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Niche segregation in sandy beach animals: an analysis with surface-active peracarid crustaceans on the Atlantic coast of Spain

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Abstract Several species of sandy beach invertebrates regularly switch between burial in the sand during the day and surface activity at night to feed on stranded organic matter. Because all species consume essentially the same type of food (i.e., wrack) deposited over a restricted area, the potential for competition exists. Conversely, spatial and temporal segregation of surface activity behaviour is predicted to allow for niche separation. Here, we tested whether such behavioural niche separation occurs in three species of sympatric crustaceans (the talitrid amphipods *Talitrus saltator* (Montagu 1808) and *Talorchestia brito* Stebbing 1891, and the oniscoidean isopod *Tylos europaeus* Arcangeli 1938). We also assessed whether surface activity is modulated by weather, sea conditions and moon phases. Surface activity was measured over three consecutive moon phases on an exposed beach on the Atlantic Coast of Spain using pitfall traps along three transects from the foredunes to the swash. Adults of the amphipod *T. saltator* and the isopod *T. europaeus* overlapped spatially and temporally in their surface activity for most of the night. By contrast, the activity of *T. brito* was strongly disjunct in time and concentrated into significantly shorter bouts around dawn or dusk. Niche differentiation was also evident along the space axis, where *T. brito* occurred distinctly lower on the beach. Although several environmental factors (e.g., air and sand temperature, humidity, atmospheric pressure, wind speed and wind direction) were correlated with surface activity, this was highly variable amongst species, life stages, and synodic phases, and did not obscure the fundamental mosaic of spatio-temporal heterogeneity amongst species. Nocturnal feeding on beach wrack creates the potential for competition amongst sympatric crustaceans which can, however, be mitigated by behaviour patterns that separate consumers in time and space.

Introduction

Mobility, orientation and rhythmic activity are key adaptive traits of invertebrates on sandy shores. These behavioural attributes have primarily evolved in response to the highly dynamic nature of the habitat and the unpredictability of potential food supply, composed mainly by stranded macroalgae and animals, phytoplankton and microbes decomposing wrack (Schlacher et al. 2008). Both activity and orientation are frequently synchronised with predictable, cyclic environmental drivers such as light and tides, and modulated by endogenous triggers and climatic factors (Palmer 1995; Scapini et al. 1997; Ugolini et al. 2002a, b; Nardi et al. 2003). Sandy beach organisms can also differ in their expression of behavioural traits, both amongst species and amongst populations, due to specific adaptations to local habitat and other environmental conditions (Scapini et al. 1993, 2005, Ugolini et al. 2002b; Nardi et al. 2003; Marques et al. 2003).

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These behavioural traits are often strongest in species typical of the upper beach, where the assemblages are usually dominated by air-breathing, scavenging crustaceans and insects. These organisms are typically associated with stranded algal wrack which supplies food and provides a refuge against desiccation and predation (Dugan et al. 2003; Olabarria et al. 2007; Rodil et al. 2008). Consequently, beaches that receive large inputs of wrack can harbour dense populations of scavenging arthropods such as talitrid amphipods, oniscoidean isopods (Genus *Tylos*) and carabid beetles (e.g., Fallacci et al. 1996; Scapini et al. 2002; Colombini et al. 2003; Jaramillo et al. 2003).

Many arthropods of the upper beach regularly switch between a fossorial lifestyle during the day and surface activity at night. For example, talitrid amphipods and oniscoidean isopods are buried between the drift line and the base of the foredune during the day and emerge at dusk to move across the beach surface (Scapini et al. 1995). The position on the beach face where the animals bury into the sand is influenced by tidal amplitude and sediment attributes such as temperature, grain size and water content (Beverly and Branch 1979; Ugolini et al. 1995; Fallaci et al. 1996; Pavesi et al. 2007). Nocturnal emergence, activity and movement, are influenced by a multitude of extrinsic factors, including season (Scapini et al. 2002; Nardi et al. 2003; Nasri and Morgan 2006), synodic phase (Mezzetti et al. 1994; Fallaci et al. 1999), weather conditions (Scapini et al. 1997, 2002), sand temperature (Scapini et al. 1997; Fallaci et al. 1999; Cardoso 2002) and human disturbance (Nardi et al. 2003; Fanini et al. 2005); intrinsic genetic factors are also important (Scapini et al. 1995; Ketmaier et al. 2003).

Emergence, movement and distribution across the beach face are key elements in the foraging behavioural repertoire of upper-shore crustaceans. Once emerged from their diurnal burrows after sunset, animals on many European Atlantic beaches generally move seawards to feed on fresh wrack cast ashore by the swash. After the initial feeding excursion, animals then return landwards to their burial sites, generally above the reach of the swash and extending into the foredunes (Edwards and Naylor 1987; Mezzetti et al. 1994; Fallaci et al. 1999); thus, most of the nocturnal movement occurs across the shore between the dunes and the swash zone. Sandhoppers do, however, move parallel to the shoreline, favoring the exchange of genes amongst populations (Scapini et al. 1992). Surface movements can also vary ontogenetically, when juveniles and adults display different activity and movement patterns (Scapini et al. 1992; Kennedy et al. 2000; Cardoso 2002; Nardi et al. 2003; Pavesi et al. 2007).

Conventional wisdom holds that faunal assemblages of exposed, sandy shores are primarily controlled by abiotic, physical factors. Conversely, biological interactions, which are frequently prominent drivers in other intertidal environments, are thought to have less of an influence on community structure on sandy shores (Defeo and McLachlan 2005). Nevertheless, biotic interactions on sandy beaches are not necessarily rare and encompass competition (Defeo et al. 1997; McLachlan 1998; Jaramillo et al. 2003; Dugan et al. 2004), predation (Ansell 1994; Takahashi et al. 2004) and mutualism (Manning and Lindquist 2003). In the case of surface-active arthropods that forage at night on beach wrack, competitive interactions are predicted to be likely because (a) consumer populations can be dense, on some beaches resembling “herds of grazers” more akin to large ungulates on plains, (b) their food resource—wrack—can be spatially concentrated as a narrow strip of material washed ashore on top of the swash, (c) several species of crustaceans with apparently highly similar trophic profiles inhabit the same shore and (d) most of the consumers feed at night in a relatively narrow window of time. Thus, asymmetries in surface activity and in the position across the beach face where animals feed may offer a mechanism for temporal and spatial niche segregation amongst sympatric crustaceans on sandy beaches.

