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

LYDIA PNG-GONZALEZ[1], MAITE VÁZQUEZ-LUIS[2] AND FERNANDO TUYA[1]

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

Epifaunal invertebrates are sensitive to changes in the identity of the dominant host plant, so assessing differences in the structure of epifaunal assemblages is particularly pertinent in areas where seagrasses have been replaced by alternative vegetation (e.g. green seaweeds).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, particularly amphipods, between meadows dominated by the seagrass Cymodocea nodosa *and the green rhizophytic algae* Caulerpa prolifera *on shallow soft bottoms of Gran Canaria Island, determining whether patterns were temporally consistent between two times. The epifaunal assemblage structure (abundance and composition) consistently differed between both plants, those assemblages associated with* C. prolifera*-dominated beds being more diverse and abundant relative to* C. nodosa *meadows. Amphipods constituted ~70% of total crustaceans for the overall study, including 37 species belonging to 16 families. The amphipod abundance was ~3 times larger in* C. prolifera*-dominated beds than in* C. nodosa *meadows. We detected species-specific affinities; for example,* Microdeutopus stationis, Dexamine spinosa, Aora spinicornis, Ischyrocerus inexpectatus *and* Apherusa bispinosa *were more abundant in* C. prolifera*-dominated beds; while the caprellid* Mantacaprella macaronensis *dominated in* C. nodosa *meadows. However, some species, such as* Pseudoprotella phasma *and* Ampithoe ramondi, *were found in both habitats with varying abundances between times.*

Keywords: Amphipoda, epifauna, assemblage structure, ecosystem function, seagrass, Canary Islands

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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; Tuya *et al.*, 2013a). 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). At a global scale, the progressive disappearance of seagrasses has been concurrently accompanied by increases in the presence of opportunistic vegetation, such as green rhizophytic seaweeds (Thomsen *et al.*, 2012).

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 Canary Islands (Reyes *et al.*, 1995; Tuya *et al.*, 2013a). Meadows constituted by *C. nodosa* are the dominant vegetated communities on shallow soft substrates across 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, b). However, *C. nodosa* meadows are severely decreasing at local scales, mostly as a result of a range of human-mediated impacts (Martínez-Samper, 2011; Tuya *et al.*, 2013a). In these coastal areas, the decline of *C. nodosa* meadows often results in their replacement by opportunistic green algae of the genus *Caulerpa*, in particular *Caulerpa prolifera* (Forsskål) J.V. Lamouroux (Martínez-Samper, 2011; Tuya *et al.*, 2013a).

Caulerpa prolifera is a native seaweed in the Canary Islands (Haroun *et al.*, 2003), forming extensive beds on soft bottoms in waters from ~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

Corresponding author:
Lydia Png-Gonzalez
Email: lydiapng@gmail.com

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; Tuya *et al.*, 2013b). 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 and so on), so differences in the diversity, abundance and structure of invertebrate assemblages are expected between different types of vegetation within the same geographical and environmental context (Sirota & Hovel, 2006). In this sense, amphipods respond to habitat alterations and can, therefore, be used as an indicator of environmental impacts on vegetated habitats (Virnstein & Howard, 1987; Conradi *et al.*, 1997; Sánchez-Jerez *et al.*, 2000; Vázquez-Luis *et al.*, 2008, 2009).

The aim of this study was to compare the diversity, abundance and structure of epifaunal assemblages between meadows dominated by the seagrass *Cymodocea nodosa* and the seaweed *Caulerpa prolifera* on shallow soft bottoms off Gran Canaria Island, determining whether patterns were temporally consistent. Particular emphasis was concentrated on amphipods, since amphipods are one of the most quantitatively abundant and important groups of invertebrates associated with coastal vegetated habitats, while they also play an important role as trophic resources for fish populations (Sánchez-Jerez *et al.*, 1999; Vázquez-Luis *et al.*, 2009).

MATERIALS AND METHODS

Study area and sampling design

The study was carried out in Gran Canaria (Canary Islands, eastern Atlantic), at several localities (Figure 1) dominated by either subtidal mono-specific *Cymodocea nodosa* meadows or beds constituted by *Caulerpa prolifera*. Each habitat (*Cymodocea nodosa* vs *Caulerpa prolifera*-dominated beds) was randomly sampled at each of two localities, where ten replicates were collected by SCUBA divers, using a 20 × 20 cm quadrat. Macrophytes collections were performed cutting the seagrass/seaweed immediately above the sediment surface, keeping the vegetation with the associated epifauna inside unbleached woven cotton bags (Brearley *et al.*, 2008; Gartner *et al.*, 2013). Sampling was repeated twice (November 2011 and October 2012) to assess whether patterns in the diversity, abundance and structure of epifaunal assemblages between beds dominated by *Cymodocea nodosa* and *Caulerpa prolifera* were temporally consistent.

Labelled samples were preserved in a freezer (−20°C) until processing. 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 dominant groups: Crustacea, Mollusca, worms (including Annelida and Sipuncula) and other fauna (Chelicerata, Chordata and Echinodermata) were considered. Organisms were identified to the lowest possible taxonomic level and amphipods were identified to species, in most cases. The amount of vegetated biomass (expressed as grammes wet weight per 0.04 m^2) was obtained for each replicate to account for differences in the amount of habitat (vegetation) among samples. Amphipod structure was characterized using two attributes: abundance (expressed as ind m^{-2}) and species density (expressed as number of species per 0.04 m^2).

Statistical analysis

UNIVARIATE ANALYSIS

Differences in the abundance and species density of the dominant groups (here, Crustacea, Mollusca, Amphipoda, worms and other fauna) between habitats, localities within habitats and times, were tested using a three-way, permutation-based, ANCOVA, which incorporated the factors: 'Habitat' (fixed factor with two levels: *Cymodocea nodosa* vs *Caulerpa prolifera*), 'Locality' (random factor and nested within 'Habitat', 2 levels: L1 and L2), and 'Time' (fixed factor with 2 levels: November 2011 vs October 2012). 'Vegetation 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 analysis, and analyses were based on Euclidean distances (Anderson, 2001a). The significance of *P* values was determined through 4999 permutations of the raw data. 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.

