Distribution patterns of intertidal and shallow water caprellids associated with macroalgae along the Iberian Peninsula

Patrones de distribución de los caprélidos intermareales y de aguas someras asociados a macroalgas de la Península Ibérica

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ABSTRACT

This study investigated the patterns of caprellids associated with macroalgae from the intertidal and shallow waters (0-5 m) of the Iberian Peninsula. Nineteen stations and 250 samples of algae demonstrated the presence of 46 algal species (22 intertidal and 24 subtidal). Eleven caprellid species dwelled in these macroalgae with Caprella penantis and C. acanthifera being the most abundant species. Caprella acanthifera, Phtisica marina and Pseudoprotella phasma inhabited the whole Peninsula; C. danilevskii, C. equilibra, C. fretensis and C. penantis showed Atlantic distribution, whereas C. grandimana, C. hirsuta, C. liparotensis and Deutella schieckei inhabited only Mediterranean sites and the Strait of Gibraltar. Caprellid species demonstrated low substrate specificity and associated themselves with many species of algae. Subtidal subtrates contained higher numbers of caprellid species than intertidal substrates. The highest number of caprellid species occurred on the algae Stypocaulon scoparium, Cystoseira spp., Corallina elongata, Jania rubens, Codium vermilara, Cladostephus spongiosus and Asparagopsis armata. Caprellid abundances were very high, both in the intertidal and shallow subtidal zones, reaching 12200 ind/ 1000 ml

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alga. In fact, caprellids are one of the dominant groups of associated fauna in the intertidal in comparison with other taxa. In spite of the high densities, caprellid diversity (in terms of number of species) in the intertidal and very shallow bottoms of the Iberian Peninsula is very low (11 species) in comparison with total caprellid diversity including deeper areas >5 m (ca. 40 species). Canonical Correspondence Analysis showed that temperature and conductivity are the environmental variables that explain a clear Atlantic-Mediterranean gradient for caprellid distribution.

RESUMEN

Se estudió el patrón de caprélidos asociados a macroalgas del intermareal y aguas someras (0-5 m) de la Península Ibérica. Un total de 19 estaciones y 250 muestras de algas reflejaron la presencia de 46 especies de algas (22 intermareales y 24 submareales). Once especies de caprélidos se asociaron a estas macroalgas, siendo Caprella penantis y C. acanthifera las más abundantes. Caprella acanthifera, Phtisica marina y Pseudoprotella phasma se distribuyeron por toda la Península; C. danilevskii, C. equilibra, C. fretensis y C. penantis mostraron distribución Atlántica, mientras que C. grandimana, C. hirsuta, C. liparotensis y Deutella schieckei se encontraron sólo en el Mediterráneo y el Estrecho de Gibraltar. Los caprélidos mostraron baja especificidad por el sustrato y se asociaron a distintas especies de algas. Los sustratos submareales albergaron mayor número de especies que los intermareales. Las mayores diversidades de especies se encontraron en las algas Stypocaulon scoparium, Cystoseira spp., Corallina elongata, Jania rubens, Codium vermilara, Cladostephus spongiosus y Asparagosis armata. Las abundancias registradas fueron muy altas, tanto en el intermareal como el submareal, alcanzando los 12200 ind/1000 ml de alga. De hecho, los caprélidos constituyen uno de los grupos dominantes de fauna asociada en el intermareal en comparación con otros taxa. A pesar de las altas densidades, la diversidad de los caprélidos (en términos de número de especies) en el intermareal y submareal somero de la Península Ibérica es bajo (11 especies) si se compara con la diversidad total de caprélidos incluyendo aguas más profundas > 5 m (ca. 40 especies). El Análisis Canónico de Correspondencias mostró que la temperatura y la conductividad son las variables ambientales que mejor explican el claro gradiente Atlántico-Mediterráneo de distribución de caprélidos.

INTRODUCTION

Amphipods are one of the dominant groups associated with a variety of macroalgae on rocky shores (Chavanich *et al.*, 2010). Amphipods can use these algae as habitat or food, and both biological and physical factors influence the selection of macroalgae by amphipods (Chavanich, 2006; Viejo & Arrontes, 1992). Knowledge of the ecology and taxonomy of amphipod species on the coasts of the Iberian Peninsula is still fragmentary (Jimeno

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& Turón, 1995; Bellan-Santini & Ruffo, 1998). Most of the studies dealing with Caprellidea occurred along the Strait of Gibraltar (see Guerra-García & Izquierdo, 2010 for details), and information dealing with distribution, diversity and abundance patterns of caprellids along the Iberian Peninsula is scarce: Jimeno & Turón (1995) studied the ecological distribution of the Gammaridea and Caprellidea from Northeast coast of Spain on different types of substrata; Pereira et al. (2006), as part of a general study on intertidal macroinvertebrates, reported the bigeographic patterns of some caprellids along the Portuguese coast: Vázquez-Luis et al. (2009) studied the caprellid assemblages in shallow waters invaded by Caulerpa racemosa from southeastern Spain; Guerra-García et al. (2009e) and Guerra-García & Izquierdo (2010) investigated the caprellids associated with the algae Stypocaulon scoparium and Corallina elongata along the Iberian Peninsula. Guerra-García (2001) studied the habitat use of caprellids associated with different substrates (19 species of algae, 8 species of hydroids, 7 species of anthozoans, 5 species of echinoderms, 3 species of sponges, 3 species of bryozoans and 1 annelid) along the littoral of Ceuta (North Africa, Strait of Gibraltar).

Despite the lack of studies along the Atlantic and Mediterranean coasts of the Iberian Peninsula dealing with caprellids, these peracarids are dominant in number of specimens (per m² or per ml of algae) along the intertidal or shallow water zones (Guerra-García *et al.*, 2009e, 2009c). In fact, they are usually cited as part of taxa lists in ecological or biogeographical studies conducted in coastal areas not only from the Iberian Peninsula, but also world-wide (Woods, 2009). Consequently, a detailed knowledge of the species, together with adequate tools for identification, is necessary to properly address future studies.

During previous observations we detected that, in spite of their numerical dominance, the diversity of caprellids in terms of number of species in the intertidal ecosystems and very shallow waters (0-5 m) was usually low, including few species widely distributed in different algal species and with no specificity for a single substrate. Consequently, the objective of the present study was to verify this pattern by selecting a wide range of intertidal and shallow subtidal algal substrates and investigating the associated caprellids.

