Spatial patterns and seasonal fluctuations of the intertidal Caprellidae (Crustacea: Amphipoda) from Tarifa Island, Southern Spain

Distribución espacial y fluctuaciones estacionales de los caprélidos intermareales (Crustacea: Amphipoda) de la Isla de Tarifa, sur de España


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Palabras clave: Caprélidos, algas, intermareal, ecología, distribución espacio-temporal.

ABSTRACT

Tarifa Island is located in the Strait of Gibraltar, between the Mediterranean and Atlantic. The unique biogeographical position, together with the substrate heterogeneity and the protection degree resulting from its condition of marine reserve, has contributed to maintain very diverse intertidal ecosystems at their rocky shores. Under absence of anthropogenic influence, we have studied the fluctuations of macroalgae and associated caprellids during two years (December 2005 to December 2007). Samples were taken every two months from the different intertidal levels. Caprella penantis, C. liparotensis and C. equilibra were exclusively distributed in the low intertidal levels dominated by Gelidium corneum; Caprella grandimana and C. acanthifera were found in the intermediate levels of Corallina elongata, Jania rubens and Gelidium spp. and the caprellids were absent in the upper intertidal levels dominated by Fucus spiralis. The caprellid species and the main seaweeds were present during the whole year. The peaks of seaweed biomass were observed from April to June, and were coincident with the peaks in caprellid abundances. The highest caprellid fluctuations were registered in the low levels: although G. corneum maintained high biomass during the whole year, the associated C. penantis had

very low densities in winter (<50 ind/m²) and high densities (around 5,000 ind/m²) in early summer. On the other hand, the population of C. grandimana associated to intermediate levels, showed similar densities all the year round. These seasonal patterns could be related to winter storms, which mainly affect to the low intertidal levels, near the subtidal area.

RESUMEN

La Isla de Tarifa se localiza en el Estrecho de Gibraltar, entre el Mediterráneo y el Atlántico. Su posición biogeográfica singular, junto con la heterogeneidad del sustrato y el grado de protección como zona de reserva, ha contribuido a mantener ecosistemas intermareales rocosos muy biodiversos. Teniendo en cuenta la ausencia de influencia antrópica en el área de estudio, se estudiaron las fluctuaciones de las algas y caprélidos asociados durante dos años (diciembre 2005 a diciembre de 2007). Las muestras se recolectaron cada dos meses en los distintos niveles del intermareal. Caprella penantis, C. liparotensis y C. equilibra se distribuyeron exclusivamente en los niveles más bajos dominados por Gelidium corneum; Caprella grandimana y C. acanthifera se encontraron en los niveles intermedios de Corallina elongata, Jania rubens y Gelidium spp., y no se encontraron caprélidos en los niveles superiores dominados por Fucus spiralis. Las especies de caprélidos y las algas principales estuvieron presentes durante todo el año. Los picos de biomasa de algas se registraron de abril a junio, coincidiendo con los picos en las abundancias de los caprélidos. Las mayores fluctuaciones estacionales en los caprélidos se midieron en los niveles inferiores: aunque G. corneum mantuvo una biomasa elevada durante todo el año, el caprélido asociado C. penantis mostró bajas densidades en invierno (<50 ind/m²) y altas densidades (en torno a 5,000 ind/m²) a comienzos del verano. Por otra parte, la población de C. grandimana asociada a los niveles intermedios mostró densidades similares durante todo el año. Estos patrones estacionales podrían estar relacionados con los temporales de invierno, que afectan fundamentalmente a los niveles más bajos del intermareal, próximos a la zona infralitoral.

INTRODUCTION

The Straits Natural Park (Parque Natural del Estrecho) (Fig. 1) was declared a protected area in 2003. It is a maritime-terrestrial park along 54 km of coastline in Southern Spain and includes highly diverse and structured marine communities (García-Gómez et al., 2003). Inside the Park, Tarifa Island is considered as marine reserve, and constitutes the most interesting enclave of the park regarding to the marine habitat. Tarifa Island is the most southern point of Europe, just between the Mediterranean and Atlantic, with 21 hectares and 2 km of coastline. The unique biogeographical position, together with the substrate heterogeneity and the access restrictions to the
area by the military for a long time, has contributed to maintain very diverse intertidal ecosystems at their rocky shores. Guerra-García & García-Gómez (2000) reviewed the marine fauna of Tarifa Island, compiling all the literature dealing with marine communities of the area.