MULTIVARIATE ANALYSIS

Differences in the multivariate structure (which includes the composition and abundance) of assemblages between habitats

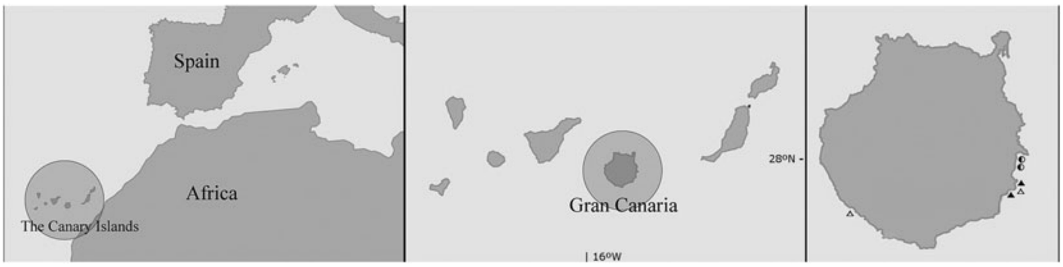

Fig. 1. Map of the study area showing the sampled localities at Gran Canaria. Triangles, *Cymodocea nodosa* meadows; circles, *Caulerpa prolifera*-dominated beds; filled symbols, November 2011; open symbols, October 2012.

(*Cymodocea nodosa* vs *Caulerpa prolifera*) were visualized through a non-metric multidimensional scaling (nm-MDS) ordination plot. The significance of these multivariate differences were tested by a three-way PERMANOVA (Anderson, 2001b), using 'Time', 'Habitat' and 'Locality' as factors, following the same design outlined above. The vegetation biomass of each replicate was, again, included as a covariate. Data were square-root transformed prior to analysis to downweight the relevance of the most abundant taxa and analyses were based on Bray–Curtis similarities. The individual contribution of each amphipod species to the dissimilarity between habitats was calculated by the SIMPER routine. All uni- and multivariate procedures were carried out by means of the PRIMER 6.0 & PERMANOVA statistical package.

RESULTS

Epifaunal assemblages

A total of 4655 epifaunal individuals, belonging to 105 taxa (Appendix), were counted, including crustaceans (3594 individuals), molluscs (777), worms (138) and other fauna (146). The abundance of crustaceans, which proved to be the dominant group (accounting for 77.2% of the total epifaunal abundance), was significantly larger in *Caulerpa prolifera*-dominated beds (1792.5 ± 181.18 ind m^{-2}, mean ± SE) than in *Cymodocea nodosa* meadows (562.5 ± 81.92 ind m^{-2}) at both sampling times (Figure 2; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 1). The species density of crustaceans was also larger in *C. prolifera*-dominated beds than in *Cymodocea nodosa* meadows (12.03 ± 0.52 vs 5.8 ± 0.47 spp. 0.04 m^{-2}, respectively) (Figure 3; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 1). The abundance of molluscs was, again, significantly larger in *Caulerpa prolifera*-dominated beds (415.63 ± 71.4 ind m^{-2}) than in *Cymodocea nodosa* meadows (70 ± 15.14 ind m^{-2}) (Figure 2; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 1), as well as the species density of molluscs (3.45 ± 0.23 vs 1.6 ± 0.2 spp. 0.04 m^{-2}, respectively) (Figure 3; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 1). Minor epifaunal fractions, such as worms, showed a different pattern between sampling times, but their abundance and species density were, on average, larger in *Caulerpa prolifera*-dominated beds (80 ± 16.32 ind m^{-2} and 1.33 ± 0.09 spp. 0.04 m^{-2}, respectively) than in *Cymodocea nodosa* meadows (26.25 ± 6.39 ind m^{-2} and 0.65 ± 0.07 spp. 0.04 m^{-2}) (Figures 2 and 3; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 1). Finally, other fauna was more abundant in *Caulerpa prolifera*-dominated beds (70 ± 20.16 ind m^{-2}) than in *Cymodocea nodosa* meadows (19.38 ± 5.02 ind m^{-2}), but without significant differences (Figure 2; three-way ANCOVA: 'Habitat', $P = 0.6590$, Table 1). The species density of other fauna

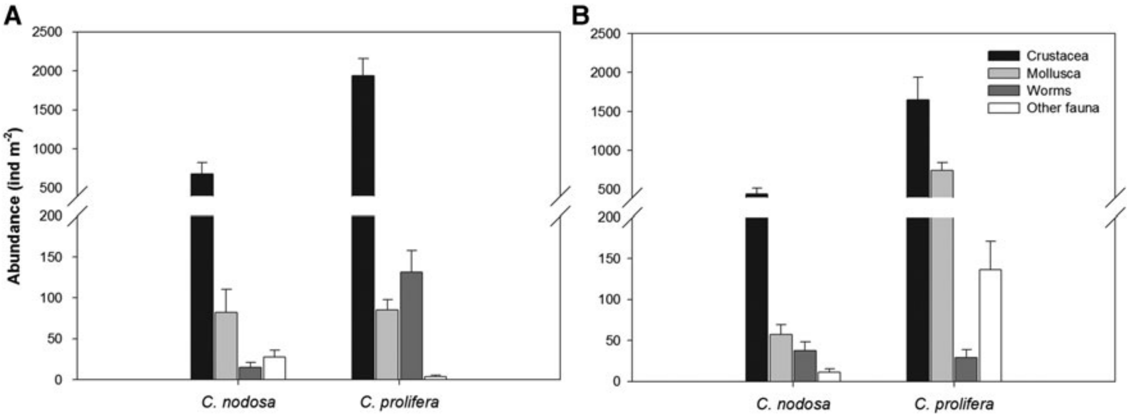

Fig. 2. Mean abundance (ind m^{-2} ±SE) of the four dominant epifaunal groups at each habitat in (A) November 2011 and (B) October 2012.