MATERIAL AND METHODS

We selected 19 stations along the Atlantic and Mediterranean coasts of the Iberian Peninsula, including the Strait of Gibraltar (Fig. 1). We chose relatively undisturbed enclaves with low human pressures to avoid the effect

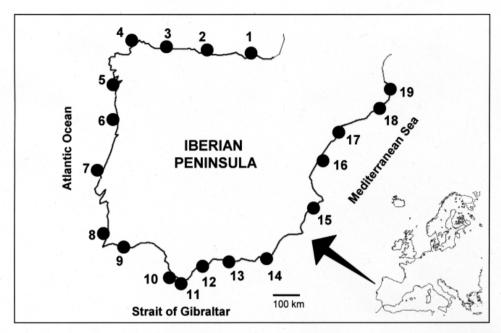


Fig. 1.—Study area showing the sampling stations along coastal Spain. Ogella (1), Oyambre (2), Cetarea (3), Baleo (4), Cabo Silleiro (5), Labruge (6), Playa Azul (7), Vale dos Homens (8), Castelo (9), Bolonia (10), Isla de Tarifa (11), Torreguadiaro (12), Cerro Gordo-Herradura (13), Cabo de Gata (14), Cala del tío Ximo (15), Benicassim-Oropesa (16), Torrent del Pi (17), Cala de Sant Françesc (18), L'Estartit (19).

Fig. 1.—Área de estudio mostrando las estaciones de muestreo a lo largo de la costa de la Península Ibérica. Ogella (1), Oyambre (2), Cetarea (3), Baleo (4), Cabo Silleiro (5), Labruge (6), Playa Azul (7), Vale dos Homens (8), Castelo (9), Bolonia (10), Isla de Tarifa (11), Torreguadiaro (12), Cerro Gordo-Herradura (13), Cabo de Gata (14), Cala del tío Ximo (15), Benicassim-Oropesa (16), Torrent del Pi (17), Cala de Sant Françesc (18), L'Estartit (19).

of anthropogenic influence on the natural biogeographical and ecological patterns of species.

Sampling occurred in the summer of 2008 (from 5th June to 5th August). We measured the following environmental parameters "in situ" at each sampling site: water temperature, pH, conductivity, dissolved oxygen and turbidity. Guerra-García & Izquierdo (2010) report the details of the physico-chemical study.

From the 19 stations of the Iberian Peninsula, we collected 250 samples of algae that included 46 algal species (22 intertidal and 24 subtidal). We collected algae from the intertidal zone directly by hand at low tide; subtidal snorkelling provided algal samples from shallow waters (1-5 meters deep). Algae were collected either individually, holdfast included (e.g., *Cystoseira*,

Codium, Bifurcaria, etc.), or, when the species constituted a turf (*Corallina*, *Jania*, *Laurencia*, etc.), by scraping the surface for a volume of approximately 200 ml. We preserved samples in 70% ethanol.

In the laboratory, using a 0.5 mm mesh sieve, we washed the samples, sorted the caprellids from the algae and identified specimens to species level. We always expressed the density of caprellids as number of individuals per volume (1000 ml) of algae because of the different structure of the algal species (see Pereira *et al.*, 2006). Volume of algae was estimated as the difference between the initial and final volume when placed into a graduated cylinder with a fixed amount of water (see Pereira *et al.*, 2006).

Possible differences in the number of caprellid species and abundance between intertidal and subtidal substrates were tested with one-way ANOVA, after verifying normality with the Kolmogorov-Smirnov test, and the homogeneity of variances with the Levene test. We established affinities among stations based on caprellid composition through cluster analysis with UPGMA (unweighted pair group method using arithmetic averages) and euclidean distances. We studied the relationships between environmental measures and caprellid assemblages by Canonical Correspondence Analysis (CCA) and we conducted univariate analyses through SPSS and multivariate analyses through the PRIMER package (Clarke & Gorley, 2001) and the PC-ORD programme (McCune & Mefford, 1997).

RESULTS AND DISCUSSION

Caprellids and algae as substrates

We collected 250 samples from the Iberian coasts and identified 46 species of algae (Table I); 135 samples were of intertidal algae (22 species), and the remaining 115 samples were of subtidal algae (24 species). The most common algal substrates along the rocky shores of the Iberian coasts are *Corallina elongata*, *Stypocaulon scoparium*, *Asparagopsis armata*, *Cladostephus spongiosus*, *Codium vermilara*, *Cystoseira tamariscifolia*, *Jania rubens*, *Gelidium corneum* and *Pterocladia capillacea*.

Eleven caprellid species inhabited these 46 species of macroalgae (Table I, Fig. 2). *Caprella penantis* and *C. acanthifera* were the most abundant species, being present in the majority of the algal substrates, followed by *Caprella danilevskii*, *C. grandimana*, *C. hirsuta* and *C. liparotensis*. The distribution of most caprellid species in the intertidal and shallow sublittoral zones was random. However, the species *Phtisica marina* and *Pseudoprotella phasma* demonstrated clear preference for subtidal habitats (Table I). Caprellid species showed low substrate specificity and were associated with several

Table I.—Mean abundance (ind/ 1000 ml seaweed) of the caprellids in the different algal substrates. n=number of samples collected of each substrate.

Tabla I.—Abundancia media (ind/ 1000 ml seaweed) de los caprélidos en los diferentes sustratos algales. n=número de muestras recolectadas en cada sustrato.