Zonation patterns of marine algae and invertebrates, especially mussels, barnacles, snails, and limpets, have been intensively studied, while only a few researches have studied the zonation patterns of rocky intertidal amphipods (but see Chavanich & Wilson, 2000). In Europe, research on caprellids’ life cycles based on field studies is limited to a few species. For example, *Pseudoprotella phasma* from the southwest coast of England showed a life span...
of 6 to 9 months with three generations per year (Hughes, 1978). Ovigerous females of *Caprella acanthifera* from Ireland were collected from April to June and October to November by Costello & Myers (1989), suggesting that *C. acanthifera* produces two generations per year or reproduces twice each year (Takeuchi & Hirano, 1991). The breeding activity of *Caprella equilibra* from a lagoon estuary of the Northern Adriatic Sea showed peaks in April and September, breeding stopped in winter and females produced more than one brood per year (Sconfietty & Luparia, 1995). The density of *Phtisica marina* from an estuarine zone of southwest Spain was higher in winter and spring than in summer and autumn; in fact, there was a complete cessation in the reproduction of this species from August to November (Guerra-García *et al*., 2000).

Recently, it has been an increasing interest in the study of growth and reproduction of caprellids reared under laboratory conditions (see Takeuchi & Hirano, 1991, 1992a,b; Cook *et al*., 2007). Takeuchi & Hirano (1991) pointed out the difficulty of estimating generation structure for caprellid amphipods based on size-frequency distribution data from monthly field samples due to the important fluctuations in the number of individuals during short periods of time. According to this, moulting cycle, growth, and maturation should be better examined under laboratory conditions. However, for management and conservation purposes, especially in protected areas, it is also essential to know and understand the spatial distribution and seasonal fluctuations of species in the field, since many factors such as habitat complexity, competition and predation among species, winter storms, etc., can severely influence life cycles; those factors can not be properly evaluated in the laboratory when rearing specimens under controlled conditions. Consequently, the purpose of this study was to examine the zonation pattern and seasonal abundance of caprellids associated to intertidal algae from Tarifa Island.

**MATERIAL AND METHODS**

All the samples were collected from the most southern point of Tarifa Island (Punta Marroquí, 36°00'00.7"N, 5°36'37.5"W). The width of the intertidal range in this location is 250 cm approximately (Fig. 1) and we considered 5 levels to establish the zonation of the intertidal algae (level 1: from zero tidal level to 0.5 m; level 2: 0.5-1 m; level 3: 1-1.5 m; level 4: 1.5-2 m and level 5: 2-2.5 m). A ruler, set square and rope were used to establish the different heights. The first height was the zero tidal level and the process was continued until the vertical height of 2.5 meters had been achieved, coinciding with upper limit of the intertidal community (see Fa...
et al., 2002; Guerra-García et al., 2006). At each height, three replicates (quadrats 20 x 20 cm) were sampled. The surface was scrapped and all specimens of algae and associate fauna were collected. Samples were taken every two months from the different intertidal levels (December 2005 to December 2007). The samples were fixed in ethanol 70-80% and brought to laboratory. Samples were sieved using a mesh size of 0.5 mm and caprellids were sorted, identified to species level and counted; abundance of caprellid species was expressed in number of individuals per m². The most abundant seaweeds were identified to species level and biomass of algae was expressed in grams of dry weight per m². In each sampling, water temperature and salinity were measured using a conductivimeter WTW LF-323.

The relationships between seaweeds and caprellids in the different intertidal levels along the studied period, were explored by Canonical Correspondence Analysis (CCA). Multivariate analyses were carried out using the PC-ORD programme (McCune & Mefford, 1997).

RESULTS

Salinity values were more or less constant (around 37 psu) along the two years of study, while water temperature ranged from 14.4ºC (February) and 19.4ºC (August and October) (Fig. 2).

Level 1 (0-0.5 m) was dominated by Gelidium corneum (=sesquipedale) and Gymnogongrus patens (Fig. 3). Level 2 (0.5-1 m) was mainly constituted by a turf of several species of Gelidium and Caulacanthus ustulatus, Valonia utricularis and Osmundea (=Laurencia) pinnatifida. Corallinacea algae (Corallina elongata and Jania rubens) were located in level 3 (1-1.5 m), level 4 was dominated by the green algae Ulva rigida and Chaetomorpha aerea, while Fucus spiralis was the only species found in level 5 (Fig. 3). The highest values of seaweed biomass were registered in level 3, followed by level 1 and 4 (Fig. 4). The intermediate levels (2-4) showed the maximum biomass values in April-June, while level 1 and 5 showed the highest values along April-August. Anyway, both studied years showed a similar pattern, with higher values of seaweed biomass during spring and beginning of summer, and lower values from late summer to winter.