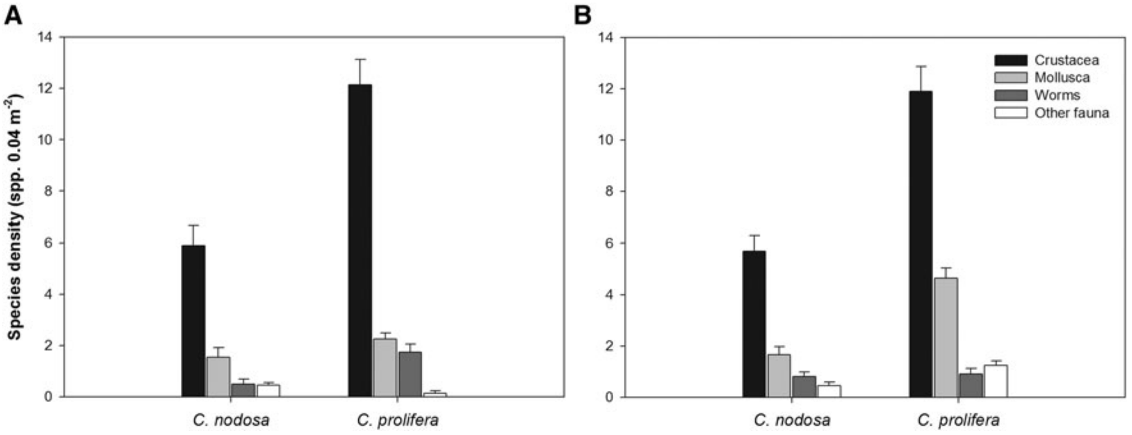

Fig. 3. Mean species density (number of species ±SE) of the four dominant epifaunal groups at each habitat in (A) November 2011 and (B) October 2012.

Table 1. Results of three-way ANCOVAs testing for differences between habitats, times and localities within habitats, for the abundance and species density of each dominant epifaunal group.

Crustacea		**Abundance**				**Species density**			
	df	**MS**	**F**	***P***	**% VC**	**MS**	**F**	***P***	**% VC**
Covariate = vegetation 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
Ti × Ha	1	80.91	0.0617	0.8100	0	0.60	0.2138	0.6791	0
Ti × Lo (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									
Covariate = vegetation biomass	1	386.81	3.3939	0.0762	4.79	0.97	0.7060	0.3910	0
Time	1	2262.20	7.8276	0.1048	19.32	4.94	4.4910	0.1550	14.54
Habitat	1	1292.50	3.9539	0.0002*	14.79	8.75	2.1964	0.0002*	17.71
Locality (Ha)	2	433.26	23.6670	0.0002	11.82	5.29	26.3780	0.0002	22.31
Ti × Ha	1	1472.90	6.7506	0.1099	24.65	2.03	2.6053	0.2347	13.26
Ti × Lo (Ha)	2	271.08	14.8070	0.0002	13.52	0.93	4.6486	0.0108	12.39
Residual	71	18.31			11.10	0.20			19.79
Total	79								
Worms									
Covariate = vegetation biomass	1	8.46	0.3701	0.5430	0	0.04	0.1204	0.7252	0
Time	1	53.98	0.3520	0.5856	0	0.09	0.0520	0.8190	0
Habitat	1	310.50	8.6372	0.0002*	20.06	3.74	9.7138	0.0002*	24.00
Locality (Ha)	2	42.50	2.5050	0.0854	7.46	0.39	1.1012	0.3414	3.04
Ti × Ha	1	254.03	2.0613	0.2672	20.24	1.66	0.9854	0.4229	0
Ti × Lo (Ha)	2	151.36	8.9221	0.0004	25.06	2.03	5.6634	0.0042	30.23
Residual	71	16.96			27.18	0.36			42.73
Total	79								
Other fauna									
Covariate = vegetation biomass	1	180.77	6.1752	0.0182	8.46	0.0024	0.0045	0.9442	0
Time	1	474.15	11.0950	0.0758	21.43	3.73	3.1454	0.2040	15.22
Habitat	1	0.63	0.0114	0.6590	0	0.08	0.0603	1.0000	0
Locality (Ha)	2	68.69	3.9334	0.0182	9.85	1.75	10.1600	0.0006	15.99
Ti × Ha	1	264.64	7.4973	0.1146	24.99	4.07	4.4363	0.1566	27.08
Ti × Lo (Ha)	2	40.02	2.2915	0.1050	9.57	1.11	6.4597	0.0024	18.08
Residual	71	17.46			25.70	0.17			23.62
Total	79								

*, significant difference at $P < 0.05$. The amount of variance (% VC) explained by each factor is included.

(0.7 ± 0.12 vs 0.45 ± 0.35 spp. 0.04 m^{-2}, respectively) (Figure 3) was not significant either (three-way ANCOVA: ‘Habitat’, $P = 1.0000$, Table 1).