	n	Ca	Cd	Ce	Cf	Cg	Ch	CI	Ср	Ds	Pm	Рр
INTERTIDAL:												
Asparagopsis armata Harvey	33	222	68	-	-	-	14	98	3364	-	-	2
Bifurcaria bifurcata R. Ross	4	-	-	-	-	-	-	-	1	-	-	-
Chaetomorpha aerea (Dillwyn) Kutzing	1	3036	-	-	-	-	-	-	-	-	-	-
Chondria scintillans G.Feldmann	2	42	-	-	-	-	-	-	50	-	-	-
Cladophora prolifera (Rothpletz) Kützing	2	-	-	-	-	-	-	-	130	-	-	-
Codium decorticatum (Woodward) M.A.Howe	1	-	1	-	-	-	-	-	-	-	-	-
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	1	-	-	-	-	177	-	-	-	-	-	-
Corallina elongata J.Ellis & Solander	57	-	1	-	-	343	224	26	378	-	-	-
Cystoseira elengans Sauvageau	1	-	539	-	-	-	15	8	8	-	-	-
Gastroclonium ovatum (Hudson) Papenfuss	1	-	-	-	-	-	-	-	5	-	-	-
Gelidium attenuatum (Turner) Thuret	4	-	-	-	-	-	-	-	1025	-	-	-
Gelidium latifolium (Greville) Bornet	2	-	-	-	-	45	34	-	820	-	-	-
Gelidium pusillum (Stackhouse) Le Jollis	5	-	-	-	-	175	7	-	188	-	-	-
Halopteris filicina (Grateloup) Kützing	1	-	-	-	-	-	-	-	-	50	-	-
Hypnea musciformis (Wulfen) Lamouroux	2	19	-	-	-	-	35	128	-	-	-	-
Laurencia papillosa (C.Agardh) Greville	4	-	-	-	-	25	-	11	-	-	-	-
Lomentaria articulata (Hudson) Lyngbye	1	-	-	1	-	-	-	-	56	-	-	-
Mastocarpus stellatus (Stackhouse) Guiry	3	10	-	-	-	-	-	-	-	-	-	-
Osmundea pinnatifida (Hudson) Stackhouse	2	1	65	-	-	-	-	-	367	-	-	-
Plocamium cartilagineum (Linnaeus) P.S.Dixon	3	6	-	-	-	-	-	3	403	-	-	-
Sargassum muticum (Yendo) Fensholt	3	-	22	-	-	-	-	-	14	-	-	3
Sargassum vulgare C. Agardh	2	154	-	-	-	-	-	-	421	-	-	-
SUBTIDAL:												
Caulerpa racemosa (Forsskål) J. Agardh	1	-	-	-	-	-	6	-	-	-	-	-
Cladostephus spongiusus (Hudson) C. Agardh	9	111	-	-	-	-	-	1	105	3	4	9
Codium bursa (Linnaeus) C. Agardh	1	3	-	-	-	3	-	-	-	-	3	-
Codium vermilara (Olivi) Delle Chiaje	12	8	-	-	-	-	-	-	226	-	-	-
Cystoseira baccata (S.G.Gmelin) P.C.Silva	4	-	3	-	-	-	-	-	14	-	-	35
Cystoseira tamariscifolia (Hudson) Papenfuss	11	27	26	-	-	16	3	163	209	-	2	16
Dictyopteris membranacea (Stackhouse) Batters	2	-	47	-	-	-	-	-	8	-	-	1
Dictyota dichotoma (Hudson) J.V. Lamouroux	4	8	17	-	-	-	-	14	8	-	10	-
Gelidium corneum (Hudson) J.V.Lamouroux	7	3	51	-	-	-	-	-	1253	-	-	7
Gigartina pistillata (S.G.Gmelin) Stackhouse	2	1	2	-	-	-	-	-	5	-	-	1
Gigartina teedii (Roth) Lamouroux	3	-	7	-	-	-	-	-	23	-	-	-
Halimeda tuna (Ellis et Solander) Lamouroux	2	100	-	-	-	-	20	-	-	5	-	-
Haliptilon virgatum (Zanardini) Garbary & H.W.Johans	3	-	4	-	-	-	-	-	3	-	-	-
Halopitys incurvus (Hudson) Batters	1	-	-	-	-	-	7	-	-	-	-	-
Jania rubens (Limnaeus) J.V. Lamouroux	12	1	1	-	-	63	58	16	6	-	-	1
Laurencia obtusa (Hudson) Lamouroux	4	31	-	-	-	-	166	-	10	-	-	-
Liagora viscida (Forsskål) C. Agardh	2	-	-	-	-	-	-	-	10	-	-	-
Padina pavonica (Linnaeus) Thivy	1	4	-	-	-	23	-	-	-	-	-	-
Polysiphonia sp	1	-	50	-	-	-	-	-	12200	-	-	-
Pterocladia capillacea (S.G.Gmelin) Bornet	9	1	122	-	-	-	-	2	423	-	-	1
Rytiphlaea tinctoria (Clemente) C.Agardh	1	33	83	-	17	-	-	-	2000	-	-	17
Sachorriza polyschides (Lightfoot) Batters	4	93	-	-	-	-	-	-	2	-	-	-
Sphaerococcus coronopifolius Stackhouse	5	7	3	-	-	1	-	-	2	-	-	-
Stypocaulon scoparium (Linnaeus) Kützing	14	135	22			143	337	4	37	36	21	

species of algae. Subtidal substrates contained higher numbers of caprellid species (4.0 ± 2.2 , Mean \pm Standard Deviation) than intertidal ones (2.4 ± 1.6) (one-way ANOVA, F=5.85, p<0.05). Caprellid abundances were very high, both in the intertidal and shallow subtidal, with a mean reaching 12200 ind/ 1000 ml algae. Although caprellid abundances measured in the

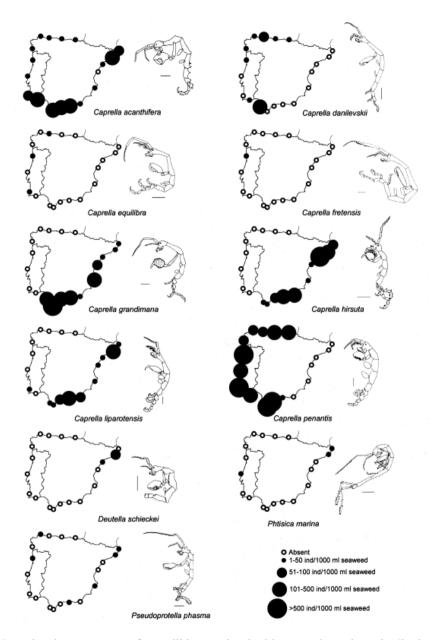


Fig. 2.—Abundance patterns of caprellids associated with macroalgae along the Iberian Peninsula. Data are expressed as ind/1000 ml algae (represented values are mean of densities of each species in the 46 algal species collected).

