows are in the left-hand side of the plot, while amphipods associated with *Caulerpa prolifera*-dominated beds are in the right-hand side. Samples collected in November 2011 were more dissimilar to each other than those obtained in October 2012

(Fig. 5). However, the structure of amphipod assemblages was only statistically significant between habitats (3-way PERMANOVA: 'Habitat', P=0.0002, Table 5).

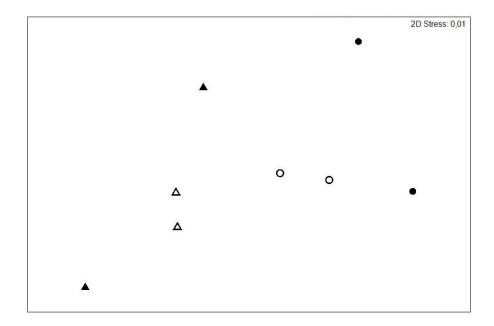


Figure 5. Two-dimensional MDS plot showing similarities in the amphipod assemblage structure between habitats and times. Each symbol corresponds to a sampling locality within habitats. Triangles: *C. nodosa*, circles: *C. prolifera*. Filled symbols: Nov'11, unfilled symbols: Oct'12.

Table 5. Results of 3-way PERMANOVA testing for differences between habitats, times and locations within habitats, for the amphipod assemblage structure. *Significant differences for P<0.05. The amount of variance (%CV) explained by each factor is included.

	df	MS	\mathbf{F}	P	%CV
Covariate = Le	af				
biomass	1	1528.4	1.2753	0.2314	2.97%
Time	1	4796.5	1.4492	0.3056	9.45%
Habitat	1	8107.8	2.4173	0.0002*	18.48%
Locality(Ha)	2	4431.1	19.278	0.0002	21.18%
TixHa	1	2188.6	0.86856	0.4874	0%
TixLo(Ha)	2	3125.6	13.598	0.0002	25.76%
Residual	71	229.86			22.15%
Total	79				

The amphipod species which most contributed to dissimilarities between habitats were: Microdeutopus stationis, Dexamine spinosa, Aora spinicornis, Mantacaprella macaronensis, Pseudoprotella phasma, Ampithoe ramondi, Ischyrocerus inexpectatus and Apherusa bispinosa. These species made up ca. 60% of the total abundance of amphipods. Amphipod assemblages showed a clear segregation, with different species contributing to the dissimilarity between habitats. For example, the abundance of M. stationis, D. spinosa and A. spinicornis was significantly larger in C. proliferadominated beds (Fig. 6a, b, c; 3-way ANCOVA: 'Habitat', P<0.05, Table 6), while the new species of caprellid M. macaronensis (Fig. 7; Vázquez-Luis et al., 2013; in revision) significantly dominated in C. nodosa meadows (Fig. 6d; 3-way ANCOVA: 'Habitat', P=0.0002, Table 6). The other caprellid species, P. phasma, also showed larger abundances in C. nodosa meadows, although the difference with respect to C. prolifera-dominated beds was not statistically significant (Fig. 6e; 3-way ANCOVA: 'Habitat', P=0.6612, Table 6). The gammarid A. ramondi was found in both habitats, with larger abundances in C. prolifera-dominated beds, but without significant differences (Fig. 6f; 3-way ANCOVA: 'Habitat', P=0.6800, Table 6). Finally, I. inexpectatus and A. bispinosa were more abundant in C. prolifera-dominated beds, but no significant differences were detected between habitats, probably masked by the high variability between localities (Fig. 6g, h; 3-way ANCOVA: 'Habitat', P>0.05, Table 6).

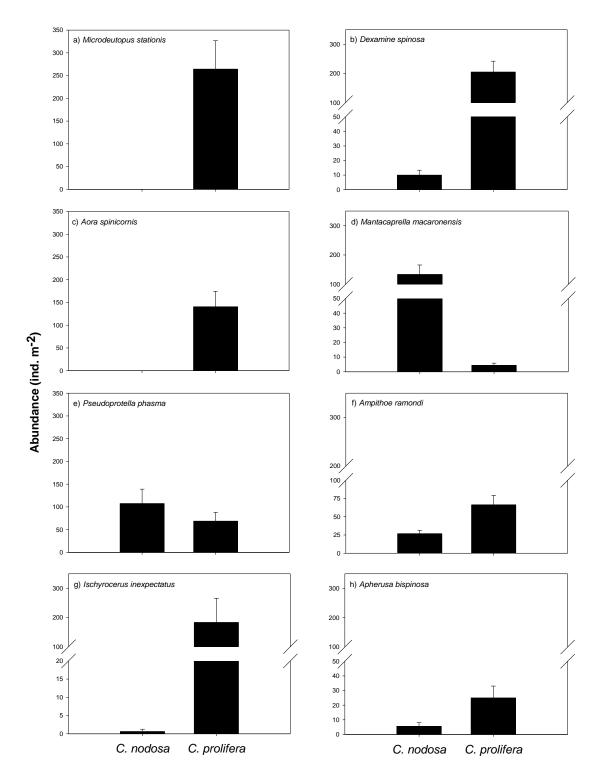


Figure 6. Mean abundance (ind. $m^{-2} \pm SE$) of the most important amphipod species at each habitat.

Table 6. Results of 3-way ANCOVAs testing for differences between habitats, times and localities within habitats, for the abundance of the most important amphipod species. *Significant differences for P < 0.05. The amount of variance (%CV) explained by each factor is included.