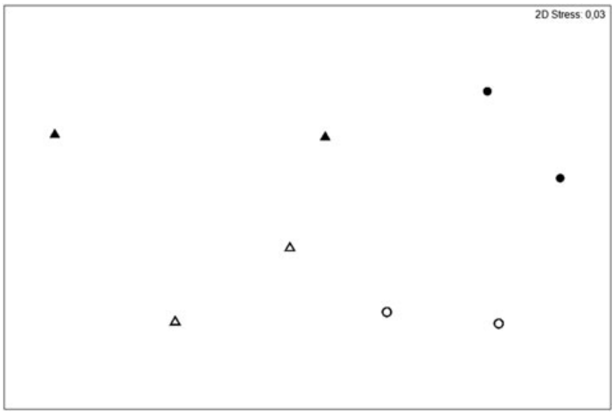

Fig. 4. Two-dimensional nm-MDS plot showing similarities in the epifaunal assemblage structure between habitats and times. Each symbol corresponds to a sampling locality within each habitat. Triangles, *Cymodocea nodosa*; circles, *Caulerpa prolifera*. Filled symbols, November 2011; open symbols, October 2012.

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

Table 2. Results of three-way PERMANOVA testing for differences in the epifaunal assemblage structure between habitats, times and localities within habitats.

	df	**MS**	**F**	***P***	**% VC**
Covariate = vegetation 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
Ti × Ha	1	7014.8	1.8769	0.2272	13.87
Ti × Lo (Ha)	2	4610.3	10.515	0.0002	19.12
Residual	71	438.47			18.92
Total	79				

*, significant differences for $P < 0.05$. The amount of variance (% VC) explained by each factor is included.

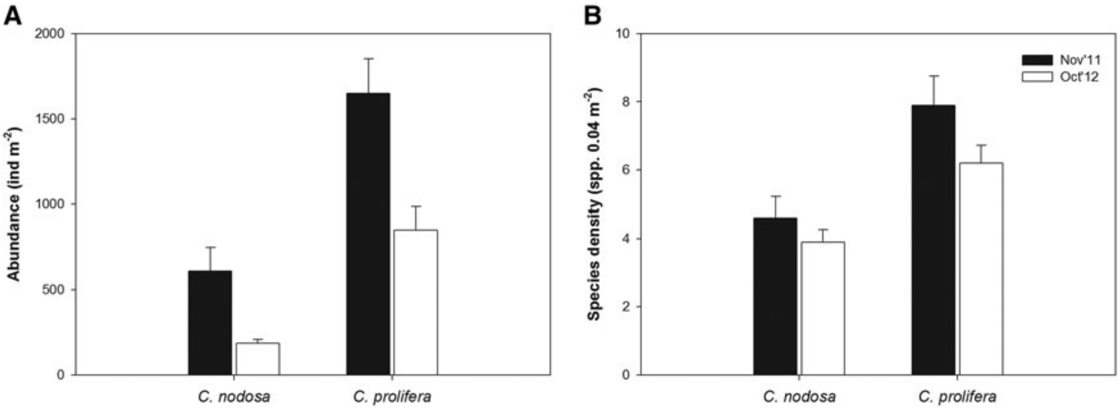

Fig. 5. (A) Mean abundance (ind m^{-2} ±SE) and (B) mean species density (number of species ±SE) of amphipods at each habitat and time.

Table 3. Results of 3-way ANCOVAs testing for differences in the total abundance and species density of amphipods between habitats, times and localities within habitats.

		Total abundance				**Total species density**			
	df	MS	F	*P*	% VC	MS	F	*P*	% VC
Covariate = vegetation 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
Ti × Ha	1	12.32	0.0123	0.9186	0	0.02	0.0004	0.9896	0
Ti × Lo (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								

*, significant difference at $P < 0.05$. The amount of variance (% VC) explained by each factor is included.

side of the plot. In addition, samples corresponding to November 2011 are in the top half of the plot, whereas those corresponding to October 2012 are in the bottom half (Figure 4). This multivariate response, however, was only statistically significant between habitats (three-way PERMANOVA: 'Habitat', $P = 0.0002$; Table 2).

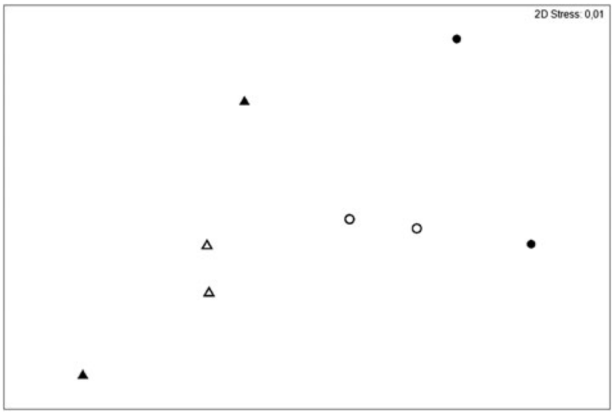

Fig. 6. Two-dimensional nm-MDS plot showing similarities in the amphipod assemblage structure between habitats and times. Each symbol corresponds to a sampling locality within habitats. Triangles, *Cymodocea nodosa*; circles, *Caulerpa prolifera*. Filled symbols, November 2011; open symbols, October 2012.

Amphipod assemblages

A total of 41 amphipod species, belonging to 16 families, were collected (Appendix). The abundance of amphipods constituted ~70% of total crustaceans for the overall study; amphipod abundance was significantly larger in *Caulerpa prolifera*-dominated beds (1248.13 ± 136.83 ind m^{-2}, mean ± SE) than in *Cymodocea nodosa* meadows (396.88 ± 77.36 ind m^{-2}) at both sampling times (Figure 5A; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 3). A similar pattern

Table 4. Results of three-way PERMANOVA testing for differences in the amphipod assemblage structure between habitats, times and locations within habitats.

	df	MS	F	*P*	% VC
Covariate = vegetation 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
Ti × Ha	1	2188.6	0.86856	0.4874	0
Ti × Lo (Ha)	2	3125.6	13.598	0.0002	25.76
Residual	71	229.86			22.15
Total	79				

*, significant differences for $P < 0.05$. The amount of variance (% VC) explained by each factor is included.