Fig. 2.—Patrones de abundancia de los caprélidos asociados a las macroalgas de la Península Ibérica. Los datos se expresan en ind/1000 ml de alga (los valores representan la media de las densidades de cada especie en las 46 espeices de algas recolectadas).

intertidal (584.2 ind/1000 ml alga \pm 207.9) were usually higher than those measured in the subtidal (283.9 \pm 106.6), differences were not significant (one-way ANOVA, F=1.69, p=0.2). The highest number of caprellid species occurred on the algae Stypocaulon scoparium, Cystoseira spp., Corallina elongata, Jania rubens, Codium vermilara, Cladostephus spongiosus and Asparagopsis armata. These results are in agreement with those obtained by Guerra-García (2001), who studied habitat use for the Caprellidea from Ceuta, North Africa. Guerra-García (2001) collected a total of 55 species that were potential substrates for the Caprellidea (19 species of algae, 8 hydroids, 9 ascidians, 7 anthozoans, 5 echinoderms, 3 sponges, 3 bryozoans and 1 annelid) from 0-40 m. depth, together with sediments from 5-15 m. A total of 22 caprellid species in 5 genera were collected along the coast of Ceuta (only several km long). However, if we restrict the results to algal substrates collected from intertidal or very shallow waters (<5m), the species collected in Ceuta are the same to those collected in the present study along the whole Iberian Peninsula. This interpretation supports the idea of a very similar community of caprellids along intertidal and shallow sublittoral zones in our latitudes.

Caprellids are one of the dominant groups of associated fauna in the intertidal in comparison with other taxa, in terms of number of specimens per volume or biomass of algae (see Guerra-García et al., 2009e, 2009c). Despite the high densities, the present study demonstrates that caprellid diversity (in terms of number of species) along the intertidal and very shallow bottoms of the Iberian Peninsula is very low (11 species) in comparison with total caprellid diversity including deeper areas >5 m from Spain and Portugal (ca. 40 species, unpublished data). Consequently, caprellids are much more important in our ecosystems in terms of biomass than in terms of number of species. Other studies have reported large biomasses of caprellids. Caprella penantis associated with macroalgae reaches 12000 ind/m² (Guerra-García et al., 2009e, 2009c; Guerra-García & Izquierdo, 2010). Conradi (1995) reported densities up to 10595 ind/100g of Caprella equilibra associated with the bryozoan Bugula neritina in Algeciras Bay, Cádiz, Southern Spain. Ashton et al. (2010) reported a density of 319000 ind/m² of Caprella mutica at a fish farm on the west coast of Scotland. In fact, caprellids constitute an important component of many fishes' diet (Woods, 2009).

Distributional patterns

In terms of biogeographical patterns, *Caprella acanthifera*, *Phtisica marina* and *Pseudoprotella phasma* occur along the whole Peninsula; *C. danilevskii*,

C. equilibra, C. fretensis and C. penantis show an Atlantic distribution, whereas C. grandimana, C. hirsuta, C. liparotensis and Deutella schieckei inhabit only Mediterranean sites and the Strait of Gibraltar. These general results agree with those obtained exclusively for Stypocaulon scoparium and Corallina elongata (Guerra-García et al., 2009e; Guerra-García & Izquierdo, 2010). Pereira et al. (2006) conducted a biogeographical study of intertidal macroinvertebrates and their association with macroalgal distribution along the Portuguese coast. These authors found distributions of the species Caprella danilevskii, C. penantis, C. liparotensis, C. acanthifera and Phtisica marina similar to the present study; but these authors also found occasionally C. mitis and C. dilatata, and abundantly C. andreae, especially in the southern stations, including Vale dos Homens and Castelo. We collected many algal samples at these stations and did not find any specimens belonging to C. andreae. Specimens of C. andreae from this 2006 study should be re-examined. They could be large specimens of C. penantis. Caprella andreae usually inhabits turtle caparaces, not intertidal zones (pers. observ.).

Bellan-Santini & Ruffo (1998) reported *C, hirsuta* and *C. grandimana*, considered as Mediterranean endemics by Krapp-Schickel (1993), on the Atlantic African coast from Cape Spartel to Cape Blanc. The present study, however, reveals that these two species are strictly restricted to Mediterranean conditions. Although both species could have been found along the Atlantic coast of Morocco, due to the Mediterranean influence along the Strait of Gibraltar, such a finding is not enough to consider that these two species are not endemic to the Mediterranean (Guerra-García *et al.*, 2009e). For example, specimens of the Mediterranean endemic *Patella ferruginea* Gmelin, 1971 have been found recently on the Atlantic coast of the Strait of Gibraltar (pers. observ.). Despite the similar distribution of *C. grandimana* and *C. hirsuta* along the whole Mediterranean coast, the maps of distribution (see Fig. 2) reveal that there could be competition between the two species: the stations in which *C. grandimana* is more abundant, *C. hirsuta* shows lower abundances, and vice versa.

Caprella penantis and *C. danilevskii* also show an interesting distribution pattern, being exclusively distributed in the Atlantic stations and Strait of Gibraltar. The lower oxygen values and higher temperatures of the Mediterranean seem inadequate for these species. As discussed by Guerra-García *et al.* (2009e), *C. penantis* is now much less abundant in the Mediterranean than some years ago, and we cannot disregard the possibility that this species could be disappearing from the Mediterranean intertidal due to global warming. At the Iberian Peninsula, the species *C. penantis* is replaced by *C. liparotensis* along the Mediterranean. Both species share

a similar morphology, but *C. liparotensis*, although usually associated with clean water, a preference similar to that of *C. penantis* (see Guerra-García & García-Gómez, 2001), seems to be able to tolerate lower oxygen concentrations and higher temperatures than does *C. penantis*.

Multivariate analysis

The Mediterranean coast is characterised by higher seawater temperature and conductivity and lower values of oxygen concentration and turbidity. Atlantic stations are much more exposed, contributing to increased turbidity and oxygen because of greater wave action (see Guerra-García & Izquierdo, 2010 for more details of physico-chemical measures). Cluster analysis based on caprellid composition (mean values of abundance in all the algal substrates) shows two distinct groups, one formed by Atlantic stations, and the other by the Mediterranean and Strait of Gibraltar sites (Fig. 3). With this figure, we can confirm that intertidal and shallow water caprellid fauna of the Strait of Gibraltar is more similar to the Mediterranean than to the Atlantic. The alga *Stypocaulon scoparium* exhibits the same pattern (Guerra-García *et al.* 2009e) but *Corallina elongata* does not (Guerra-García & Izquierdo, 2010). In the present study, considering the 46 species of algae as a whole, we obtained the same pattern as that obtained for *S. scoparium*.