		Mianada	utomus sta	·tionia		Danamin			
	ae	-	utopus sta		0/ CV	Dexamin MS		- D	0/ CV
Commists I softismess	df 1	MS 325.79	F 1.1317	P 0.2856	%CV 2.07%	MS 606.04	F 18.6590	P 0.0008	%CV 9.61%
Covariate = Leaf biomass	1								
Time	1	563.44	1.8731	0.2866	8.20%	1313.80	17.8540	0.0500	21.20%
Habitat	1	2414.9	2.7502	0.0002*	21.68%	1183.10	16.9750	0.0002*	21.98%
Locality(Habitat)	2	1173	51.703	0.0002	22.87%	88.29	5.6029	0.0056	6.84%
TimexHabitat	1	581.46	2.7391	0.2214	15.53%	388.08	6.6477	0.1155	17.49%
TimexLo(Habitat)	2	262.44	11.568	0.0002	15.29%	69.65	4.4201	0.0150	8.63%
Residual	71	22.69			14.36%	15.76			14.25%
Total	79								
		Aora sp	inicornis	=		Mantacaj	prella maco	ironensis	-
	df	MS	F	P	%CV	MS	F	P	%CV
Covariate = Leaf biomass	1	119.41	2.2410	0.1502	4.29%	0.0065	0.0001	0.9942	0%
Time	1	277.33	0.6036	0.5068	0%	368.48	0.9490	0.4310	0%
Habitat	1	1436.90	10.5870	0.0002*	31.24%	1126.80	2.9057	0.0002*	26.20%
Locality(Habitat)	2	176.93	10.8940	0.0002	13.38%	518.80	66.7480	0.0002	26.57%
TimexHabitat	1	160.31	0.4498	0.5641	0%	106.09	0.3643	0.6086	0%
TimexLo(Habitat)	2	446.38	27.4850	0.0002	32.07%	366.21	47.1160	0.0002	32.59%
Residual	71	16.24			19.02%	7.77			14.65%
Total	79								
		Pseudop	rotella ph	asma	-	Ampithoe ramondi			
	df	MS	F	P	%CV	MS	F	P	%CV
Covariate = Leaf biomass	1	18.06	0.0821	0.7754	0%	37.21	2.0019	0.1674	3.75%
Time	1	259.49	0.7038	0.4774	0%	275.43	2.2711	0.2426	16.18%
Habitat	1	28.76	0.0433	0.6612	0%	24.28	0.7197	0.6800	0%
Locality(Habitat)	2	887.31	43.9170	0.0002	38.93%	41.30	3.5043	0.0382	9.44%
TimexHabitat	1	27.01	0.0995	0.7282	0%	168.45	1.7604	0.2983	17.77%
TimexLo(Habitat)	2	337.75	16.7170	0.0002	34.50%	117.89	10.0040	0.0006	26.21%
Residual	71	20.20			26.56%	11.79			26.66%
Total	79								
		Ischyroc	erus inex _l	pectatus		Apherusa	bispinosa	_	
	df	MS	F	P	%CV	MS	F	P	%CV
Covariate = Leaf biomass	1	80.94	0.4627	0.4382	0%	80.94	0.4627	0.4590	0%
Time	1	574.97	0.8736	0.4360	0%	574.97	0.8736	0.4336	0%
Habitat	1	789.99	1.6073	0.2470	14.13%	789.99	1.6073	0.2540	14.13%
Locality(Habitat)	2	649.69	19.8570	0.0002	24.76%	649.69	19.8570	0.0002	24.76%
TimexHabitat	1	369.51	0.7336	0.4693	0%	369.51	0.7336	0.4709	0%
TimexLo(Habitat)	2	628.32	19.2040	0.0002	35.63%	628.32	19.2040	0.0002	35.63%
Residual	71	32.72			25.49%	32.72			25.49%

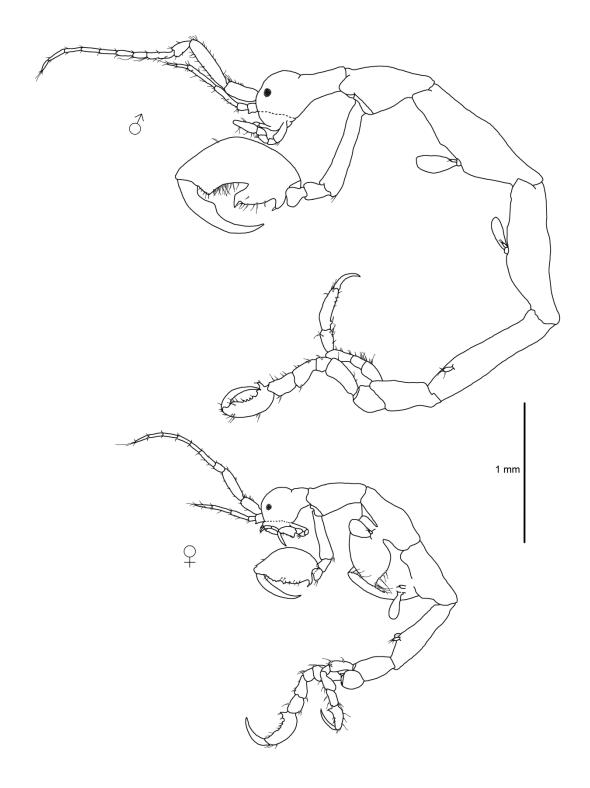


Figure 7. *Mantacaprella macaronensis* n. sp. Lateral view of holotype male (4.5 mm) and paratype female (2.7 mm). Scale bar: 1 mm.