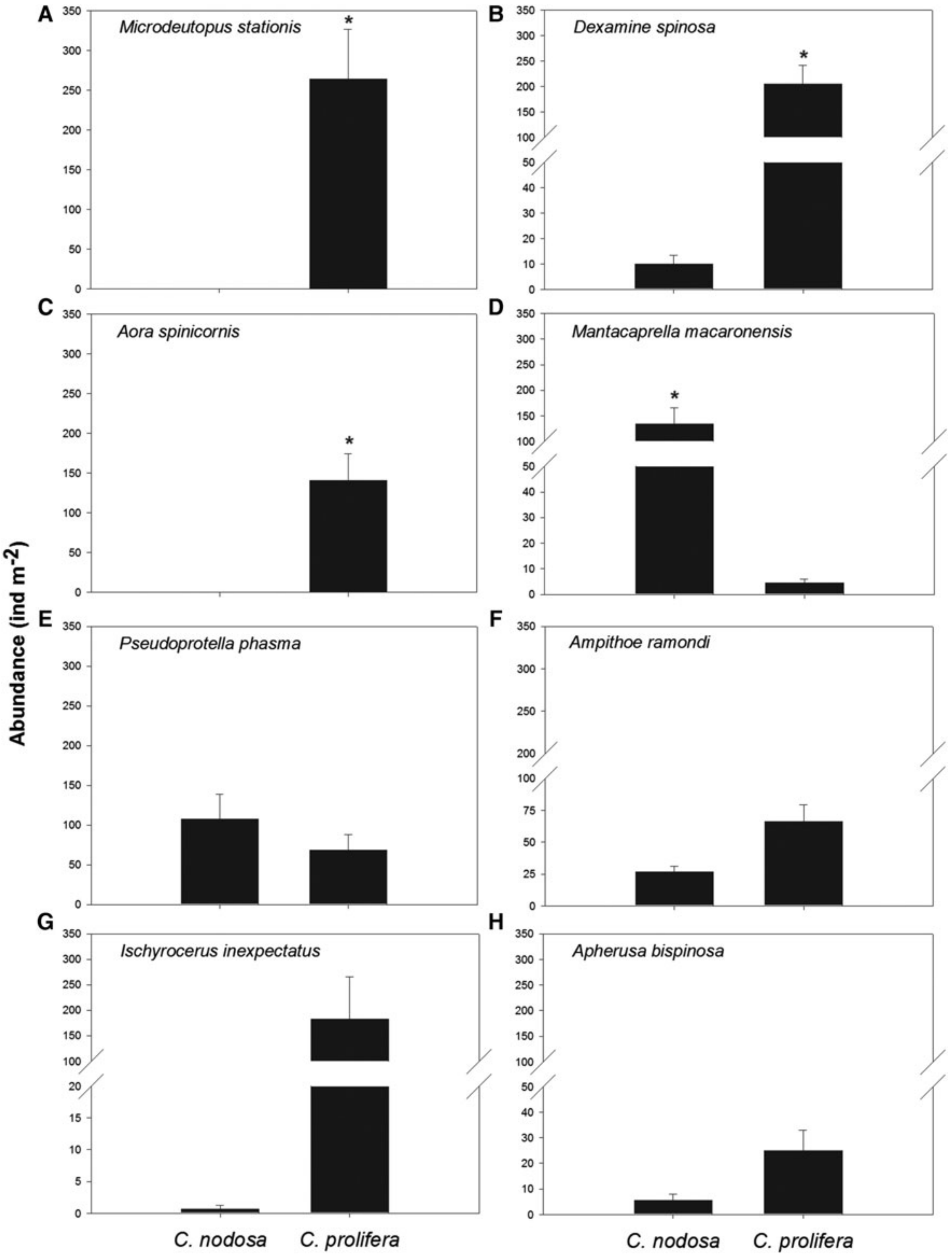

Fig. 7. Mean abundance (ind m^{-2} ± SE) of the most important amphipod species at each habitat. *, significant differences.

was found for amphipod species density (7.05 ± 0.47 vs 4.25 ± 0.38 spp. 0.04 m^{-2}, respectively; Figure 5B), but differences were not statistically significant (three-way ANCOVA: 'Habitat', $P = 0.3406$, Table 3).

The two-dimensional MDS plot showed a clear segregation of amphipod assemblages 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 (Figure 6). However, the structure of amphipod assemblages was only significantly different between habitats (three-way PERMANOVA: 'Habitat', $P = 0.0002$, Table 4).

The amphipod species which most contributed to dissimilarities between habitats were: *Microdeutopus stationis*,

Table 5. Results of three-way ANCOVAs testing for differences in the abundance of the most important amphipod species between habitats, times and localities within habitats.

		Microdeutopus stationis				*Dexamine spinosa*			
	df	MS	F	P	% VC	MS	F	P	% VC
Covariate = vegetation biomass	1	325.79	1.1317	0.2856	2.07	606.04	18.6590	0.0008	9.61
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 (Ha)	2	1173	51.703	0.0002	22.87	88.29	5.6029	0.0056	6.84
Ti × Ha	1	581.46	2.7391	0.2214	15.53	388.08	6.6477	0.1155	17.49
Ti × Lo (Ha)	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 spinicornis				*Mantacaprella macaronensis*			
Covariate = vegetation 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 (Ha)	2	176.93	10.8940	0.0002	13.38	518.80	66.7480	0.0002	26.57
Ti × Ha	1	160.31	0.4498	0.5641	0	106.09	0.3643	0.6086	0
Ti × Lo (Ha)	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								
		Pseudoprotella phasma				*Ampithoe ramondi*			
Covariate = vegetation 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 (Ha)	2	887.31	43.9170	0.0002	38.93	41.30	3.5043	0.0382	9.44
Ti × Ha	1	27.01	0.0995	0.7282	0	168.45	1.7604	0.2983	17.77
Ti × Lo (Ha)	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								
		Ischyrocerus inexpectatus				*Apherusa bispinosa*			
Covariate = vegetation 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 (Ha)	2	649.69	19.8570	0.0002	24.76	649.69	19.8570	0.0002	24.76
Ti × Ha	1	369.51	0.7336	0.4693	0	369.51	0.7336	0.4709	0
Ti × Lo (Ha)	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
Total	79								

*, significant differences for $P < 0.05$. The amount of variance (% VC) explained by each factor is included.