On ocean-exposed Atlantic beaches of the northern Iberian Peninsula, three peracarid crustaceans are abundant—two sympatric talitrid amphipods: *Talitrus saltator* (Montagu 1808) and *Talorchestia brito* Stebbing 1891, and the oniscoidean isopod *Tylos europaeus* Arcangeli 1938 (Lastra et al. 2006). These species show distinct shifts between diurnal burial in the sand and nocturnal surface activity, and all feed on beach wrack (Fallaci et al. 1999; Colombini et al. 2002, 2003).

Yet, temporal and spatial pattern of surface activity of *T. saltator*, *T. brito* and *T. europaeus* have not been reported for populations on these beaches, nor is it known to which extend the three co-occurring species overlap when active on a mesotidal (3.5 m range) beach-face. Consequently, we measured spatio-temporal patterns of surface activity of adults and juveniles in relation to moon phases, tides and weather conditions. If differences in the timing and position of activity were sufficiently large and consistent amongst the sympatric species, their niches would be effectively segregated in space and time—this is the predictive hypothesis tested here.

Methods

Study site

Nocturnal activity patterns of peracarid crustaceans were measured at Praia de Serans (42°41′N, 09°01′W) located at the NW Atlantic Coast of Spain (Fig. 1). It is a reflective beach, 1 km long and ca. 100 m wide (Lastra et al. 2006). Tides are semidiurnal and mesotidal, with a maximum amplitude of 3.5 m. Annual rainfall ranges from 1,000 to

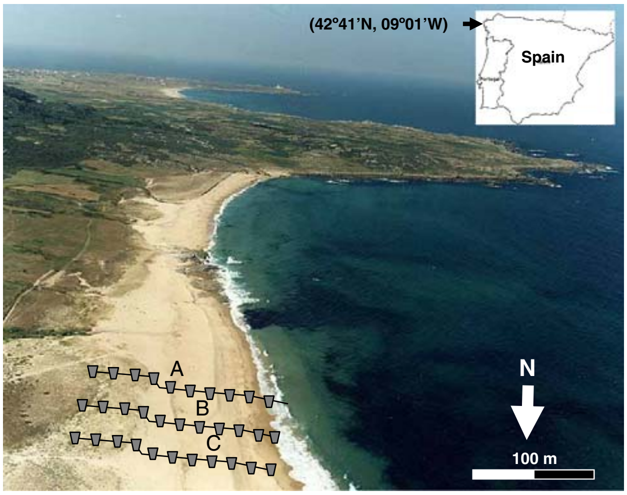

Fig. 1 Geographic position of the beach, Praia de Espiñeirido, on the Atlantic coast of Spain (*inset*) and spatial layout of the sampling design on the beach (*main panel*). Surface-active peracarid crustaceans (talitrid amphipods and oniscoidean isopods) were captured at night in pitfall traps (grey symbols) arranged at 4 m intervals along transects extending from the foredunes to the swash. Three transects (*A*, *B*, *C*) spaced 40 m apart were sampled. The size of pitfall traps (actual opening diameter: 15 cm) is greatly exaggerated for visual clarity

1,400 mm and air temperatures vary from 5 to 30°C. Water temperature is 10–12°C in winter and 18–20°C in summer (M. Lastra, unpublished data).

The beach is backed by small foredunes up to 3 m in height and up to 50 m wide. These foredunes are vegetated at 30–60% ground cover, with the dominant species including *Ammophila arenaria* subsp. *australis* (L.), *Elymus farctus* subsp. *boreoatlanticus* (Simonet & Guinochet) Melderis, *Eryngium maritimum* (L.), *Euphorbia paralias* (L.) and *Pancratium maritimum* (L.). The macroinvertebrate community of the intertidal beach is relatively poor in species (9) and low in abundance (mean: 56 ind. m^{-1}). The lower and middle zones of the beach are occupied by polychaetes (*Nephtys cirrosa* Ehlers, *Scolelepis squamata* Müller), isopods (*Eurydice pulchra* Leach and *E. affinis* Hansen) and amphipods (*Haustorius arenarius* Slabber, *Pontocrates arenarius* Bate). The supratidal zone is dominated by the semiterrestrial crustaceans *Talitrus saltator, Talorchestia brito* and *Tylos europaeus* (Lastra et al. 2006). The distribution of *T. saltator* extends several metres into the foredunes, particularly during storms and in winter (M. Lastra, personnel observation).

Field collections

Surface-active crustaceans were sampled during the first quarter moon of 19–20 May 2002 (neap tide) and two consecutive spring tides, one at full moon (27–28 May 2002) and one at new moon (10–11 June 2002). Sampling was, therefore, contained to a short period (22 days) to avoid possible confounding with seasonal factors that could influence activity in beach arthropods (Scapini et al. 2002; Jaramillo et al. 2003; Nardi et al. 2003).

Animals were captured in pitfall traps which were plastic funnels, 15 cm in diameter and 18 cm in height. Traps were placed at 4-m interval along 3 transects spaced 40 m apart along the beach (Fig. 1). Transects covered the entire intertidal zone (drift line to swash) and the proximal part of the foredunes. Near the swash, the placement of traps followed the tidal excursion of the swash position, with traps removed on incoming tides and more traps added as the swash zone moved downshore on the ebbing tide. One trap was placed at the base of the foredune and two additional traps were added further inland up to 8 m into the dunes. All traps were filled with seawater up to 5 cm below the rim and then buried flush with the sand surface. Behavioural features were tracked only during nocturnal hours (Jaramillo et al. 2003), as adult stages of the talitrid amphipods studied and both adults and juvenile individuals of *T. europaeus* exhibit a prevalently nocturnal rhythm of activity (Williams 1980; Fallaci et al. 1996, 1999; Colombini et al. 1996; Nasri and Morgan 2006). Sampling started 1 h before sunset and finished 1 h after sunrise. The traps were emptied hourly, with all samples collected within 15 min of the full hour by a team of 5–6 field workers. Captured individuals were preserved in 70% ethanol in situ. Environmental variables measured at hourly frequency included air and sand temperature, humidity, atmospheric pressure, wind speed and direction. There was no rain during any sampling event, no significant light pollution was evident, and the beach was not groomed nor was wrack-removed.

Laboratory and data analysis

Adults of *T. saltator* and *T. brito* were analysed separately. Juveniles of these two species lacked distinct differential characters. They could not be separated with confidence and were excluded from the analysis. By contrast, adult and juvenile *T. europaeus* could be separated accurately by the presence of sexual characters such as brood plates and penis structures and were analysed separately.