A total of 7,227 caprellids of five species were collected during the present study from the intertidal of Tarifa Island: Caprella penantis, C. liparotensis and C. equilibra, distributed exclusively in level 1, Caprella grandimana, especially abundant in level 3 but also present in level 2 and 4, and Caprella acanthifera, distributed in levels 3 and 4 (Table 1). Caprellids were absent in level 5. The highest abundances were registered in level 1.
Fig. 2.—Data (Mean ± SD) of temperature and salinity in the study area.
Fig. 2.—Datos (Media ± DE) de temperatura y salinidad en el área de estudio.

Fig. 3.—Macroalgal species in each intertidal level (L1-L5) and their relative abundance.
Fig. 3.—Especies de macroalgas en cada nivel intermareal (L1-L5) y su abundancia relativa.
with maximum values in April-June and very low values in December-February (Fig. 5). In general, caprellids also showed higher abundances in spring and beginning of summer, similarly to seaweeds. However, patterns of abundance of caprellids associated to level 3 were not so clear as in level 1. *Caprella penantis* and *C. grandimana* were the dominant caprellids; *Caprella penantis* showed clearly the seasonal pattern of abundance peaks in April and June and very low densities in December and February, while *Caprella grandimana* showed abundances ranging from 100-1,000 ind/m² along the whole year. Figure 6 and table 2 show the results of the CCA analysis. The first axis absorbed almost all the variance explained by the data, and correlated positively with *Gelidium corneum* and *G. patens* and negatively with *Corallina elongata, Jania rubens, Valonia utricularis, Osmundea pinnatifida* and the algal turf. This axis 1 separated clearly samples of level 1 (L1) dominated by *C. penantis* from the other levels (L2, L3 and L4). Axis 2 mainly correlated with green algae (*Chaetomorpha aerea* and *Ulva rigida*), separating level 4 dominated by *C. acanthifera* from levels 2 and 3 dominated by *C. grandimana.*
Table 1.—Caprellid species found during the study and their abundance along the year (seasonal fluctuations) and zonation in the different intertidal levels (L1-L5).

Tabla 1.—Especies de caprélidos encontrados durante el estudio y su abundancia a lo largo del año (fluctuaciones estacionales) y zonación en los diferentes niveles del intermareal (L1-L5).

<table>
<thead>
<tr>
<th>Caprellid species</th>
<th>Dec</th>
<th>Feb</th>
<th>Apr</th>
<th>Jun</th>
<th>Aug</th>
<th>Oct</th>
<th>Dec</th>
<th>Feb</th>
<th>Apr</th>
<th>Jun</th>
<th>Aug</th>
<th>Oct</th>
<th>Dec</th>
<th>1</th>
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<tbody>
<tr>
<td>Caprella acanthifera (Leach, 1814)</td>
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<td>Caprella equilibra (Say, 1818)</td>
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<td>Caprella grandimana (Mayer, 1882)</td>
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<td>Caprella lapurotenis (Haller, 1879)</td>
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<tr>
<td>Caprella penartzis (Leach, 1814)</td>
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Table 2.—Summary of the results of the CCA analysis. *p<0.05, **p<0.01, ***p<0.001

Tabla 2.—Resumen de los resultados del análisis ACC. *p<0.05, **p<0.01, ***p<0.001

<table>
<thead>
<tr>
<th></th>
<th>Axis 1</th>
<th>Axis 2</th>
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<tbody>
<tr>
<td>Eigenvalue</td>
<td>0.98</td>
<td>0.04</td>
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<tr>
<td>Caprellid-seaweed correlation</td>
<td>0.99</td>
<td>—</td>
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<tr>
<td>Percentage of species variance</td>
<td>54.5</td>
<td>2.2</td>
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<tr>
<td>Correlation with seaweeds</td>
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<tr>
<td><em>Gelidium corneum</em></td>
<td>0.99***</td>
<td>—</td>
</tr>
<tr>
<td><em>Gymnogongrus patens</em></td>
<td>0.63**</td>
<td>—</td>
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<tr>
<td><em>Valonia utricularis</em></td>
<td>−0.3*</td>
<td>—</td>
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<tr>
<td>Turf</td>
<td>−0.4*</td>
<td>−0.4*</td>
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<tr>
<td><em>Osmundea pinnatifida</em></td>
<td>−0.3*</td>
<td>−0.3*</td>
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<tr>
<td><em>Corallina elongata</em></td>
<td>−0.3*</td>
<td>—</td>
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<tr>
<td><em>Jania rubens</em></td>
<td>−0.3*</td>
<td>—</td>
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<tr>
<td><em>Ulva rigida</em></td>
<td>—</td>
<td>0.83***</td>
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<tr>
<td><em>Chaetomorpha aerea</em></td>
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<td>0.85***</td>
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DISCUSSION