4. Discussion

4.1. Overall epifaunal assemblage response

Our results have indicated clear differences in the multivariate structure, in terms of abundance and diversity (here quantified through the species density), of epifaunal assemblages between habitats dominated by the seagrass Cymodocea nodosa and the green seaweed Caulerpa prolifera, and patterns of differences have been consistently through times. Larger abundances and species densities were found, unexpectedly, in C. prolifera-dominated beds, since caulerpenyne seems to reduce macrophyte palatability and act as deterrent against some herbivore species (Erickson et al., 2006). In accordance with our results, previous studies have demonstrated that seabeds dominated by Caulerpa prolifera may particularly benefit crustacean assemblages (Sánchez-Moyano et al., 2007a), revealing the importance of this vegetated habitat for the maintenance of the biodiversity in coastal areas under considerable human impacts (Sánchez-Moyano et al., 2001b). A previous study conducted in the Canaries also recorded higher macrofaunal diversity in mixed bottoms of C. prolifera and C. nodosa than in mono-specific C. nodosa meadows (Monterroso et al., 2012). Differences in the structure, abundance and diversity of epifaunal assemblages may be due to changes in the structural complexity of the habitat (e.g. plant identity, plant morphology, floral and faunal epiphytes) (Virnstein and Howard, 1987; Taylor and Cole, 1994; Bologna, 1999), which plays an important role as space available for shelter against predators; but also due to changes in the hydrodynamic properties of the habitat. In the Mediterranean, Hendriks et al. (2010) demonstrated that, seasonally, Caulerpa species are able to attenuate water flow, trap particles and protect the sediment from erosion even better than seagrasses (particularly C. prolifera vs. C. nodosa), thus seabeds constituted by Caulerpa spp. might affect the associated fauna compared to seagrass meadows; favoring macrofaunal assemblages mainly dominated by crustaceans and polychaetes (Hendriks et al., 2010; Monterroso et al., 2012).

Differences within invertebrate assemblages are expected between different types (identities) of vegetation within the same geographical and environmental context (Sirota and Hovel, 2006). Low epifaunal abundances associated with C. nodosa meadows may be explained by space limitation, so the architecture of C. nodosa would be less important for fauna that are limited by space in comparison to other seagrasses, such as Posidonia sinuosa and Amphibolis griffithii, which have a higher leaf surface area and algal epiphyte biomass (Gartner et al., 2013). Epifaunal assemblages are also subjected to substrate competitive exclusion due to source limitation (Duffy and Harvilicz, 2001) and to fish predatory pressure. Seagrasses provide a paramount role as habitat for nearshore fish assemblages (Espino et al., 2011a). In the study region, C. nodosa meadows play a 'nursery' role for the early stages of numerous fish species (Espino et al., 2011a, 2011b). The abundance of fishes is ca. 3-4 times larger in C. nodosa than in C. prolifera dominated beds (unpublished data). Epifaunal organisms, particularly crustaceans, are the main constituent of diets of seagrass-associated fishes (Yamada et al., 2010; Horinouchi et al., 2012). Hence, it is worth noting that the contrasting abundance patterns of epifaunal and fish assemblages between C. nodosa and C. prolifera bottoms might fits a classical 'predation' model, where a large abundance of predators (here, fishes) remove large quantities of prey (here, epifauna) and so explain decreasing abundance of prey in such habitats (here, C. nodosa seagrass meadows) (Verdiell-Cubedo et al., 2007).

4.2. Amphipod assemblage response

The amphipod assemblage structure has significantly differed between habitats at both sampling times, showing a mean abundance of amphipods ca. 3 times larger in Caulerpa prolifera-dominated beds (1248.13 \pm 136.83 ind. m⁻², mean \pm SE) than in Cymodocea nodosa meadows (396.88 ± 77.36 ind. m⁻²). Our results of amphipods abundance do not agree, for example, with those reported by Vázquez-Luis et al. (2009) for the same habitats (313.89 \pm 75.63 ind. m⁻² in *C. prolifera* and 494.44 \pm 160.17 ind. m^{-2} in C. nodosa, mean \pm SE). Regarding the diversity of amphipods, in C. nodosa seagrass meadows at Gran Canaria we have recorded values of 16 amphipod species in November 2011 and 17 in October 2012, which are comparable or even lower than the number of amphipod species reported by several studies carried out in the Mediterranean Sea and the adjacent Atlantic coasts in C. nodosa meadows (28 species, Sánchez-Jerez et al., 1999; 13 species in September and 21 in March, Vázquez-Luis et al., 2009). On vegetated bottoms dominated by C. prolifera, a total of 27 and 20 amphipod species (in November 2011 and October 2012, respectively) were identified, which contrast with the 17 amphipod species recorded by Sánchez-Moyano et al. (2007) and values of 6 and 18 species reported by Vázquez-Luis et al. (2009) for the same habitat (in September and March, respectively). The variation within the total number of amphipod species among studies show a more diverse epifaunal community in C. prolifera-dominated beds at Gran Canaria.

Several authors have stated that amphipods are able to actively select their host habitat (Hay et al., 1990; Poore, 2005; Poore and Hill, 2006), a fact that is related to differences on vegetation palatability and food preferences by herbivores (Ortega et al., 2010). However, although the active selection appears important, it is not sufficient by itself to explain differential patterns of epifaunal distribution (Virnstein and Howard,

1987). The presence of diverse amphipods on plant species may result from ecological processes unrelated to herbivore preferences or the quality of that host for growth and survival, but from the variation in the risk of predation among hosts (Poore, 2005). As reported above, the susceptibility of amphipods to fish predation commonly varies across algal species, usually decreasing with increased structural complexity of the host or with the presence of secondary metabolites that are deterrent to omnivorous fish (Poore, 2005; Verdiell-Cubedo et al., 2007; Vázquez-Luis et al., 2010).