The mean number of individuals over all traps and transects per time interval were used to compare abundance between species within each synodic phase (Student′s *t*-test for paired data). Circular statistics were used to calculate the mean angles of activity (i.e., the mean hour of activity) during the nocturnal period, as well as the circular standard deviation of the data around this angle (Oriana 3.01 statistical package). The mean vector and Rayleigh's *z* were calculated to test whether the data showed a uniform circular distribution or whether they were concentrated. A longer mean vector (and the resulting larger value of *z*) denotes greater concentration of the data around the mean, and thus less likelihood of the data being uniformly distributed (Zar 1996).

The spatial distribution of individuals across the dune-swash gradient was numerically described by the centre of abundance, calculated as the mean position of the population: $MP = \Sigma(n_i \; L_i)/\Sigma n_i$ where n_i is the abundance (number per trap) at beach level L_i (Schlacher and Wooldridge 1994). MP values were calculated separately for each transect and for each hourly catch. The reference point for the calculation of MP was the most landward located trap in the foredunes ($L_1 = 0$ m) with successive beach levels at 4-m interval towards the swash (i.e., $L_2 = 4$ m, $L_3 = 8$ m, etc.).

To test for the differences in surface activity and the position of the centre of abundance, we used a three-way model ANOVA with Species (3 levels) and Moon phase (3 levels) as fixed factors, and Hour (10 levels) as a random factor. To test for differences in activity and beach position between juveniles and adults of *T. europaeus*, we used a three-way model ANOVA with Life stage (2 levels) and Moon phase (3 levels) as fixed factors and Hour (10 levels) as a random factor. No data transformations were required, as variances were homogenous (Cochran's test). ANOVA was followed by Student–Newman–Keuls tests (SNK) to identify significant differences amongst means. In addition, multiple regression analysis, employing backward elimination of predictors, was used to investigate the influence of environmental variables on catch rates (Fallaci et al. 1996; Zar 1996). Wind direction data were split in sea–land and shore-parallel directions, and then transformed into Cartesian co-ordinates (sin and cosine of the angle) by making the *x*-axis pointing shore-parallel and *y*-axis sea–land orientated (Fallacci et al. opus cit.).

The Bray-Curtis (BC) concordance function was used as the numerical measure of similarity for distributions amongst species and hence as a measure of niche partitioning. BC is the most widely used resemblance function in multivariate, ecological assemblage analysis. Its chief advantages are that it is not influenced by double-absences, and it is constrained to range from zero to 1, where both the minimum and maximum value have a straightforward biological interpretation (Clarke et al. 2006).

Similarity coefficients between species pairs were calculated on standardised abundance data for each species using total catches per transect and night. Standardisation was done because the test of interest was to which degree the *pattern* of activity (time axis) or the *pattern* of distribution (space axis) differed amongst species. In cases where species had different abundances—typically the case—numerical similarity measures for two species whose distribution matched exactly would be artificially deflated if no standardisation was performed (Clarke and Gorley 2006).

Tests for niche partitioning amongst species were based on ANOSIM (analysis of similarity; Clarke 1993) analysis. These tests contrasted three dimensions of species occurrences: (a) differences in spatial distributions across the beach-face irrespective of time (space partitioning), (b) differences in the temporal pattern of surface activity (partitioning of niches in time) and (c) combination of spatial and temporal differentiation. There were three replicate transects sampled during each of three moon phases, and the ANOSIM test was a two way, crossed design, with 'Species' and 'Moon Phase' as factors.

Results

Environmental conditions

Temperature, air humidity, atmospheric pressure and wind conditions (Table 1) varied significantly amongst sampling dates. Air and sand temperatures were higher during the quarter moon than during both the full- and new moon (SNK test: air temperature, Quarter moon > Full moon = New moon; sand temperature; $P < 0.05$; Quarter moon > Full moon > New moon; $P < 0.05$). Atmospheric pressure during the new moon collections was higher than

Table 1 Summary statistics of environmental variables: mean (±SD) during the sampling dates

	Sand temperature (°C)	Air temperature (°C)	Wind velocity (m/s)	Air pressure (mb)	Air humidity (%)	Tide times and heights
First quarter moon neap tide	15.7 ± 0.9	18.7 ± 2.1	1.9 ± 0.99	1,022 ± 2.9	97.6 ± 2.8	22:31: 3.19 m
	(14; 16.7)	(15.4; 22.3)	(0; 3)	(1,018; 1,026)	(92; 100)	05:04: 1.31 m
Full-moon spring tide	13.6 ± 0.8	15.1 ± 0.7	3 ± 1,05	1,023 ± 1.7	94.7 ± 5.3	23:43: 0.67 m
	(12; 15)	(14.3; 16.4)	(2; 5)	(1,020; 1,024)	(82; 100)	05:58: 3.81 m
New-moon spring tide	12.4 ± 2.1	15.0 ± 1.4	1.2 ± 1.4	1,026 ± 1.5	97.9 ± 3	22:50: 0.88 m
	(10; 15)	(12.8; 17.8)	(0; 3)	(1,024; 1,027)	(90; 100)	04:58: 3.52 m

Minimum and maximum values in brackets

during full and quarter moons (SNK test: New moon > Full moon = Quarter moon; $P < 0.05$). Wind velocity was greater during full moon than during quarter and new moon phases (SNK test: Full moon > Quarter moon = New moon; $P < 0.05$). Landward winds blew mainly during the first quarter moon, whereas wind direction during the full moon was mainly shore-parallel. Wind direction varied significantly over the three synodic phases (SNK test: sea–land wind, Quarter moon > Full moon = New moon; $P < 0.05$; shore-parallel wind, Full moon > New moon > Quarter moon; $P < 0.05$). No differences in air humidity were detected between sampling dates.

Patterns of activity

Higher number of statistical differences in the number of surface-active individuals between species was observed during neap tide phase (Table 2). Surface activity differed significantly amongst species, but species to species contrasts were inconsistent at different moon phases (i.e., ANOVA significant interaction Species × Moon phase, $F_{4,36} = 3.64$, $P = 0.014$; Table 3). A total of 28,881 individuals were caught over the three sampling dates. Catches were higher during the quarter moon at 12,273 individuals compared with 7,515 and 9,093 during the full and new moon, respectively. During all synodic phases, *T. saltator* numerically dominated the catches, comprising 57–63% of the total catch, while the congener *T. brito* was less abundant (6–21%) as was the isopod *T. europaeus* at 17–37% of all individuals.