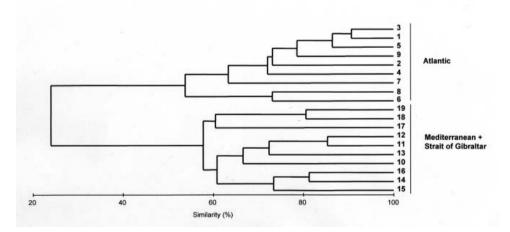


Fig. 3.—Cluster analysis based on caprellid abundances (see Table I). Fig. 3.—Análisis de cluster basado en la abundancia de caprélidos (véase Tabla I).

Canonical Correspondence Analysis showed that temperature, conductivity and oxygen are the environmental variables that better explain caprellid distribution, showing a clear Atlantic-Mediterranean gradient (Fig. 4, Table II). Furthermore, the pattern obtained with the 46 algal species supports the patterns previously obtained for *C. elongata* and *S. scoparium*.

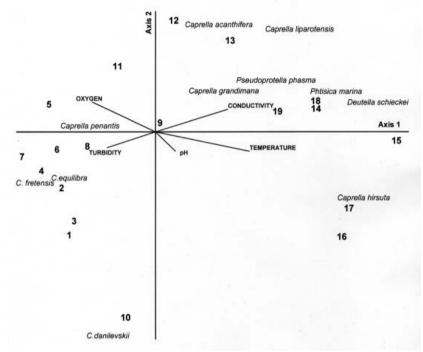


Fig. 4.—Graph representation of the stations and caprellids with respect to the first two axes of the Canonical Correspondence Analysis (CCA) (see also Table II).

Fig. 4.—Representación gráfica de las estaciones y los caprélidos con respecto a los dos primeros ejes del Análsis Canónico de Correspondencias (CCA) (ver también Tabla II).

	Axis 1	Axis 2	Axis 3
Eigenvalue Species-environment correlation	$0.67 \\ 0.93$	$0.19 \\ 0.79$	$0.06 \\ 0.38$
Percentage of species variance	32.8	9.0	2.9
Correlation with environmental variables			
Temperature (°C)	0.90***		
pH	_	-0.59 * *	0.84***
Oxygen (mg/l)	-0.66**		0.57**
Conductivity (mS/cm)	0.81***	0.60**	
Turbidity (ntu)			

Table II.—Summary	of the result	s of the CCA	análisis. **p<0.0	01, ***p<0.001
Tabla II.—Resumen	de los resulta	ados del análi	s CCA. **p<0.01	, ***p<0.001

Ecological and taxonomical remarks on the caprellid species found during the present study

Caprella acanthifera Leach, 1814

Taxonomy

Krapp-Schickel & Vader (1998) showed that the taxon Caprella acanthifera, usually considered to be one 'highly variable' species, consists of a number of closely related species. They defined two group of species, those lacking an axillary spine near the insertion of gnathopod 2 (the 'C. acanthifera group') and those characterized by the presence of this axillary spine ('the C. armata-group'). In their paper, Krapp-Schickel & Vader (1998) focused on the *acanthifera*-group and studied the taxa with an axillary spine: they redefined Caprella acanthifera Leach 1814 sensu stricto, and described Caprella stella from the aboral surface of starfishes in the Azores (15-32 m depth), and C. cavediniae from among algae in the Mediterranean (1.5-5 m depth). Guerra-García et al. (2001a) described two new species belonging to this C. armata group: Caprella monai collected from hydroids and sediments, and Caprella takeuchii collected from intertidal algae and sediment substrate under intertidal boulders, both species highly setose. Guerra-García et al. (2001b; 2002b) described the species Caprella caulerpensis, C. pseudorapax and C. sabulensis, closely related to 'C. acanthifera group' species, based on material collected from the sediments of the Strait of Gibraltar. The C. armata group (including form discrepans, see Krapp-Schickel, 1993) remains in need of revision, but a detailed study will likely reveal the existence of several species inside the group.

Taking into account that the 'acanthifera complex' is not completely resolved yet, in the present study we have considered all the studied specimens under the taxon Caprella acanthifera sensu lato. We have observed morphological differences among specimens along the Iberian Peninsula, including the form C. acanthifera sensu stricto, with rounded projections, and morphological varieties matching the form discrepans, but most of the specimens lack an axillary spine. On the other hand, several specimens found during the present study could probably belong to Caprella takeuchii, based mainly on the presence of abundant setae. However, adult specimens of C. acanthifera often have gnathopods and/or bodies densely overgrown with filiform algae, elliptic diatoms and suctorian protozoans such as Ephelota (Krapp-Schickel & Vader, 1998), which easily might be confused with setae, making difficult the differentiation between the two species. A detailed morphological and molecular study of the material collected from the whole Iberian Peninsula, together with other Mediterranean and Atlantic areas should be undertaken to clarify the taxonomic status of all specimens of *C. acanthifera sensu lato* found along the Iberian Peninsula.

Ecology

Caprella acanthifera sensu stricto lives mainly at 0-10 m depth, although Krapp-Schickel & Vader (1998) reported the species at 33 m. It dwells among brown algae, on sponges, hydroids, ascidians, anthozoans, bryozoans, seagrasses and sediments (Krapp-Schickel, 1993; Jimeno & Turón, 1995; Krapp-Schickel & Vader, 1998; Guerra-García, 2001; González *et al.*, 2008; Vázquez-Luis *et al.*, 2009). This species inhabits areas with little water movement and rich detritus (Krapp-Schickel & Vader; Guerra-García & García-Gómez, 2001). In the present study, we found the species clinging to 24 species of algae.

Biology

Muñoz-Cobo (1981) and Moreira (2003) found the highest densities of this species in summer months. Jimeno (1993) found ovigerous females during April, June, August and September. Guerra-García *et al.* (2009a) studied the seasonal fluctuations of intertidal caprellids from Tarifa Island, Southern Spain, and found *C. acanthifera* throughout the whole year, with maximum densities in June. In terms of clinging behaviour, *C. acanthifera* spends most of the time in an "upright" posture, with a considerable scraping and grooming (Guerra-García *et al.*, 2002a). According to the dietary analysis conducted by Guerra-García & Tierno de Figueroa (2009) *C. acanthifera* feeds mainly on detritus, but also on diatoms and even polychaetes.

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied and discussed the fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Devonshire, England. *Other records*: Atlantic Ocean (from Norway to Azores). Mediterranean, Adriatic and Black Seas (McCain & Steinberg, 1970; Krapp-Schickel & Vader, 1998).

Location of type material: The holotype is lost. Krapp-Schickel & Vader (1998) established a neotype using the type of *C. calva* Bate, 1856 from Plymouth.