Dexamine spinosa, *Aora spinicornis*, *Mantacaprella macaronensis*, *Pseudoprotella phasma*, *Ampithoe ramondi*, *Ischyrocerus inexpectatus* and *Apherusa bispinosa*. These species made up ~60% of the total abundance of amphipods. We detected species-specific affinities for the two habitats; for example, the abundance of *Microdeutopus stationis*, *D. spinosa* and *A. spinicornis* was significantly larger in *C. prolifera*-dominated beds (Figure 7A, B, C; three-way ANCOVA: 'Habitat', $P < 0.05$, Table 5), while the caprellid *Mantacaprella macaronensis* significantly dominated in *Cymodocea nodosa* meadows (Figure 7D; three-way ANCOVA: 'Habitat', $P = 0.0002$, Table 5). The other caprellid species, *P. phasma*, also showed larger abundances in *C. nodosa* meadows, although the difference with respect to *Caulerpa prolifera*-dominated beds was not statistically significant (Figure 7E; three-way ANCOVA: 'Habitat', = 0.6612, Table 5). The gammarid *Ampithoe ramondi* was found in both habitats, with larger abundances in *C. prolifera*-dominated beds, that were otherwise not statistically different (Figure 7F; three-way ANCOVA: 'Habitat', = 0.6800, Table 5). Finally, *I. inexpectatus* and *Apherusa 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 (Figure 7G, H; three-way ANCOVA: 'Habitat', >0.05, Table 5).

DISCUSSION

Epifaunal assemblages

Our results have demonstrated 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*. Larger abundances and species densities were found in *C. prolifera*-dominated beds; this was unexpected, since caulerpenyne seems to reduce macrophyte palatability and act as a 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.*, 2007), 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 *Cymodocea nodosa* than in mono-specific *C. nodosa* meadows (Monterroso *et al.*, 2012).

Differences in the structure, abundance and diversity of epifaunal assemblages may result from changes in the structural complexity of the habitat, including host plant attributes (e.g. plant morphology, associated floral and faunal epiphytes, etc.) (Virnstein & Howard, 1987; Taylor & Cole, 1994; Bologna & Heck Jr, 1999), which play 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 Sea, 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 Cymodocea nodosa*). Hence, the replacement of *C. nodosa* meadows by *Caulerpa prolifera* may involve a significant change in the hydrodynamic properties of the sea-floor, modifying the local ecosystem functioning and affecting associated fauna compared with seagrass meadows. The high accumulation of detritus in *C. prolifera*-dominated beds plays an important role as a trophic resource for marine invertebrates, and can affect the overall trophic web (Vázquez-Luis *et al.*, 2009), favouring macrofaunal assemblages mainly dominated by crustaceans and polychaetes (Hendriks *et al.*, 2010; Monterroso *et al.*, 2012) and, probably, several facultative species which could also be found in infaunal environments.

Differences within invertebrate assemblages are expected between different types of vegetation within the same geographical and environmental context (Sirota & Hovel, 2006). Low epifaunal abundances associated with *Cymodocea nodosa* meadows may be explained by space limitation; the architecture of *C. nodosa* is less complex 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 & Harvilicz, 2001) and to fish predatory pressure. Seagrasses play an important role in providing 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, b). The abundance of fish is ~3–4 times larger in *C. nodosa*- than in *Caulerpa prolifera*-dominated beds (Tuya *et al.*, 2013b). Epifaunal organisms, particularly crustaceans, are the main constituent of diets of seagrass-associated fish (Yamada *et al.*, 2010; Horinouchi *et al.*, 2012). Hence, it is worth noting that the contrasting abundance patterns of epifaunal and fish assemblages between *Cymodocea nodosa* and *Caulerpa prolifera* bottoms might fits a classical 'predation' model, where a large abundance of predators (here, fish) remove large quantities of prey (here, epifauna) and so explain the decreasing abundance of prey in such habitats (here, *Cymodocea nodosa* seagrass meadows) (Verdiell-Cubedo *et al.*, 2007).

Amphipod assemblages

The amphipod assemblage structure differed between habitats at both sampling times, including larger abundances of amphipods (~3 times) in *Caulerpa prolifera*-dominated beds than in *Cymodocea nodosa* meadows. This outcome disagrees with amphipod abundances reported by Vázquez-Luis *et al.* (2009) for the same habitats, at two different seasons (September 2004 and March 2005), in the western Mediterranean Sea (313.89 ± 75.63 ind m^{-2} in *Caulerpa prolifera* and 494.44 ± 160.17 ind m^{-2} in *Cymodocea nodosa*, mean ± SE). The variation of amphipod abundances between both studies, especially in bottoms constituted by *Caulerpa prolifera*, may be due to the difference in the sampling seasons or merely due to the difference between the sampling areas (Canary Islands in the Atlantic Ocean vs Alicante in the Mediterranean Sea).