T. saltator was the most abundant species irrespective of the synodic phase (Fig. 2). *T. brito* was always the least abundant species, but mean abundances at new and full moon were not significantly different ($P > 0.05$) from that of adult individuals of *T. europaeus* (SNK test: Quarter moon: *T. saltator* > *T. europaeus* > *T. brito*, $P < 0.05$; Full and new moon: *T. saltator* > *T. europaeus* = *T. brito*, $P < 0.05$). In total, most of *T. saltator* and *T. europaeus* individuals were captured during the quarter moon (41.23 and 54.26%, respectively), whereas 51.53% of the total number of *T. brito* were captured during the new moon.

Table 2 Summary of paired Student's *t*-tests for differences in surface activity between species and life stages during each of three synodic phases

	Neap tide	Full moon	New moon
T. saltator			
T. brito	***	*	NS
T. europaeus (adults)	**	**	**
T. europaeus (juveniles)	***	**	**
T. brito			
T. europaeus (adults)	*	NS	NS
T. europaeus (juveniles)	NS	NS	NS
T. europaeus (adults)			
T. europaeus (juveniles)	**	*	*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. NS non-significant

Table 3 Summary of three-factor analysis of variance contrasting activity and position across the beach face

Source	*df*	Activity		Position across beach face	
		F	*P*	*F*	*P*
Species	2	**12.46**	0.004	**47.89**	0.000
Moon phase	2	3.38	0.057	**25.62**	0.000
Hour	9	**10.63**	0.000	**8.98**	0.000
Species × Moon phase	4	**3.64**	0.014	**2.76**	0.042
Species × Hour	18	**7.03**	0.000	1.65	0.053
Moon phase × Hour	18	**3.32**	0.000	**3.38**	0.000
Species × Moon phase × Hour	36	**1.73**	0.011	0.89	0.651
Residual	180				
Total	269				

Species and Moon phase were orthogonal and fixed factors and Hour was a random factor

Surface activity of the species varied through synodic phases and sampling times during the nocturnal activity (significant interaction Species × Moon phase × Hour, $F_{36,180} = 1.73, P = 0.011$; Table 3). The surface activity of *T. brito* was highly concentrated during dusk and dawn when these coincided with low tides (Table 4). *T. saltator* was longer active on the beach close to sunrise than adults of *T. europaeus*, reflected in larger abundances of this amphipod at dawn during the quarter moon and full moon (Fig. 2).

Adults of *T. europaeus* were significantly (significant main effect of Life stage, $F_{1,9} = 13.26$, $P = 0.005$) more abundant than juveniles during all moon phases (Fig. 2). Maximum abundance of adults was recorded during the quarter moon (SNK test: Quarter moon > Full moon = New moon, $P < 0.01$), whereas no significant differences in the abundance of juveniles between moon phases was detected.

Environmental drivers of activity

The influence of environmental variables on surface activity varied across species and synodic phases (Table 5). At first quarter moon, catches of *T. saltator* were positively related to air humidity, atmospheric pressure, tidal elevation and wind speed, but were negatively affected by air temperature, shore-parallel and landward winds. Weather and tides influenced the activity of *T. brito* in opposite ways to its congener *T. saltator*: *T. brito* showed reduced