Caprella danilevskii Czerniavskii, 1868

Taxonomy

The distinctive male abdomen, the absence of grasping spines on the percopods and the short dactylus of male gnathopod 2 distinguish this species clearly from other species of *Caprella*. The morphology of this species is quite constant all over the world; nevertheless, Guerra-García & Takeuchi (2004) studied material from Tasmania and found some males showing very elongate antenna 1, perconites 1 and 2, basis and propodus of gnathopod 2. The Atlantic specimens found during the present study are all similar in morphology, and no distinct morphological varieties could be detected.

Ecology

The species lives on algae, bryozoans, seagrasses, sponges and tunicates (Krapp-Schickel, 1993; Guerra-García, 2001). Guerra-García (2001) collected specimens from different species of algae in areas of high hydrodynamics. In fact, the species is mainly found in very exposed areas with low sedimentation (Guerra-García & García-Gómez, 2001). In the present study, we found the species clinging to 20 species of algae.

Biology

Caprella danilevskii, similar to C. *penantis*, appears to have acquired the ability to attach to the substrate using gnathopod 1 in a "parallel" posture rather than in the "upright" posture used by species living in calmer waters. This species feeds mainly by scraping (see Takeuchi & Hirano, 1995; Guerra-García *et al.*, 2002a). A study of the diet revealed the presence of detritus (main component) in the digestive tract, but copepods, diatoms and dinoflagelates were also present. *Caprella danilevskii* is one of the most studied caprellid species in terms of life history, based on Japanese specimens (Takeuchi & Hirano, 1991, 1992).

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Black Sea. *Other records*: Atlantic, Mediterranean, South Africa, South Arabian coast, Bermuda, Venezuela, Brazil, Hawaii, northeastern

Pacific, and Australia (see McCain and Steinberg, 1970; Krapp-Schickel, 1993; Díaz *et al.*, 2005). Doubtfully considered cosmopolitan.
Location of type material: Unknown (McCain & Steinberg, 1970).

Caprella equilibra Say, 1818

Taxonomy

Specimens of *C. equilibra* have a distinctive ventral projection between gnathopods 2, characteristic of this species. During the present study, only a few specimens were found at Atlantic stations. All specimens possessed the ventral projection. Although this species is constant in most of its characteristics around the world, McCain (1968) reported a variant living on gorgonians along the coast of North and South Carolina, USA, in which the projection is reduced or absent; this variant could probably be a different species.

Ecology

Caprella equilibra dwells on seagrasses, algae, sponges, hydroids, bryozoans, ascidians, alcyonarians, molluscs or even other crustaceans such as *Squilla empusa*, from the intertidal to 3000 meters depth (Krapp-Schickel, 1993; Guerra-García & Takeuchi, 2004; Díaz *et al.*, 2005). This species is also associated with artificial devices such as aquaculture nets, water duct pipes, power plants, and floating substrates (e.g. buoys and drift algae) (Takeuchi & Sawamoto, 1998; Thiel *et al.*, 2003).

Biology

Caprella equilibra feeds principally by filtering, frequently using grooming behaviour, in the "upright" position (Guerra-García *et al.*, 2002a). The dietary analysis of this species shows detritus as the main food component, but also an important contribution from copepods, hydroids and algae (Guerra-García & Tierno de Figueroa, 2009). Krapp-Schickel (1993) reported predation using gnathopods 1 and rarely gnathopods 2 on *Ampithoe*, *Jassa* and small polychaetes. Dewey (1970) conducted a complete study on the feeding habitats of *C. equilibra*. Sánchez-Moyano *et al.* (unpublished data) studied the annual life cycle of *C. equilibra* from an estuarine zone of Southern Spain, and reported breeding throughout the year, with the main reproductive peaks occurring in early spring and early fall. Guerra-García *et al.* (2009a) found the species in the intertidal zone of Tarifa Island from February to April.

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: South Carolina, USA. *Other records*: Atlantic Ocean, Mediterranean, Black Sea, Indian Ocean, Pacific Ocean (McCain & Steinberg, 1970; Krapp-Schickel, 1993).

Location of type material: Academy of Natural Sciences, Philadelphia (McCain & Steinberg, 1970).

Caprella fretensis Stebbing, 1878

Taxonomy

Only one specimen (adult male) was found during the present study. This species can be clearly distinguished by the setae on antenna 1 and gnathopod 2.

Ecology

Caprella fretensis lives on algae, seagrasses, sand and muds (Marques & Bellan-Santini, 1985; Guerra-García, 2001; Guerra-García & Takeuchi, 2002). The species is not common and seems to have a restricted distribution.

Biology

Unknown

Biochemistry

Unknown

General distribution

Type locality: Salcombe Estuary, England. *Other records*: British Isles, France, North of Spain and Portugal (Chevreux & Fage, 1925; Anadón, 1975; Marques & Bellan-Santini, 1985; Arresti *et al.*, 1986).

Location of type material: Unknown.

Caprella grandimana Mayer, 1882

Taxonomy

Guerra-García et al. (2001a) redescribed specimens collected from intertidal pools of Tarifa Island in detail. The taxonomic position of C. grandimana has been unclear since its original description by Maver (1882). Since then this species was considered a variety or subspecies of C. acanthifera (Mayer, 1890). Chevreux (1913) and McCain & Steinberg (1970) considered C. grandimana as C. hirsuta f. longimana. Finally, Cavedini (1982) considered C. grandimana again as a different species and established the synonymy between C. grandimana and C. hirsuta f. longimana. After their redescription, Guerra-García et al. (2001a) agreed with Cavedini (1982) in considering C. grandimana as a valid species. In fact, C. hirsuta and C. grandimana not only differ in morphological characters, but also in the number of chromosomes (C. hirsuta 2n=26, C. grandimana 2n=22) (Libertini, comm. pers.). Although males of both species can easily be distinguished by clear differences in gnathopod 2, females are quite similar and can apparently only be distinguished by the setation of pereopods, which are much more setose in specimens of C. hirsuta.

In the present study morphological differences were observed between specimens of *C. grandimana* collected from the Strait of Gibraltar (more robust and setose) than those collected from some Mediterranean stations such as Cala del tío Ximo (smaller specimens with less setae). A detailed morphological study together with molecular tools should be undertaken to clarify if there is intraspecific variation inside the species, or the specimens belong to different species.