The main intertidal seaweeds of Tarifa Island showed a perennial behaviour. The species were present along the whole year, although maximum values of biomass were registered during spring and beginning of summer for most of the algae. This fact probably determined that the main caprellid species, i.e. *Caprella penantis* and *C. grandimana* were also present throughout the year. Seasonal fluctuations of caprellids were, in general terms, coincident with seasonality of the seaweeds, having higher biomass from April to June. However, in spite of the important biomass decrease of level 3 algae (*Corallina elongata* and *Jania rubens*) in summer due to high temperatures, density of caprellids (mainly that of *C. grandimana*) maintained values above 1000 ind/m$^2$. On the other hand, *Gelidium corneum* showed similar biomass values throughout all the year round and caprellids

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associated (mainly *C. penantis*) showed important fluctuations with more than 5,000 ind/m² in April-June and less than 200 ind/m² in December-February. These patterns indicate that caprellid density in the intertidal is not only influenced by distribution of algae as substrate, but also by external factors, such as hydrodynamics, oxygen, weather conditions, competition or predation. Probably, the level 1, very close to the subtidal, is more exposed to wave action, and is more sensitive to winter storms, which are likely to negatively affect to the population of *C. penantis*, according to the decrease of its biomass during the winter period. Oppositely, *C. grandimana* from level 3 was able to maintain high densities in

the platforms of *Corallina elongata*. Level 3 is not so affected by waves during winter storms. Furthermore, *C. penantis* is especially sensible to environmental stress (Guerra-García & García-Gómez, 2001; Guerra-García *et al.*, 2009a), while *C. grandimana* seems to be more resistant (Baeza-Rojano *et al.*, unpublished data).

Under favourable conditions, according to the literature, populations of some caprellid species can reach high densities, even higher than 300,000 ind/m$^2$, although there may be considerable temporal and spatial variation depending upon a range of biophysical factors, such as temperature and food supply (Woods, 2009). In the present study *Caprella penantis* showed densities of more than 10,000 ind/m$^2$ in June, and this species, together with *C. grandimana*, were present all the year round; in fact, caprellid reproduction may be continuous throughout the year (Woods, 2009). Some temperate species exhibit peak abundances in spring/summer and marked declines in winter (Keith, 1971; Thom *et al.*, 1995; Ashton, 2006), as those registered in the present study, whilst others such as *Phtisica marina* exhibit peak abundances in winter and spring (Guerra-García *et al.*, 2000). On the other hand, temporal patterns of caprellid populations have also been shown to be positively correlated with the seasonal cycles of the biomass of the host that they inhabit (see Woods, 2009 for details). The present study confirms this trend but also shows that other factors are also involved, probably related with winter storms. Some authors have also pointed predation pressure as an important factor (Duffy & Hay, 2000). *Caprella penantis* and *C. grandimana*, the most abundant species found in the intertidal of Tarifa Island, are also the most common species in other areas of the Strait of Gibraltar (Guerra-García *et al.*, 2009b), being *C. penantis* also common in intertidal ecosystems of the Atlantic coasts of the Iberian Peninsula (Pereira *et al.*, 2006). Although in the present study *C. penantis* has been restricted to level 1 associated to *Gelidium corneum*, in other localities *C. penantis* can reach high densities also on *Corallina elongata*.

Summarising, the results of this study indicate that the distribution of the intertidal caprellids from the Strait of Gibraltar shows a clear tidal zonation, with some species living near the subtidal and others in intermediate tidal levels. The dominant caprellid species reproduce continuously during the whole year and their seasonal fluctuations (with peaks of abundance in April-June) are directly related to seasonality of the main seaweed in which they are associated to. Further experimental studies are still needed to understand other factors (such as competition, predation and weather conditions) causing zonation of caprellids and seasonal changes in their abundance.
ACKNOWLEDGEMENTS

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