In the current study, some species seem to show a preference for specific habitats and, in overall, it is possible to distinguish gammarid species associated with C. prolifera-dominated beds, while caprellids are associated with C. nodosa meadows. Within gammarids, individuals belonging to the family Aoridae (here, Aora spinicornis and Microdeutopus stationis) have been exclusively found in C. prolifera-dominated beds. This outcome contrasts with previous records; for example, A. spinicornis has been found among hydroids, phanerogams and algae, and on sandy bottoms as well (Ruffo, 1982); whilst M. stationis has been almost exclusively found on fine sand, particularly among the phanerogams Cymodocea and Posidonia, with some records on coralligenous habitats (Ruffo, 1998). However, other authors found also larger abundances of *Microdeutopus* spp. in *Caulerpa* beds and on rocky habitats (Roberts and Poore, 2005; Vázquez-Luis et al., 2008, 2009), with preference for low hydrodynamic regimes and high sedimentation rates (Conradi et al., 1997; Guerra-García and García-Gómez, 2005). Other species significantly more abundant in C. prolifera-dominated beds was the free-living, herbivore Dexamine spinosa, which is very common within algal canopies within the shallow subtidal (Lincoln, 1979; Ruffo, 1982). Apherusa bispinosa and Ischyrocerus inexpectatus were also collected in higher abundance in C. prolifera-dominated beds. Consistent with our results, Farlin et al. (2010) reported that ischyrocerids, such as *I. inexpectatus*, tend to feed more on algae than on seagrasses. As the previous gammarids, *Ampithoe ramondi* was, again, more abundant in *C. prolifera*-dominated beds than in *C. nodosa* meadows, although differences were not so great. Ampithoids are, cosmopolitan, herbivorous amphipods, which usually occur in shallow subtidal zones amongst native seaweeds and seagrasses (Lincoln, 1979; Ruffo, 1982; Poore, 2005; Vázquez-Luis et al., 2008, 2009), tending to feed more on seagrasses (Farlin et al., 2010). The caprellid *Pseudoprotella phasma* has been mostly found inhabiting *C. nodosa* meadows, although this species might also be found among algae, but rarely associated with hydroids (Ruffo, 1993).

Finally, it is important to highlight the new genus, new species, of caprellid, *Mantacaprella macaronensis*, which show a clear preference on *C. nodosa* seagrass meadows, but also occurring in *C. prolifera*-dominated beds. This species was firstly recorded in Cape Verde, in natural rocky and artificial habitats (shipwrecks), in 2009; and together with the results of the current study, *M. macaronensis* has been recently described by Vázquez-Luis et al. (in revision). The relatively high abundances found in the Canary Islands and Cape Verde reflects the lack of detailed studies on benthic fauna in the region, namely on amphipods, and therefore this new species is expected to be also present in other islands of the Macaronesian region.

In conclusion, our study shows that *Caulerpa prolifera*-dominated beds have a more abundant and diverse epifaunal assemblage, which significantly differs from *Cymodocea nodosa* meadows and is temporally consistent. According to the biodiversity related to *Cymodocea nodosa* seagrass meadows, this study has been used as an important tool for the taxonomical and ecological description of the new genus, new species, of caprellid, since *Mantacaprella macaronensis* has resulted one of the dominant amphipods inhabiting these meadows. This reflects the lack of knowledge on

Macaronesian invertebrates, like amphipods, and the need of further taxonomical studies to better characterise the biodiversity of this region and to design adequate programmes of management and conservation.

Acknowledgements

This study was financially supported by the UE project "Changes in submerged vegetation: assessing how ecosystems services shift from frondose to depauperate systems dominated by opportunistic seaweeds (ECOSERVEG)". We acknowledge T. Sánchez and F. Espino for their help during fieldwork. Special thanks to J.M. Guerra-García and his team for their welcome at the Marine Biology's lab (Universidad de Sevilla).

References

- Anderson, M.J., 2001a. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32-46.
- Anderson, M.J., 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58, 626-639.
- Barberá, C., Tuya, F., Boyra, A., Sanchez-Jerez, P., Blanch, I., Haroun, R.J., 2005. Spatial variation in the structural parameters of *Cymodocea nodosa* seagrass meadows in the Canary Islands: A multiscaled approach. Botanica Marina 48, 122-126.
- Box, A., Sureda, A., Tauler, P., Terrados, J., Marbà, N., Pons, A., Deudero, S., 2010. Seasonality of caulerpenyne content in native *Caulerpa prolifera* and invasive *C. taxifolia* and *C. racemosa* var. *cylindracea* in the western Mediterranean Sea. Botanica Marina 53, 367-375.
- Brearley, A., Kendrick, A.J., Walker, D., 2008. How does burrowing by the isopod *Limnoria agrostisa* (Crustacea: *Limnoriidae*) affect the leaf canopy of the southern Australian seagrass *Amphibolis griffithii*? Marine Biology 156, 65-77.

- Conradi, M., López-González, P.J., García-Gómez, C., 1997. The amphipod community as a bioindicator in Algeciras Bay (Southern Iberian Peninsula) based on a spatiotemporal distribution. Marine Ecology 18 (2), 97-111.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.
- Duarte, C.M., 2000. Marine biodiversity and ecosystem services: An elusive link. Journal of Experimental Marine Biology and Ecology 250, 117-131.
- Duarte, C.M., 2002. The future of seagrass meadows. Environmental Conservation 29 (2), 192-206.
- Duffy, J.E., Hay, M.E., 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs 70, 237-263.
- Duffy, J.E., Harvilicz, A.M., 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. Marine Ecology Progress Series 223, 201-211.
- Duffy, J.E., 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology Progress Series 311, 233-250.
- Erickson, A.A., Paul, V.J., Van Alstyne, K.L., Kwiatkowski, L.M., 2006. Palatability of macroalgae that use different types of chemical defenses. Journal of Chemical Ecology 32, 1883-1895.
- Espino, F., Tuya, F., Brito, A., Haroun, R., 2011a. Ichthyofauna associated with *Cymodocea nodosa* meadows in the Canarian Archipelago (central eastern Atlantic): Community structure and nursery role. Ciencias Marinas 37 (2), 157-174.
- Espino, F., Tuya, F., Brito, A., Haroun, R., 2011b. Variabilidad espacial en la estructura de la ictiofauna asociada a praderas de *Cymodocea nodosa* en las Islas Canarias, Atlántico nororiental subtropical. Revista de Biología Marina y Oceanografía 46 (3), 391-403.
- Farlin, J.P., Lewis, L.S., Anderson, T.W., Lai, C.T., 2010. Functional diversity in amphipods revealed by stable isotopes in an eelgrass ecosystem. Marine Ecology Progress Series 420, 277-281.
- Gartner, A., Tuya, F., Lavery, P.S., McMahon, K., 2013. Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. Journal of Experimental Marine Biology and Ecology 439, 143-151.
- Guerra-García, J.M., García-Gómez, J.C., 2005. Assessing pollution levels in sediments of a harbour with two opposing entrances. Environmental implications. Journal of Environmental Management 77, 1-11.