Ecology

The ecology of *C. grandimana* is poorly known (Krapp-Schickel, 1993). The species lives on algae at 0-10 m depth (Krapp-Schickel, 1993; Jimeno & Turón, 1995). In the present study, we have found the species clinging to 11 species of algae. Guerra-García *et al.* (2009c) reported this species as one of the most abundant crustaceans associated with the alga *Corallina elongata*.

Biology

Caprella grandimana feed mainly on detritus, copepods and diatoms (Guerra-García & Tierno de Figueroa, 2009). The life history of this species is known under laboratory conditions (see Baeza-Rojano *et al.*,

2011). Seasonal fluctuations in natural conditions for two years show high densities in the intermediate levels of the intertidal throughout the entire year (Guerra-García *et al.*, 2009a).

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Naples. *Other records*: Mediterranean endemic: France, Italy-Tyrrhenian Sea, Monaco, Israel, Strait of Gibraltar (Krapp-Schickel, 1993; Guerra-García *et al.*, 2009c).

Location of type material: Unknown.

Caprella hirsuta Mayer, 1890

Taxonomy

Guerra-García *et al.* (2000b) redescribed this species based on specimens collected from the Strait of Gibraltar, and reported several differences with previous descriptions. Likely these differences are due more to the lack of details in the original description of Mayer (1890) than to intraspecific variation. All specimens studied from the Mediterranean Iberian Peninsula showed a similar morphology; male gnathopod 2 clearly distinguishes males of *C. hirsuta* from other species. Pereopods of males and females are more setose in *C. hirsuta* than in other related species, such as *C. grandimana*.

Ecology

Caprella hirsuta has been found on *Balanus*, hydroids, Asteroidea and algae from 0-30 m deep. The species seems to prefer habitats with abundant detritus (Guerra-García *et al.*, 2000b; Vázquez-Luis *et al.*, 2009), and specimens from the Strait of Gibraltar are usually sediment-covered (Guerra-García *et al.*, 2000b). In the present study, we found the species clinging to 13 species of algae.

Biology

This species feeds mainly on detritus, but Guerra-García & Tierno de Figueroa (2009) found, in addition, a low proportion of diatoms and dinoflagellates in the digestive tract.

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Gulf of Naples. *Other records*: Mediterranean endemic: France, Sardinia, Italy-Tyrrhenian Sea, Sicily, Israel, Tunisia (Krapp-Schickel, 1993; Guerra-García *et al.*, 2000b).

Location of type material: Zoological Museum, Copenhagen

Caprella liparotensis Haller, 1879

Taxonomy

Guerra-García & Takeuchi (2002) redescribed this species in detail based on material from the Strait of Gibraltar. Krapp-Schickel & Takeuchi (2005) described *Caprella wirtzi* from Cape Verde, a species very close (or morphologically similar) to *C. liparotensis*. Specimens of *C. liparotensis* examined during the present study showed consistant morphological characteristics. At some stations, *C. liparotensis* shared substrates with *C. penantis*. Although adult males are clearly different, females and juveniles of both species are rather similar and can be confused. Future detailed morphological studies are necessary to look for constant and valid characters to differentiate females of *C. liparotensis* and *C. penantis*.

Ecology

Krapp-Schickel (1993) suggested that *C. liparotensis* is always associated with hydroids. However, Guerra-García (2001) found the species clinging to different species of algae. In fact, during the present study, we found *C. liparotensis* associated with 12 species of algae. *C. liparotensis* mainly exists in very exposed areas with low sedimentation (Guerra-García & García-Gómez, 2001).

Biology

This species can be considered a detritivore, but also copepods and even hydroids are present in the digestive trait (Guerra-García & Tierno de Figueroa, 2009). Guerra-García *et al.* (2009a) studied the seasonal fluctuations of intertidal caprellids from Tarifa Island and found *C. liparotensis* in the period April-June.

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Lipari, Italy. *Other records*: Coast of Portugal, Mediterranean, Adriatic and Black Seas (Krapp-Schickel, 1993; Guerra-García & Takeuchi, 2002).

Location of type material: Unknown (see Krapp-Schickel & Takeuchi, 2005).

Caprella penantis Leach, 1814

Taxonomy

Caprella penantis is one of the most taxonomically problematic caprellids throughout the world, since this species has been recorded as several different species or subspecies from the temperate regions of the world. Most taxonomic studies on this caprellid have pointed out the need for genetic studies to determine its identity status at each locality (McCain, 1968; Laubitz, 1972; Guerra-García et al., 2006; Cabezas et al., 2010). Mayer's monographs (1890, 1903) described nineteen forms of the "acutifrons" group (forms typica, minor, tabida, tibada, neglecta, gibbosa, andreae, carolinensis, virginia, lusitanica, natalensis, porcellio, simulatrix, testudo, angusta, incisa, vertucosa, borealis and cristibrachium). Several of these forms have already been given specific rank. The study of Cabezas et al. (2010), based on RAPD analyses, showed that all C. penantis forms from the Iberian Peninsula, including forms with the projection in gnathopod 2 (*testudo* and *lusitanica*) and without this projection (*simulatrix*) seem to be very similar from the molecular point of view, suggesting that there is no clear evidence to support species differentiation. The presence/absence of the projection seems not to be related with species differentiation but with phenotypic intraspecific variation. Presently, the material from the Iberian Peninsula, together with material from other world areas, is being studied by mtDNA (COI) (Cabezas et al., in prep.).

Ecology

This species lives on red and brown algae, seagrasses such as *Posidonia*, hydroids, alcyonarians, zoantharians, bryozoans, sponges, echinoderms (*Arbacia*), decapods (*Libinia*) and mussels (McCain, 1968; Krapp-Schickel, 1993; Díaz *et al.*, 2005). We found *C. penantis* showing very low substrate-specificity, as it was associated with 34 species of algae. Guerra-García *et al.* (2009c) reported *C. penantis* as one of the most common species associated with *C. elongata* along the Strait of Gibraltar.

Ecological characteristics of the habitat could be a main influence on the morphological variation among populations of *C. penantis*. Bynum (1980), for example, conducted a morphometric study using *C. penantis* from coastal and estuarine sites in North Carolina and found a gradient of forms related to the degree of exposure to turbulence. Body parts and appendages associated with grasping the substrate of a caprellid species are capable of modification depending on the degree of wave exposure, thus exhibiting ecological plasticity or "ecotopic variation" (Caine, 1989; Guerra-García, 2001).