The diversity of amphipods recorded in *Cymodocea nodosa* seagrass meadows at Gran Canaria (16 amphipod species in November 2011 and 17 in October 2012) are comparable, or even lower, than the number of amphipod species reported by several studies from the Mediterranean Sea (28 species, Sánchez-Jerez *et al.*, 1999; 13 species in September and 21 in March, Vázquez-Luis *et al.*, 2009). On bottoms dominated by *Caulerpa prolifera*, a total of 27 and 20 amphipod species (November 2011 and October 2012, respectively) were identified by our study, which contrast with 17 amphipod species recorded by Sánchez-Moyano *et al.* (2007) in Algeciras Bay, and values of 6 and 18 species reported by Vázquez-Luis *et al.* (2009), at two different seasons, also in the Mediterranean Sea. The variation within the total number of amphipod species among studies show a more diverse assemblage of amphipods 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 & Hill, 2006), a fact that is related to differences in palatability and food preferences by herbivores (Ortega *et al.*, 2010). However, although the active selection appears important, it is not sufficient to explain differential patterns of epifaunal distribution and abundance among host plants (Virnstein & Howard, 1987). The presence of diverse amphipods on plant species may result from ecological processes unrelated to herbivore preferences or the quality of the host for growth and survival, but from 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 preference for specific habitats. Overall, it is possible to distinguish between gammarids, typically associated with *C. prolifera*-dominated beds, and caprellids, typically associated with *Cymodocea nodosa* meadows. Within gammarids, individuals belonging to the family Aoridae (here, *Aora spinicornis* and *Microdeutopus stationis*) have been exclusively found in *Caulerpa prolifera*-dominated beds. This outcome contrasts with previous records from the Mediterranean Sea. For example, *A. spinicornis* has been found among hydroids, phanerogams and algae, and on sandy and muddy bottoms as well (Ruffo, 1982; Conradi & López-González, 1999); whilst *M. stationis* has been almost exclusively found on fine sand, particularly among the phanerogams *Cymodocea nodosa* and *Posidonia oceanica*, with some records on coralligenous habitats (Ruffo, 1998) and macrophytes (Conradi & López-González, 1999). However, other authors have also found large abundances of *Microdeutopus* spp. in *Caulerpa* beds and on rocky habitats (Roberts & Poore, 2005; Vázquez-Luis *et al*., 2008, 2009), with preference for environments with low hydrodynamic regimes and high sedimentation rates (Conradi *et al*., 1997; Guerra-García & García-Gómez, 2005). In our study, other species significantly more abundant in *C. prolifera*-dominated beds was the free-living, herbivore, *Dexamine spinosa*, which is very common within algal canopies in the shallow subtidal zone (Lincoln, 1979; Ruffo, 1982), but also on sandy bottoms with bio-detritus (Conradi & López-González, 1999). *Apherusa bispinosa* and *Ischyrocerus inexpectatus* were also collected in higher abundances in *C. prolifera*-dominated beds. Consistent with our results, Farlin *et al.* (2010) reported that ischyrocerids, such as *Ischyrocerus inexpectatus*, tend to feed more on algae than on seagrasses. As with the previous gammarids, *Ampithoe ramondi* was, again, more abundant in *C. prolifera*-dominated beds than in *Cymodocea nodosa* meadows, although differences were not so high. 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), which contrasts with our results. The caprellid *Pseudoprotella phasma* has been found in both habitats, but mainly inhabiting *C. nodosa* meadows; this species might also be found among algae (Ruffo, 1993), with a preference for environments with high hydrodynamics (Conradi & López-González, 2001). Finally, the caprellid *Mantacaprella macaronensis* has shown a clear preference for *C. nodosa* seagrass meadows, with few abundances occurring in *Caulerpa prolifera*-dominated beds. This caprellid species has also been found in rocky habitats from the Macaronesian archipelago of Cape Verde (Vázquez-Luis *et al*., 2013).

In conclusion, our study shows that *Caulerpa prolifera*-dominated beds have a more abundant and diverse epifaunal assemblage than *Cymodocea nodosa* meadows, which is also reflected on amphipod assemblages, and is temporally consistent. Therefore, *C. prolifera* meadows seem to be a favourable habitat for epifauna in soft vegetated habitats in the Canary Islands.

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Correspondence should be addressed to:
Lydia Png-Gonzalez
Centro en Biodiversidad y Gestión Ambiental, Marine Sciences Faculty, Campus Tafira, Universidad de Las Palmas de Gran Canaria, 35017 Tafira, Las Palmas, Spain
email: lydiapng@gmail.com

APPENDIX

Abundances (ind m^{-2} ± SE) of epifaunal organisms at each habitat and time. The total abundance and number of species are also included.

Dominant group	Group	Species	November 2011		October 2012	
			Cymodocea nodosa	*Caulerpa prolifera*	*C. nodosa*	*C. prolifera*
Crustacea	Amphipoda	*Amphilochus neapolitanus*	3.75 ± 3.75	2.5 ± 2.5	–	1.25 ± 1.25
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
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	*Autonoe longipes*	–	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	*Cheiriphotis* sp.	–	6.25 ± 6.25	–	–
Crustacea	Amphipoda	*Corophium* sp.	–	2.5 ± 2.5	–	–
Crustacea	Amphipoda	*Dexamine spinosa*	10 ± 6.12	55 ± 16.2	10 ± 4.56	355 ± 96.46
Crustacea	Amphipoda	*Elasmopus* sp.	–	1.25 ± 1.25	–	–
Crustacea	Amphipoda	*Ericthonius punctatus*	33.75 ± 15.99	97.5 ± 67.78	1.25 ± 1.25	–
Crustacea	Amphipoda	*Harpinia* sp.	–	7.5 ± 4.33	–	2.5 ± 2.5
Crustacea	Amphipoda	*Ischyrocerus inexpectatus*	1.25 ± 1.25	352.5 ± 307.61	–	–
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	*Liljeborgia* sp.	–	6.25 ± 4.73	–	1.25 ± 1.25
Crustacea	Amphipoda	*Lysianassina longicornis*	–	–	–	21.25 ± 16.38
Crustacea	Amphipoda	*Maera inaequipes*	–	1.25 ± 1.25	–	–
Crustacea	Amphipoda	*Mantacaprella macaronensis*	235 ± 125.62	6.25 ± 3.75	27.5 ± 7.77	2.5 ± 1.44
Crustacea	Amphipoda	*Medicorophium minimum*	–	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	*Microjassa cumbrensis*	–	23.75 ± 16.5	–	–

Continued

Appendix. Continued.