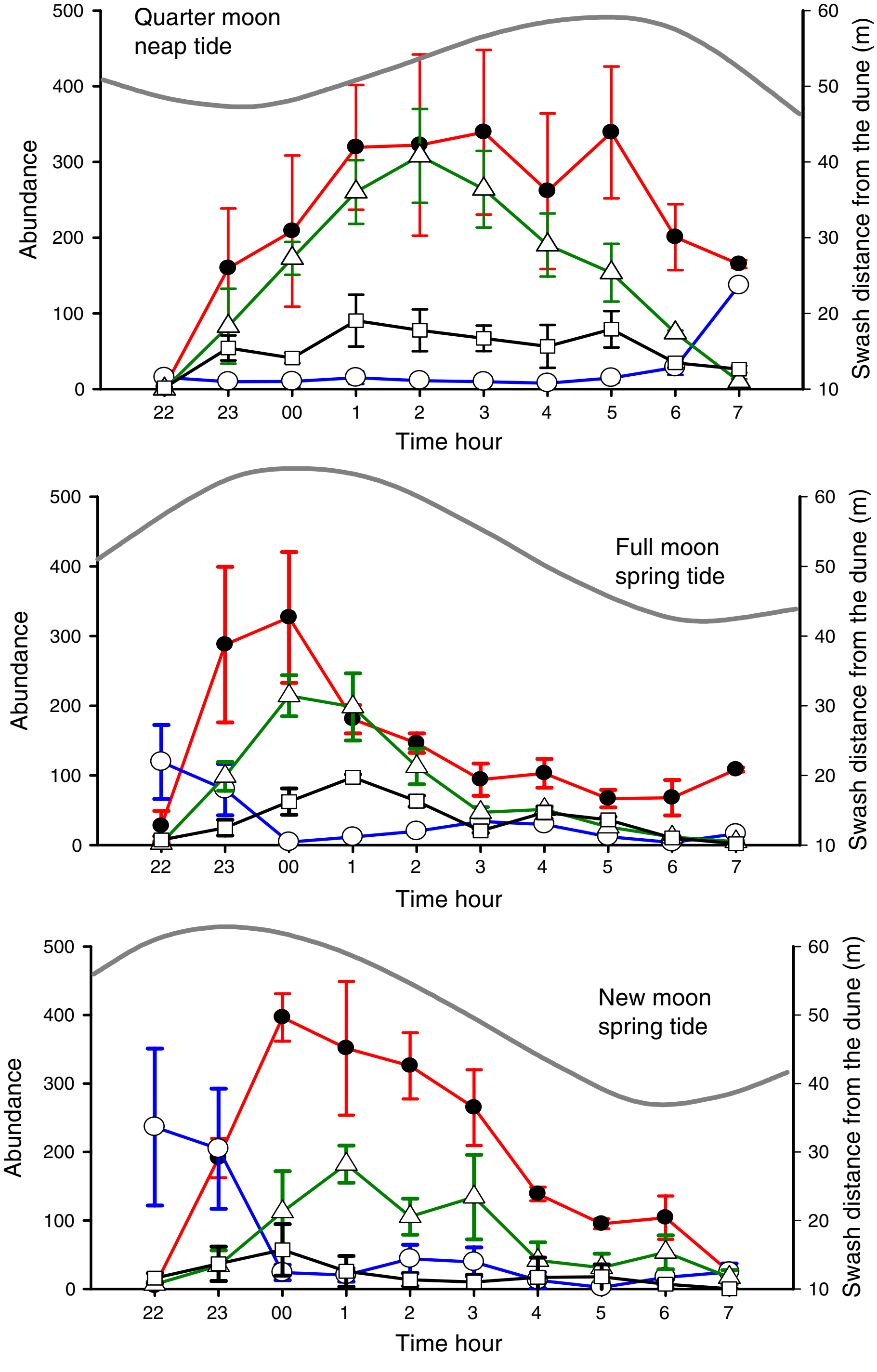

Fig. 2 Mean (±SE) abundance of the two species of amphipods and the two life stages of the isopod *Tylos europaeus* across the beach face during each of three Moon phases. *Solid circles T. saltator*; *open circles T. brito*; *open triangles T. europaeus* adults; *open squares T. europaeus* juveniles. *Grey solid line* indicates the reach of the swash

activity at incoming tides, moist air and higher wind speeds. Adults of the isopod *T. europaeus* showed similar relationships between activity levels and environmental conditions to *T. saltator*. By contrast, the activity of juveniles of *T. europaeus* was positively related to air humidity and shore-parallel winds, but negatively to sand temperature, tidal elevation and wind speed (Table 5).

During the full-moon spring tide, the activity of *T. brito* was negatively affected by atmospheric pressure and wind speed, whereas wind direction, either shore-parallel or sea–land orientated, had a positive effect. The same environmental variables had an opposite effect on the activity of *T. saltator*, whose activity was positively related with atmospheric pressure, wind speed, tidal elevation, air temperature and air humidity (Table 5). There were no significant relationships between the activity of *T. europaeus*, either for adults or juveniles, and any environmental variable during full moon.

Table 4 Summary of circular statistics for activity levels

	Mean vector (time, hour)	Length of mean vector	Circular standard deviation (time)	Raleygh test (*z*)
First quarter moon: high tide: 22:30; low tide: 05:04				
T. saltator	02:42	0.857	±02:07	167.9
T. brito	05:17	0.740	±02:58	80.0
T. europaeus (adults)	02:22	0.855	±01:53	335.2
T. europaeus (juveniles)	02:37	0.831	±02:20	39.8
Full moon: low tide: 23:43; high tide: 05:58				
T. saltator	01:29	0.795	±02:35	173.9
T. brito	00:12	0.759	±02:50	45.2
T. europaeus (adults)	01:07	0.905	±01:42	272.3
T. europaeus (juveniles)	00:58	0.838	±01:42	29.1
New moon: low tide: 22:50; high tide: 04:58				
T. saltator	01:44	0.871	±02:01	384.9
T. brito	23:32	0.825	±02:22	222.5
T. europaeus (adults)	02:02	0.870	±02:01	87.1
T. europaeus (juveniles)	01:49	0.875	±01:58	72.5

M.H. mean hour of activity, *r* length of the mean vector, *z* Rayleigh's value. A longer mean vector (and the resulting larger value of *z*) denotes greater concentration of the data around the mean hour. Rayleigh's *z* tests indicate whether the data showed a uniform circular distribution or whether they were concentrated. All *z* values were significant at $P < 0.001$

During the new-moon spring tide, fewer significant relationships between the environmental variables and the surface activity of the three peracarid crustaceans were detected. Catches of *T. saltator* were negatively correlated with increases in sand and air temperatures and positively with wind conditions. Air temperature showed a significant positive correlation with the activity of *T. brito*, while the activity of adult *T. europaeus* was positively related to flooding tides and wind (Table 5).

Distribution across the beach face

The distribution of adults across the dune-swash gradient differed significantly amongst species, but inconsistently over moon phases (Species × Moon phase interaction, $F_{2,36} = 2.76$, $P = 0.042$). During all moon phases, the centre of abundance of *T. brito* was located lower on the beach near the swash zone (Fig. 3). Most of adult individuals of *T. brito* were located lower on the shore than *T. saltator* and *T. europaeus*, with a subtle difference in mean position between moon phases (SNK tests: Quarter moon: *T. brito* > *T. saltator* = *T. europaeus*, $P < 0.05$; Full moon: *T. brito* > *T. saltator* > *T. europaeus*; New moon: *T. brito* > *T. europaeus* = *T. saltator*, $P < 0.05$).

Distributions across the beach of each species also varied across the three synodic phases. Adults of *T. brito* were located significantly lower on the beach during the quarter moon neap tide, compared to a more landward position during the full moon and new-moon spring tides (SNK test: Quarter moon > New moon > Full moon, $P < 0.05$; Fig. 3). *T. saltator* showed a similar pattern, with a mean position during the neap tide closer to the swash than that observed during full and new moon phases (SNK test: Quarter moon > New moon = Full moon, $P < 0.05$). Adults of *T. europaeus* were also located lower on the beach during the quarter moon (SNK test: Quarter moon > New moon > Full moon; $P < 0.05$), whereas juveniles of this species occurred lower on the beach than adults, and this result was consistent over the three moon phases studied (significant main effect of Life stage, $F_{1,9} = 8.21$, $P = 0.019$; Fig. 3).

Niche partitioning

The spatial distribution of the three species was broadly comparable, being centred between the drift line and the upper limit of the swash zone. There was only a moderate degree of spatial separation between the two congeneric amphipods ($R = 0.383$), and no detectable difference between juveniles and adults of *T. europaeus* ($R = 0.123$; Fig. 4; Table 6). The spatial distribution of *T. brito* differed significantly from that exhibited by the other species and life stages studied ($R = 0.296$–0. 543), and it generally occurred lower on the beach.