- Harlin, M.M., 1980. Seagrass Epiphytes. In: McRoy, P., Phillips, R. (Eds.), Handbook of Seagrass Biology: An ecosystem perspective. Garland STPM Press, New York, pp. 117-151.
- Haroun, R., Gil-Rodríguez, M.C., Wildpret de la Torre, W., 2003. Plantas Marinas de las Islas Canarias. Canseco Editores, 319 p.
- Hay, M.E., Duffy, J.E., Fenical, W., 1990. Host-plant specialization decreases predation on a marine amphipod: An herbivore in plant's clothing. Ecology 71 (2), 733-743.
- Hendriks, I.E., Bouma, T.J., Morris, E.P., Duarte, C.M., 2010. Effects of seagrasses and algae of the *Caulerpa* family on hydrodynamics and particle-trapping rates. Marine Biology 157, 473-481.
- Horinouchi, M., Tongnunui, P., Furumitsu, K., Nakamura, Y., Kanou, K., Yamaguchi, A., Okamoto, K., Sano, M., 2012. Food habits of small fishes in seagrass habitats in Trang, southern Thailand. Fisheries Science 78, 577-587.
- Hughes, A.R., Williams, S.L., Duarte, C.M., Heck, K.L., Waycott, M., 2009. Associations of concern: Declining seagrasses and threatened dependent species. Frontiers in Ecology and the Environment 7 (5), 242-246.
- Jung, V., Thibaut, T., Meinesz, A., Pohnert, G. (2002). Comparison of the wound-activated transformation of caulerpenyne by invasive and noninvasive *Caulerpa* species of the Mediterranean. Journal of Chemical Ecology 28 (10), 2091–2105.
- Lincoln, R.J., 1979. British Marine Amphipoda: Gammaridea. British Museum (Natural History), 671 p.
- Martínez-Samper, J., 2011. Análisis espacio-temporal de las praderas de *Cymodocea nodosa* (Ucria) Ascherson en la isla de Gran Canaria. Master thesis, Universidad de Las Palmas de Gran Canaria.
- Meinesz, A., 1999. From the discovery of the Alga in Monaco to its arrival in France. In: Meinesz, A. (Eds.), Killer Algae. The University of Chicago Press, Chicago, pp. 1-22.
- Monterroso, O., Riera, R., Núñez, J., 2012. Subtidal soft-bottom macroinvertebrate communities of the Canary Islands. An ecological approach. Brazilian Journal of Oceanography 60 (1), 1-9.
- Ortega, I., Díaz, Y.J., Martín, A., 2010. Feeding rates and food preferences of the amphipods present on macroalgae *Ulva* sp. and *Padina* sp. Zoologica baetica 21, 45-53.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck Jr., K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S., 2006. A global crisis for seagrass ecosystems. BioScience 56 (12), 987-996.

- Pavón-Salas, N., Herrera, R., Hernández-Guerra, A., Haroun, R., 2000. Distributional pattern of seagrasses in the Canary Islands (Central-East Atlantic Ocean). Journal of Coastal Research 16 (2), 329-335.
- Poore, A.G.B., 2005. Scales of dispersal among hosts in a herbivorous marine amphipod. Austral Ecology 30, 219-228.
- Poore, A.G.B., Hill, N.A., 2006. Sources of variation in herbivore preference: among-individual and past diet effects on amphipod hosts choice. Marine Biology 149, 1403-1410.
- Reyes, J., Sansón, M., Afonso-Carrillo, J., 1995. Distribution and reproductive phenology of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Canary Islands. Aquatic Botany 50, 171-180.
- Roberts, D.A., Poore, A.G.B., 2005. Habitat configuration affects colonization of epifauna in a marine algal bed. Biological Conservation 127, 18-26.
- Ruffo, S., 1982. The Amphipoda of the Mediterranean. Part 1: Gammaridea (Acanthonotozomatidae to Gammaridae). Mémoires de l'Institut Océanographique, Monaco 13, 364 p.
- Ruffo, S., 1989. The Amphipoda of the Mediterranean. Part 2: Gammaridea (Haustoriidae to Lysianassidae). Mémoires de l'Institut Océanographique, Monaco 13, 221 p.
- Ruffo, S., 1993. The Amphipoda of the Mediterranean. Part 3: Gammaridea (Melphidippidae to Talitridae), Ingolfiellidea, Caprellidea. Mémoires de l'Institut Océanographique, Monaco 13, 242 p.
- Ruffo, S., 1998. The Amphipoda of the Mediterranean. Part 4. Mémoires de l'Institut Océanographique, Monaco 13, 150 p.
- Sánchez-Jerez, P., Barberá Cebrián, C., Ramos Esplá, A.A., 1999. Comparison of the epifauna spatial distribution in *Posidonia oceanica*, *Cymodocea nodosa* and unvegetated bottoms: Importance of meadow edges. Acta Oecologica, 20 (4), 391-405.
- Sánchez-Jerez, P., Barberá-Cebrián, C., Ramos-Esplá, A.A., 2000. Influence of the structure of *Posidonia oceanica* meadows modified by bottom trawling on crustacean assemblages: Comparison of amphipods and decapods. Scientia Marina 64 (3), 319-326.
- Sánchez-Moyano, J.E., Estacio, F.J., García-Adiego, E.M., García-Gómez, J.C., 2001a. Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna. Aquatic Botany 70, 163-174.
- Sánchez-Moyano, J.E., García-Adiego, E.M., Estacio, F.J., García-Gómez, J.C., 2001b. Influence of the density of *Caulerpa prolifera* (Chlorophyta) on the composition of