Dominant group	**Group**	**Species**	**November 2011**		**October 2012**	
			Cymodocea nodosa	***Caulerpa prolifera***	***C. nodosa***	***C. prolifera***
Crustacea	Amphipoda	*Microprotopus longimanus*	–	35 ± 23.63	–	–
Crustacea	Amphipoda	*Peltocoxa mediterranea*	–	–	–	1.25 ± 1.25
Crustacea	Amphipoda	*Pereionotus testudo*	1.25 ± 1.25	–	–	–
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	*Stenothoe monoculoides*	11.25 ± 7.18	–	3.75 ± 2.39	–
Crustacea	Amphipoda	Unidentified	–	3.75 ± 3.75	3.75 ± 2.39	16.25 ± 7.47
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	Brachyura	2.5 ± 1.44	11.25 ± 5.54	1.25 ± 1.25	21.25 ± 9.44
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
Crustacea	Decapoda	Larva	–	2.5 ± 1.44	–	3.75 ± 2.39
Crustacea	Isopoda	*Astacilla* sp.	–	–	1.25 ± 1.25	1.25 ± 1.25
Crustacea	Isopoda	*Cymodoce* sp.	–	6.25 ± 3.75	1.25 ± 1.25	10 ± 3.54
Crustacea	Isopoda	Chaetiliidae sp. 1	1.25 ± 1.25	–	221.25 ± 106.29	2.5 ± 1.44
Crustacea	Isopoda	*Stenosoma lancifer*	–	1.25 ± 1.25	–	6.25 ± 3.75
Crustacea	Isopoda	Unidentified 1	18.75 ± 11.25	3.75 ± 3.75	11.25 ± 8.0	–
Crustacea	Isopoda	Unidentified 2	6.25 ± 6.25	–	5 ± 3.54	17.5 ± 10.9
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	Tanaidacea	*Apseudes talpa*	–	–	–	5 ± 3.54
Crustacea	Tanaidacea	*Apseudes* sp.	–	–	–	–
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
Mollusca	Bivalvia	Cardiidae sp. 1	–	6.25 ± 3.75	–	–
Mollusca	Bivalvia	Unidentified 1	–	10 ± 5.4	3.75 ± 3.75	10 ± 2.04
Mollusca	Bivalvia	Unidentified 2	–	3.75 ± 1.25	1.25 ± 1.25	12.5 ± 4.33
Mollusca	Gastropoda	*Alvania* sp.	43.75 ± 25.2	–	6.25 ± 4.73	257.5 ± 91.3
Mollusca	Gastropoda	*Anachis* sp.	–	1.25 ± 1.25	–	–
Mollusca	Gastropoda	*Bittium* sp.	3.75 ± 3.75	1.25 ± 1.25	–	190 ± 84.29
Mollusca	Gastropoda	*Cerithiopsis* sp.	–	–	1.25 ± 1.25	6.25 ± 4.73
Mollusca	Gastropoda	Eulimidae sp. 1	–	–	–	2.5 ± 1.44
Mollusca	Gastropoda	*Mitrella* sp.	2.5 ± 1.44	33.75 ± 11.61	–	1.25 ± 1.25
Mollusca	Gastropoda	Nudibranchia	–	1.25 ± 1.25	–	–
Mollusca	Gastropoda	Nystiellidae sp. 1	8.75 ± 5.91	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	Rissoinae sp. 1	–	–	16.25 ± 7.18	177.5 ± 44.37
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
Mollusca	Gastropoda	*Vexillum zebrinum*	11.25 ± 8.26	5 ± 3.54	–	–
Mollusca	Gastropoda	*Volvarina* sp.	–	–	1.25 ± 1.25	1.25 ± 1.25
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
Other fauna	Pycnogonida	Unidentified	27.5 ± 14.79	–	10 ± 5.4	48.75 ± 14.34
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	*Aonides oxycephala*	–	1.25 ± 1.25	–	–
Worms	Polychaeta	*Aponuphis bilineata*	–	1.25 ± 1.25	–	–
Worms	Polychaeta	*Demonax brachychona*	–	6.25 ± 6.25	–	–
Worms	Polychaeta	*Desdemona* sp.	–	2.5 ± 1.44	–	–
Worms	Polychaeta	*Exogone naidina*	–	2.5 ± 1.44	–	–

Continued

Appendix. Continued.

Dominant group	Group	Species	November 2011		October 2012	
			Cymodocea nodosa	*Caulerpa prolifera*	*C. nodosa*	*C. prolifera*
Worms	Polychaeta	*Nereididae* sp. 1	–	11.25 ± 5.54	–	–
Worms	Polychaeta	*Platynereis dumerilii*	–	2.5 ± 1.44	–	21.25 ± 12.31
Worms	Polychaeta	*Polyophthalmus pictus*	2.5 ± 2.5	76.25 ± 42.79	–	–
Worms	Polychaeta	*Sabellidae* sp. 1	–	1.25 ± 1.25	–	–
Worms	Polychaeta	*Salvatoria* sp.	1.25 ± 1.25	–	–	1.25 ± 1.25
Worms	Polychaeta	*Schroederella laubieri*	–	1.25 ± 1.25	–	–
Worms	Polychaeta	*Streptosyllis bidentata*	5 ± 2.89	–	–	–
Worms	Polychaeta	*Syllis* sp.	6.25 ± 4.73	–	–	–
Worms	Sipunculidea	Unidentified	–	–	–	–
Total abundance			768.75 ± 397.01	1975 ± 338.83	513.75 ± 196.1	2561.25 ± 769.91
Total number of species			36	65	37	58