In comparison to the moderate spatial separation amongst species, there was a considerably stronger degree of segregation in time (Fig. 4; Table 6). Circular statistics indicated that all species showed significant concentration of activity around some hour during the night (Fig. 5; Table 6). Most activity of the amphipod *T. brito* occurred when the activity of the other species was low around low tide, indicating good separation of niches ($R = 0.963$–1.00), with little overlap between *T. brito* and either *T. saltator* or *T. europaeus*. Juveniles and adults of

Table 5 Summary of stepwise multiple regression analyses relating catches of surface-active individuals (dependent variable) to a range of environmental variables as possible predictors

	Air temperature (°C)	Sand temperature (°C)	Air humidity (%)	Atmospheric pressure (mm Hg)	Tidal elevation (m)	Wind speed (m/s)	Wind direction (shore-parallel)	Wind direction (sea–land)	R^2
First quarter moon									
Talorchestia brito	–	–	−1.74	−8.46	−7.20	−4.01	5.84	–	0.983
Talitrus saltator	−0.87	–	1.53	6.40	5.08	3.06	−4.66	−0.54	0.999
Tylos europaeus (adults)	−0.26	–	0.82	4.38	3.00	2.22	−3.04	–	0.998
Tylos europaeus (juveniles)	–	−1.85	0.91	–	−2.05	−1.45	1.50	−0.57	0.974
Full moon									
Talorchestia brito	–	–	–	−2.40	–	−2.59	4.36	1.07	0.872
Talitrus saltator	0.61		2.43	2.79	−2.37	3.02	−4.01	−1.92	0.999
Tylos europaeus (adults)	–	–	–	–	–	–	–	–	–
Tylos europaeus (juveniles)	–	–	–	–	–	–	–	–	–
New moon									
Talorchestia brito	0.82	–	–	–	–	–	–	–	0.679
Talitrus saltator	−1.07	−1.29	–	–	–	–	2.34	0.54	0.960
Tylos europaeus (adults)	−0.94	–	–	–	0.65	–	1.26	–	0.947
Tylos europaeus (juveniles)	–	–	–	–	–	–	–	–	–

Only significant ($P < 0.05$) regression coefficients are shown

T. europaeus were surface active at the same time ($R = 0.185$; Table 6).

Discussion

Different environmental variables affected the activity of the three sympatric peracarid crustaceans in different ways. In addition, the three species differed in temporal activity pattern and spatial distribution across the beach face over the three consecutive synodic phases, strongly suggesting segregation of niches.

During neap tide, larger numbers of individuals were recorded and their position was closer to the swash zone than that observed during spring tides. High densities of surface-active talitrids during neap tides have been reported for several beaches worldwide (Benson and Lewis 1976; Cardoso 2002; Jaramillo et al. 2003). For example, Cardoso (2002) found larger abundances of *Pseudorchestoidea brasiliensis* on a Brazilian beach during neap tides, with a more seaward position than that observed during spring tide. Larger abundance of *Orchestoidea tuberculata, Tylos spinulosus* and the beetle *Phalerisida maculata* during neap tide were also found by Jaramillo et al. (2003) on a Chilean beach.

Variability in activity patterns may be under endogenous control or represent responses to environmental factors (Scapini et al. 1997, 2002; Williams 1980; Edwards and Naylor 1987; Mezzetti et al. 1994). In fact, larger abundances during neap tide could indicate a moon-dependant rhythm (endogenous or exogenous), but may equally reflect an effect of the higher temperatures measured during this particular sampling occasion (Table 1). Temperatures during our study ranged between 10 and 25°C, which is within the range where locomotion of *T. saltator* is not inhibited (Bregazzi 1972a, b; Bregazzi and Naylor 1972). A negative temperature effect on the activity of *T. europaeus* was reported by Fallaci et al. (1996), indicating that more *Tylos* were surface active when air temperature was between 13 and 20°C. *T. brito* is more sensitive to desiccation and temperature stress (Scapini et al. 2002; Fallaci et al. 1999; Colombini et al. 2002) which could be a factor in determining the lower shore position of this species observed by us. Correlations between the activity of talitrids and sand temperature have been reported in previous studies (Cardoso 2002; Scapini et al. 1997). We found no significant influence of this variable on activity, but the range of temperatures during our study was probably too small (Table 1).

In contrast, air humidity, wind direction and atmospheric pressure did affect the activity of all three species, although the magnitude and intensity of these effects were highly variable amongst species. Air humidity had a positive effect on the activity of *T. saltator* and *T. europaeus* during the quarter moon. During all collections, humidity was always above 90% irrespective of wind conditions. Fallaci et al. (1996) reported decreased activity of *T. europaeus* on Tyrrhenian beaches at humidity below