Caprella penantis clearly prefers oxygenated waters with high hydrodynamics and low organic matter (Guerra-García & García-Gómez, 2001). Furthermore, Guerra-García *et al.* (2009b) proposed usisng the species as an interesting biomonitor of trace metal contaminantion.

Biology

Caprella penantis is morphologically similar to C. *danilevskii* and appears to have acquired the ability of attaching to the substrate using gnathopod 1 in a "parallel" posture rather than in the "upright" posture used by species living in calmer waters; the species feeds mainly by scraping (see Takeuchi & Hirano, 1995; Guerra-García *et al.*, 2002a). The diet is varied, including detritus, copepods, other amphipods, macroalgae, diatoms and dinoflagellates (Guerra-García & Tierno de Figueroa, 2009). Guerra-García *et al.* (2009a) found the species during the entire year in the intertidal zone of Tarifa Island, with maximum numbers by the end of spring and beginning of summer.

Biochemistry

Guerra-García *et al.* (2004, 2009d, 2010) studied fatty acid composition, together with contents of C, N, H, S, Na, K, Ca and Mg for intertidal specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: Devonshire, England. *Other records*: Atlantic Ocean, Indian Ocean, Pacific Ocean, Mediterranean Sea (Krapp-Schickel, 1993). Considered a cosmopolitan species.

Location of type material: Unknown.

Deutella schieckei Cavedini, 1982

Taxonomy

Cavedini (1982) described this species based on material from Sardinia. We found specimens of this species only in some Mediterranean stations. All the specimens were very constant in their morphological characteristics.

Ecology

This species dwells on algae in shallow waters along the Spanish Mediterranean coasts (Jimeno & Turón, 1995; Vázquez-Luis *et al.*, 2009). We found the species associated with four algal species.

Biology

Unknown

Biochemistry

Unknown

General distribution

Type locality: Sardinia: Capo Caccia. *Other records*: Mediterranean coast of Spain. Mediterranean endemic.

Location of type material: Museo Civico di Storia Naturale di Verona.

Phtisica marina Slabber, 1769

Taxonomy

Although this species is very common in this area, we found only a few specimens. Probably, the reason is that this species is much more abundant below 10 m depth than in the area 0-5 m (see Guerra-García, 2001). All the specimens examined from algae during the present study show a similar morphology, and we could not distinguish different forms. The presence

of developed pereonites 3 and 4 make the morphological recognition of this species easy. Study of species belonging to the "Phtisicidae group" is of special relevance in understanding the phylogeny of the Caprellidea (Takeuchi, 1993; Ito *et al.*, 2008).

Ecology

Phtisica marina inhabits algae, seagrasses, hydroids, anthozoans, sponges, ascidians, bryozoans, annelids, echinoderms and sediments from 0 to 660 m (Krapp-Schickel, 1993; Guerra-García, 2001). High densities of this species are associated with the invader species *Caulerpa racemosa* (Vázquez-Luis *et al.*, 2009). This species is able to inhabit waters with high values of silting, suspended solids and organic matter (Guerra-García & García-Gómez, 2001), but also inhabits unpolluted environments (Guerra-García, 2001). Gonzalez *et al.* (2008) reported that perturbations can favor *P. marina* and increase its density after trawling activities.

Biology

Phtisica marina attaches to the substrate in the "upright" position, with low percentage of grooming time, suggesting a predatory mode of life (Guerra-García *et al.*, 2002a). Frequent cannibalism occurs for this species (Guerra-García *et al.*, 2002a). Although traditionally *P. marina* has been considered a predator, a recent study of its diet revealed that, besides copepods and amphipods, the species feeds on diatoms, dinoflagellates and a high proportion of detritus (Guerra-García & Tierno de Figueroa, 2009). Guerra-García *et al.* (2000a) studied the seasonal fluctuations of *P. marina* inhabiting the perennial algae *Cystoseira usenoides* and *Sargassum vulgare* in an estuarine zone of Southern Spain and found the highest densities during winter and spring. Du Sel *et al.* (2000) report *Phtisica marina* as the main prey for the cuttlefish *Sepia officinalis* during its first 3 months of life.

Biochemistry

Guerra-García *et al.* (2004) have studied and discussed fatty acid composition for specimens of this species collected from the Strait of Gibraltar.

General distribution

Type locality: The island of Walcheren, province of Zeeland, The Netherlands. *Other records*: Atlantic Ocean, Pacific Ocean and Mediterranean Sea (Krapp-Schickel, 1993).

Location of type material: Unknown.

Pseudoprotella phasma (Montagu, 1804)

Taxonomy

Several specimens of this species exist along the Iberian Peninsula, all of them having a similar pattern of morphological characteristics.

Ecology

The species lives from 0-2450 m depth (see Guerra-García, 2004), and dwells on, anthozoans and sediment (Guerra-García, 2001). High densities of this species are associated with the invader species *Caulerpa racemosa* (Vázquez-Luis *et al.*, 2009). Although Krapp-Schickel (1993) reported the species rarely associated with hydroids, Guerra-García (2001) found that hydroids were the preferred substrate for this species in Ceuta. In fact, during the present study, although we found the species living in only11 algal species, we found that is the dominant species, together with *C. liparotensis*, on intertidal and shallow water (max. 5 m depth) hydroids. Prato & Biandolino (2005) reported *P. phasma* as the dominant species found in detritus, sand, mud and algae in the Taranto Seas. This species prefers sites characterized by moderate silting and suspended solids (Guerra-García & García-Gómez, 2001) but can be found also in unpolluted environments (Guerra-García, 2001).

Biology

Pseudoprotella phasma attaches to the substrate in the "upright" position, with a low percentage of grooming, suggesting a predatory mode of life similar to *P. marina* (Guerra-García *et al.*, 2002a). Copepods, amphipods and polychaetes constitute a high proportion of its diet, together with hydroids, diatoms and detritus (Guerra-García & Tierno de Figueroa, 2009). Di Camillo *et al.* (2008) considered this species as cleptocomensal on the hydroids *Eudendrium* spp. Hughes (1978) studied the life history of this species, and Guerra-García *et al.* (2000a) reported the highest densities of the species during May and June. This species exhibits parental care (pers. observ.). Schucksmith *et al.* (2009) showed that the invader species *Caprella mutica* could successfully displace *P. phasma* when resource space is limited.

Biochemistry

Unknown

General distribution

Type locality: South coast of Devonshire, England. *Other records*: Atlantic Ocean and Mediterranean Sea (Krapp-Schickel, 1993). *Location of type material*: Unknown.

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