- the macrofauna in a meadow in Algerias Bay (Southern Spain). Ciencias Marinas 27 (1), 47-71.
- Sánchez-Moyano, J.E., García-Asencio, I., García-Gómez, J.C., 2007. Effects of temporal variation of the seaweed *Caulerpa prolifera* cover on the associated crustacean community. Marine Ecology 28, 324-337.
- Sirota, L., Hovel, K.A., 2006. Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA. Marine Ecology Progress Series 326, 115-131.
- Smyrniotopoulos, V., Abatis, D., Tziveleka, L-A., Tsitsimpikou, C., Roussis, V., Loukis, A., Vagias, C., 2003. Acetylene sesquiterpenoid esters from the green alga *Caulerpa prolifera*. Journal of Natural Products 66, 21-24.
- Taylor, R.B., Cole, R.G., 1994. Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. Marine Ecology Progress Series 115, 271-282.
- Thomsen, M.S., Wernberg, T., Engelen, A.H., Tuya, F., Vanderklift, M.A. et al., 2012. A meta-analysis of seaweed impacts on seagrasses: Generalities and knowledge gaps. PloS ONE 7(1): e28595.
- Tuya, F., Martín, J.A., Luque, A., 2006. Seasonal cycle of a *Cymodocea nodosa* seagrass meadow and of the associated ichthyofauna at Playa Dorada (Lanzarote, Canary Islands, eastern Atlantic). Ciencias Marinas 32 (4), 695-704.
- Tuya, F., Hernandez-Zerpa, H., Espino, F., Haroun, R., 2013. Drastic decadal decline of the seagrass *Cymodocea nodosa* at Gran Canaria (eastern Atlantic): Interactions with the green algae *Caulerpa prolifera*. Aquatic Botany 105, 1-6.
- Vázquez-Luis, M., Sanchez-Jerez, P., Bayle-Sempere, J.T., 2008. Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea. Marine Environmental Research 65, 416-426.
- Vázquez-Luis, M., Sanchez-Jerez, P., Bayle-Sempere, J.T., 2009. Comparison between amphipod assemblages associated with *Caulerpa racemosa* var. *cylindracea* and those of other Mediterranean habitats on soft substrate. Estuarine, Coastal and Shelf Science 84, 161-170.
- Vázquez-Luis, M., Sanchez-Jerez, P., Bayle-Sempere, J.T., 2010. Effects of *Caulerpa racemosa* var. *cylindracea* on prey availability: an experimental approach to predation of amphipods by *Thalassoma pavo* (Labridae). Hydrobiologia 654, 147-154.
- Vázquez-Luis, M., Guerra-García, J.M., Carvalho, S., Png-Gonzalez, L., 2013. A new genus and species of Caprellidae (Crustacea: Amphipoda) from Canary Islands and Cape Verde. Zootaxa (*in revision*)

- Verdiell-Cubedo, D., Oliva-Paterna, F.J., Torralva-Forero, M., 2007. Fish assemblages associated with *Cymodocea nodosa* and *Caulerpa prolifera* meadows in the shallow areas of the Mar Menos coastal lagoon. Limnetica 26 (2), 341-350.
- Virnstein, R.W., Howard, R.K., 1987. Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. II. Comparisons between drift algae and three species of seagrasses. Bulletin of Marine Science 41 (1), 13-26.
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck Jr., K.L., Hughes, A.R., Kendrick, G., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. PNAS 106, 12377-12381.
- Yamada, K., Hori, M., Tanaka, Y., Hasegawa, N., Nakaoka, M., 2010. Contribution of different functional groups to the diet of major predatory fishes at a seagrass meadow in northeastern Japan. Estuarine, Coastal and Shelf Science 86, 71-82.

Appendix 1. Abundances (ind. per m-2 \pm SE) of epifaunal organisms at each habitat and time. The total abundance and number of species are also included.