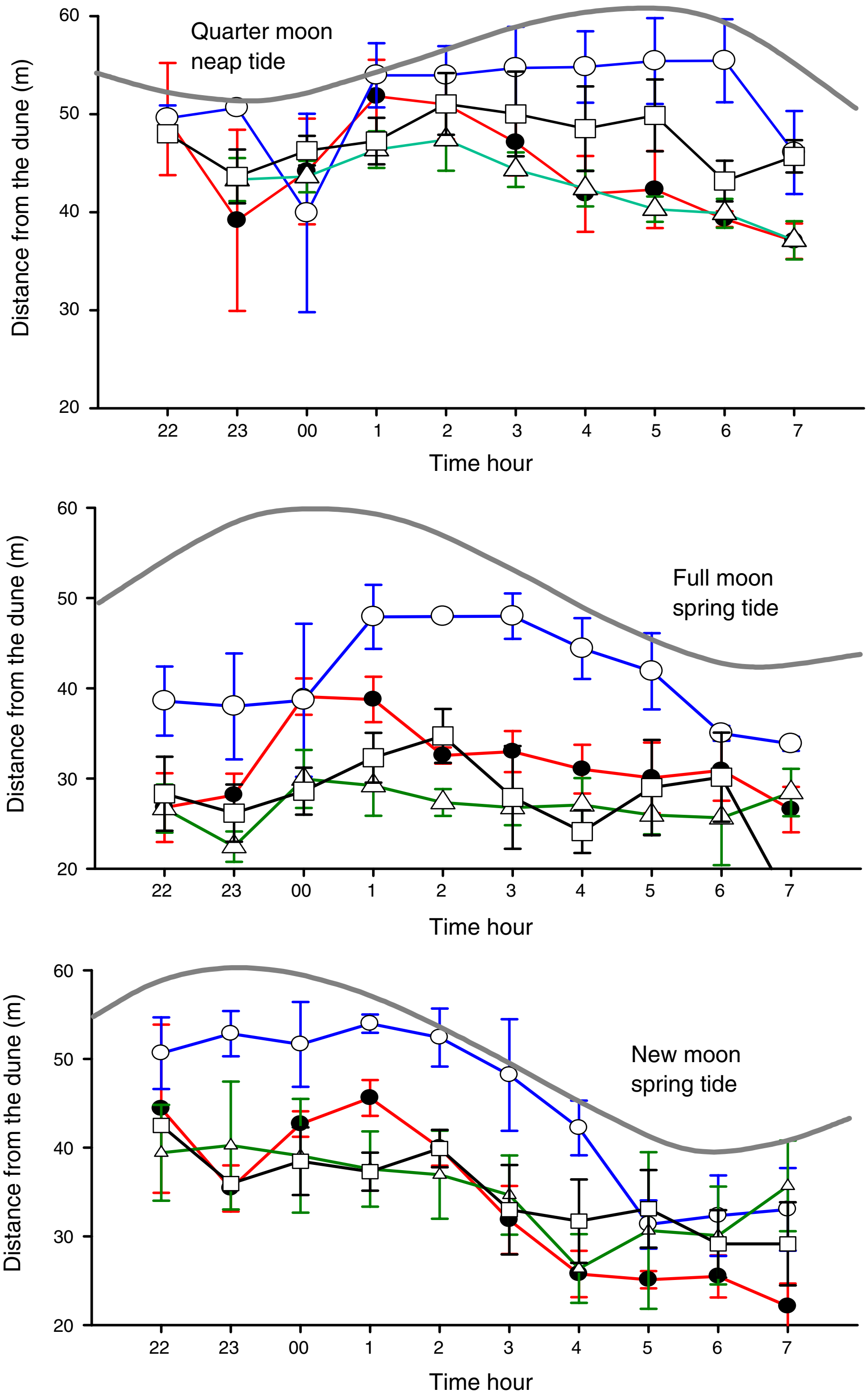

Fig. 3 Mean (±SE) position of the two species of amphipods and the two life stages of the isopod *Tylos europaeus* across the beach face during each of three Moon phases. Distances were measured from the first trap set at the base of the foredune. *Solid circles T. saltator*; *open circles T. brito*; *open triangles T. europaeus* adults; *open squares: T. europaeus* juveniles. *Grey solid line* indicates the reach of the swash

70% or above 90%. Effects of wind were different depending on species and synodic phase. For example, stronger winds had negative effects on the activity of *T. brito* during both quarter and full moons, whereas *T. saltator* became more abundant during stronger winds. Effects of wind direction on activity were heterogeneous since the same wind direction had positive effects on activity during one synodic phase, but negative ones during another phase. Similarly, the same wind direction apparently affected species differently. For example, shore-parallel winds during quarter and full moons were positively correlated with catches of *T. brito*, but captures of *T. saltator* decreased under these conditions. Fallaci et al. (1996) reported a positive effect of humid seaward winds on the

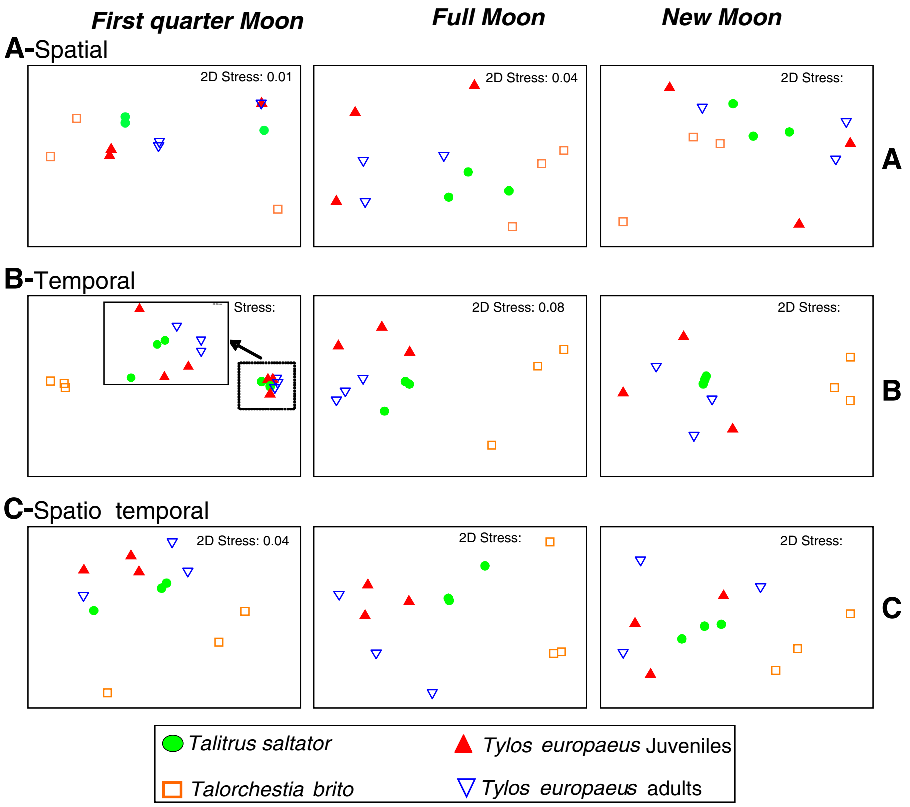

Fig. 4 Ordinations (non-metric multidimensional scaling) derived from Bray–Curtis similarities in the distributions of the three peracarid crustaceans expressed as **a** overlap in the spatial distribution across the dune-swash gradient, **b** overlap in the pattern of surface activity, and **c** overlap in their spatio-temporal occurrence

Table 6 Summary of ANOSIM (analysis of similarities), contrasting temporal (A), spatial (B) and spatio-temporal (C) distribution patterns amongst the three species of surface-active peracarid crustaceans

	A—Temporal		B—Spatial		C—Spatio-temporal	
	R	*P*	*R*	*P*	*R*	*P*
Global test	**0.597**	0.000	**0.207**	0.027	**0.426**	0.000
T. brito vs. *T. saltator*	**0.963**	0.000	**0.383**	0.017	**0.679**	0.000
T. brito vs. *T. europaeus*—juveniles	**0.988**	0.000	**0.296**	0.047	**0.642**	0.002
T. brito vs. *T. europaeus*—adults	**1.000**	0.000	**0.543**	0.006	**0.840**	0.000
T. saltator vs. *T. europaeus*—juveniles	0.086	0.258	0.198	0.117	0.272	0.062
T. saltator vs. *T. europaeus*—adults	**0.506**	0.002	0.278	0.077	**0.432**	0.028
T. europaeus juveniles vs. adults	0.185	0.147	0.123	0.773	0.049	0.403

High (>0.7) values of the *R*-statistics denote substantial partitioning of niches, whereas lower (<0.3) *R*-values are indicative of niches which are not well differentiated in space, time or both

activity of *T. europaeus*. In this study, seaward and shore-parallel winds (originated from low pressure fronts) were humid. Atmospheric pressure was positively correlated with catches of *T. saltator*, but negatively with those of *T. brito*. Scapini et al. (1997) suggested that the effect of air pressure on activity pattern might imply that animals are able to anticipate weather changes. Fallaci et al. (1999) linked this relationship with storm events on the French Atlantic coast. No storm events occurred during our field work, and atmospheric pressure was roughly typical of a high pressure situation. Any influence of air pressure on the activity levels of talitrids could thus be restricted to low pressure conditions acting as an escape response from extreme weather events.