			Novem	ber 2011	Octol	ber 2012
Functional group	Group	Species	C. nodosa	C. prolifera	C. nodosa	C. prolifera
Worms	Nematoda	Calyptronema sp.	-	11.25 ± 6.57	-	-
Worms	Nematoda	Enoplida sp. 1	-	13.75 ± 7.74	-	-
Worms	Nematoda	Unidentified	-	-	-	3.75 ± 3.75
Worms	Oligochaeta	Unidentified	-	-	-	-
Worms	Polychaeta	Aponuphis bilineata	-	1.25 ± 1.25	-	-
Worms	Polychaeta	Platynereis dumerilii	-	2.5 ± 1.44	-	21.25 ± 12.31
Worms	Polychaeta	Nereididae sp. 1	-	11.25 ± 5.54	-	-
Worms	Polychaeta	Exogone naidina	-	2.5 ± 1.44	-	-
Worms	Polychaeta	Salvatoria sp.	1.25 ± 1.25	-	-	1.25 ± 1.25
Worms	Polychaeta	Streptosyllis bidentata	5 ± 2.89	-	-	-
Worms	Polychaeta	Syllis sp.	6.25 ± 4.73	-	-	-
Worms	Polychaeta	Demonax brachychona	-	6.25 ± 6.25	-	-
Worms	Polychaeta	Desdemona sp.	-	2.5 ± 1.44	-	-
Worms	Polychaeta	Sabellidae sp. 1	-	1.25 ± 1.25	-	-
Worms	Polychaeta	Aonides oxycephala	-	1.25 ± 1.25	-	-
Worms	Polychaeta	Polyophthalmus pictus	2.5 ± 2.5	76.25 ± 42.79	-	-
Worms	Polychaeta	Schroederella laubieri	-	1.25 ± 1.25	-	-
Worms	Sipunculidea	sp. 1	-	-	-	-
Other fauna	Pycnogonida	Unidentified	27.5 ± 14.79	-	10 ± 5.4	48.75 ± 14.34
Other fauna	Actinopterygii	Opeatogenys cadenati	-	-	1.25 ± 1.25	-
Other fauna	Asteroidea	Coscinasterias tenuispina	-	2.5 ± 2.5	-	-
Other fauna	Ophiuroidea	Unidentified	-	1.25 ± 1.25	1.25 ± 1.25	90 ± 54.04
Crustacea	Copepoda	Unidentified	-	1.25 ± 1.25	15 ± 7.36	50 ± 35.18
Crustacea	Cumacea	Unidentified	2.5 ± 2.5	7.5 ± 4.79	-	6.25 ± 3.75
Crustacea	Decapoda	Caridea	2.5 ± 2.5	13.75 ± 5.91	-	217.5 ± 132.83
Crustacea	Decapoda	Galatheoidea	-	-	-	13.75 ± 10.68
Crustacea	Decapoda	Paguroidea	-	15 ± 4.56	-	95 ± 25.41

			Novemb	ber 2011	Octob	er 2012
Functional group	Group	Species	C. nodosa	C. prolifera	C. nodosa	C. prolifera
Crustacea	Decapoda	Brachyura	2.5 ± 1.44	11.25 ± 5.54	1.25 ± 1.25	21.25 ± 9.44
Crustacea	Decapoda	Larva	-	2.5 ± 1.44	-	3.75 ± 2.39
Crustacea	Isopoda	sp. 1	1.25 ± 1.25	-	221.25 ± 106.29	2.5 ± 1.44
Crustacea	Isopoda	sp. 2	18.75 ± 11.25	3.75 ± 3.75	11.25 ± 8.0	=
Crustacea	Isopoda	sp. 3	6.25 ± 6.25	-	5 ± 3.54	17.5 ± 10.9
Crustacea	Isopoda	sp. 4	-	6.25 ± 3.75	1.25 ± 1.25	10 ± 3.54
Crustacea	Isopoda	sp. 5	-	1.25 ± 1.25	-	6.25 ± 3.75
Crustacea	Isopoda	sp. 6	-	-	1.25 ± 1.25	1.25 ± 1.25
Crustacea	Tanaidacea	Apseudes sp.	-	-	-	-
Crustacea	Tanaidacea	Apseudes talpa	-	-	=	5 ± 3.54
Crustacea	Tanaidacea	Leptochelia savignyi	-	-	=	338.75 ± 148.32
Crustacea	Tanaidacea	Tanais dulongii	=	-	1.25 ± 1.25	1.25 ± 1.25
Crustacea	Tanaidacea	Zeuxo exsargasso	-	-	-	-
Crustacea	Tanaidacea	Unidentified	-	-	-	1.25 ± 1.25
Crustacea	Ostracoda	Halocyprida	-	-	-	1.25 ± 1.25
Crustacea	Ostracoda	Myodocopida	-	26.25 ± 13.6	=	7.5 ± 4.79
Crustacea	Ostracoda	Podocopida	1.25 ± 1.25	18.75 ± 5.54	1.25 ± 1.25	-
Crustacea	Amphipoda	Caprella acanthifera	-	-	21.25 ± 6.25	1.25 ± 1.25
Crustacea	Amphipoda	Caprella liparotensis	58.75 ± 34.3	-	=	=
Crustacea	Amphipoda	Phtisica marina	23.75 ± 3.15	41.25 ± 24.86	17.5 ± 4.33	45 ± 19.04
Crustacea	Amphipoda	Pseudoprotella phasma	181.25 ± 107.25	108.75 ± 79.38	27.5 ± 9.46	36.25 ± 5.54
Crustacea	Amphipoda	Mantacaprella macaronensis	235 ± 125.62	6.25 ± 3.75	27.5 ± 7.77	2.5 ± 1.44
Crustacea	Amphipoda	Ericthonius punctatus	33.75 ± 15.99	97.5 ± 67.78	1.25 ± 1.25	-
Crustacea	Amphipoda	Ischyrocerus inexpectatus	1.25 ± 1.25	352.5 ± 307.61	-	-
Crustacea	Amphipoda	Microjassa cumbrensis	-	23.75 ± 16.5	-	-
Crustacea	Amphipoda	Ampithoe helleri	5 ± 3.54	-	-	1.25 ± 1.25
Crustacea	Amphipoda	Ampithoe ramondi	23.75 ± 14.05	32.5 ± 23.14	48.75 ± 19.83	122.5 ± 42.7
Crustacea	Amphipoda	Ampithoe sp.	3.75 ± 3.75	-	2.5 ± 2.5	-
Crustacea	Amphipoda	Aora gracilis	-	-	13.75 ± 8.0	-
Crustacea	Amphipoda	Aora spinicornis	-	231.25 ± 113.53	-	41.25 ± 34.72
Crustacea	Amphipoda	Aora sp.	-	-	5 ± 2.04	7.5 ± 7.5

			Novem	ber 2011	October 2012		
Functional group	Group	Species	C. nodosa	C. prolifera	C. nodosa	C. prolifera	
Crustacea	Amphipoda	Autonoe longipes	-	1.25 ± 1.25	-	-	
Crustacea	Amphipoda	Microdeutopus anomalus	-	-	-	62.5 ± 38.11	
Crustacea	Amphipoda	Microdeutopus damnoniensis	-	12.5 ± 10.9	-	-	
Crustacea	Amphipoda	Microdeutopus stationis	-	465 ± 235.27	-	63.75 ± 41.6	
Crustacea	Amphipoda	Microdeutopus sp.	3.75 ± 3.75	6.25 ± 6.25	=	7.5 ± 3.23	
Crustacea	Amphipoda	Cheiriphotis sp.	-	6.25 ± 6.25	=	-	
Crustacea	Amphipoda	Corophium sp.	-	2.5 ± 2.5	=	-	
Crustacea	Amphipoda	Leptocheirus mariae	-	-	-	2.5 ± 2.5	
Crustacea	Amphipoda	Leptocheirus pilosus	-	48.75 ± 45.48	1.25 ± 1.25	1.25 ± 1.25	
Crustacea	Amphipoda	Leptocheirus sp.	-	8.75 ± 8.75	-	-	
Crustacea	Amphipoda	Medicorophium minimum	-	1.25 ± 1.25	-	-	
Crustacea	Amphipoda	Apherusa bispinosa	-	-	1.25 ± 1.25	46.25 ± 6.57	
Crustacea	Amphipoda	Apherusa chiereghinii	2.5 ± 1.44	85 ± 48.95	-	10 ± 5.77	
Crustacea	Amphipoda	Apherusa vexatrix	8.75 ± 7.18	2.5 ± 2.5	-	-	
Crustacea	Amphipoda	Apherusa sp.	1.25 ± 1.25	1.25 ± 1.25	-	-	
Crustacea	Amphipoda	Lysianassina longicornis	-	-	-	21.25 ± 16.38	
Crustacea	Amphipoda	Amphilochus neapolitanus	3.75 ± 3.75	2.5 ± 2.5	-	1.25 ± 1.25	
Crustacea	Amphipoda	Peltocoxa mediterranea	-	-	-	1.25 ± 1.25	
Crustacea	Amphipoda	Dexamine spinosa	10 ± 6.12	55 ± 16.2	10 ± 4.56	355 ± 96.46	
Crustacea	Amphipoda	Liljeborgia sp.	-	6.25 ± 4.73	-	1.25 ± 1.25	
Crustacea	Amphipoda	Elasmopus sp.	-	1.25 ± 1.25	-	-	
Crustacea	Amphipoda	Maera inaequipes	-	1.25 ± 1.25	-	-	
Crustacea	Amphipoda	Harpinia sp.	-	7.5 ± 4.33	-	2.5 ± 2.5	
Crustacea	Amphipoda	Stenothoe monoculoides	11.25 ± 7.18	-	3.75 ± 2.39	-	
Crustacea	Amphipoda	Pereionotus testudo	1.25 ± 1.25	-	-	-	
Crustacea	Amphipoda	Microprotopus longimanus	-	35 ± 23.63	-	-	
Crustacea	Amphipoda	Unidentified	-	3.75 ± 3.75	3.75 ± 2.39	16.25 ± 7.47	
Mollusca	Bivalvia	Cardiidae sp. 1	-	6.25 ± 3.75	-	-	
Mollusca	Bivalvia	Unidentified1	-	10 ± 5.4	3.75 ± 3.75	10 ± 2.04	
Mollusca	Bivalvia	Unidentified2	-	3.75 ± 1.25	1.25 ± 1.25	12.5 ± 4.33	
Mollusca	Gastropoda	Bittium sp.	3.75 ± 3.75	1.25 ± 1.25	-	190 ± 84.29	

			Novemb	er 2011	Octob	er 2012
Functional group	Group	Species	C. nodosa	C. prolifera	C. nodosa	C. prolifera
Mollusca	Gastropoda	Eulimidae sp. 1	-	-	-	2.5 ± 1.44
Mollusca	Gastropoda	Cerithiopsis sp.	-	-	1.25 ± 1.25	6.25 ± 4.73
Mollusca	Gastropoda	Nystiellidae sp. 1	8.75 ± 5.91	1.25 ± 1.25	-	-
Mollusca	Gastropoda	Alvania sp.	43.75 ± 25.2	-	6.25 ± 4.73	257.5 ± 91.3
Mollusca	Gastropoda	Rissoinae sp. 1	-	-	16.25 ± 7.18	177.5 ± 44.37
Mollusca	Gastropoda	Anachis sp.	-	1.25 ± 1.25	-	-
Mollusca	Gastropoda	Mitrella sp.	2.5 ± 1.44	33.75 ± 11.61	-	1.25 ± 1.25
Mollusca	Gastropoda	Vexillum zebrinum	11.25 ± 8.26	5 ± 3.54	-	-
Mollusca	Gastropoda	Volvarina sp.	-	-	1.25 ± 1.25	1.25 ± 1.25
Mollusca	Gastropoda	Pyramidella dolabrata	-	-	1.25 ± 1.25	-
Mollusca	Gastropoda	Retusidae sp. 1	10 ± 6.12	11.25 ± 6.57	1.25 ± 1.25	77.5 ± 39.82
Mollusca	Gastropoda	Nudibranchia	-	1.25 ± 1.25	-	-
Mollusca	Gastropoda	Smaragdia viridis	-	8.75 ± 2.39	10 ± 2.04	1.25 ± 1.25
Mollusca	Gastropoda	Tricolia sp.	-	-	13.75 ± 4.73	7.5 ± 4.79
Mollusca	Gastropoda	Trochidae sp. 1	-	1.25 ± 1.25	-	-
Mollusca	Gastropoda	Turbinidae sp. 1	2.5 ± 1.44	-	1.25 ± 1.25	1.25 ± 1.25
Total abundance	•	-	768.75 ± 397.01	1975 ± 338.83	513.75 ± 196.1	2561.25 ± 769.91
Total number of sp	ecies		36	65	37	58