Significant relationships between activity levels of the three species and tidal elevation were detected (Table 4). A tidal component in the activity patterns was prominent for *T. brito* which was concentrated during ebbing tides that occurred at dusk during neap tides and at dawn during spring tides. These results agree with those reported by Fallaci et al. (1999) for a French Atlantic beach, but they contrast with those found by Williams (1983) that reported activity during incoming tide on the Isle of Man. However, Cardoso (2002) found that activity peaks of adults of

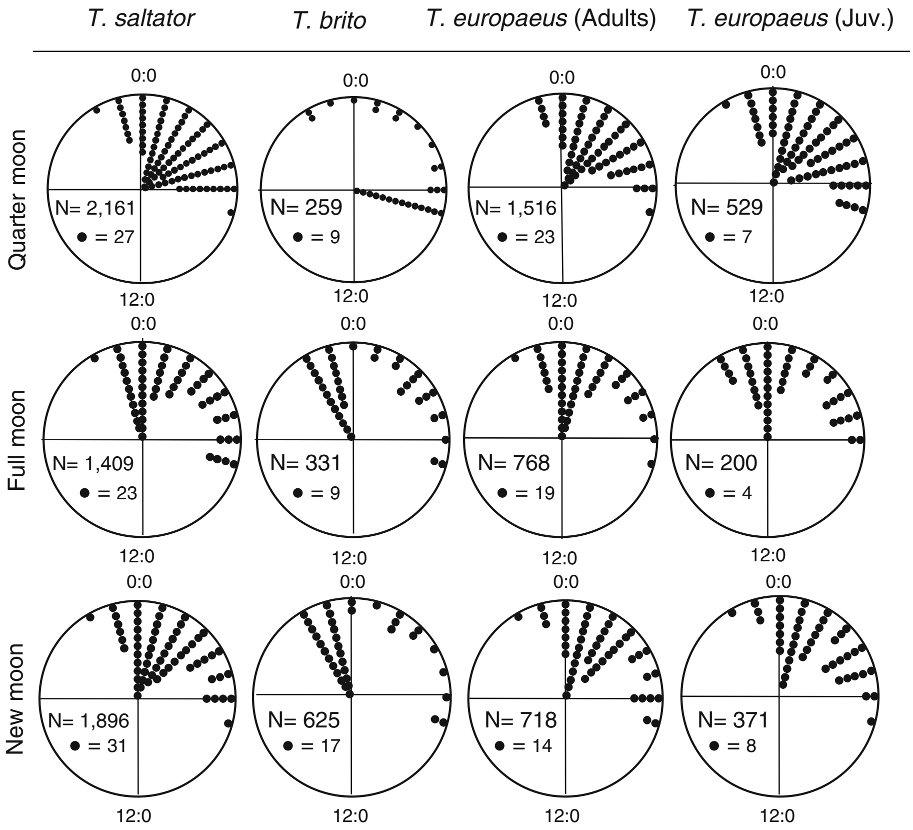

Fig. 5 Circular diagram plots of the two species of amphipods and the two life stages of the isopod *Tylos europaeus* during each of three Moon phases. Total number of individuals caught is given as *N. Each symbol* represents multiple observations according to total abundance

Pseudorchestoidea brasiliensis were not linked to tides, but to sunrise and sunset.

Niche partitioning

Temporal segregation of emergence and activity was much more important in niche partitioning of surface-active beach crustaceans than differences in their spatial distribution (Table 5). Essentially, all species occurred on the lower to middle part of the beach where swash deposits food material. Therefore, their position might be largely dictated by swash regimes, and there would be little opportunity to segregate niches across the dune-swash gradient. Nevertheless, *T. brito* occurred lower on the beach than *T. saltator* and *T. europeaus*, and its spatial distribution was significantly different from that of the other species. Previous studies have reported that the distribution of *T. brito* might be related to the patch distribution of the stranded, surf zone diatoms on which they feed (Colombini et al. 2002).

In contrast to the moderate to weak spatial separation, species activity was strongly disjoint in time (i.e., especially the strong separation of *T. brito*). Adults of *T. saltator* and *T. europaeus* overlapped in their activity, while the activity of *T. brito* differed significantly from that exhibited by the other two species. Activity of the three species varied significantly mainly during quarter moon neap tide (Table 2). It is possible that greater niche separation occurs when the beach is narrow during this tidal phase. The activity period of *T. europaeus* mainly occurred during nocturnal hours, whereas *T. saltator* was frequently active during dusk and dawn (see Scapini et al. 1997; Fallaci et al. 1999). Shifting temporal peaks of activity to reduce overlap is a strategy reported for supratidal crustaceans which occupy the same spatio-termporal niche (Williams 1980). Similarly, Colombini et al. (1998) concluded that different strategies adopted in the use of space avoid both intra- and interspecific competition.

The three species compete for the same food resource in the same area—carrion and algae stranded on the intertidal part of the beach—(Hayes 1974; Odendaal et al. 1999; Lastra et al. 2008; Colombini et al. 2009). Given the sometimes high densities of the animals feeding on the beach, competition for food is therefore probable. Competition may, however, be lowered if species partition their niches by separating their activity using different parts of the beach face (i.e., feeding in different zones), being active during different times, or a combination of spatial and temporal separation. Consequently, there are two axes which are potentially available to differentiate the niches of the surface-active amphipods and isopods—space and time.

Coexistence of sympatric species on sandy beaches has been interpreted to be facilitated by difference in surface activity in time and space (e.g., Chelazzi et al. 1983; Colombini et al. 1994; Jaramillo et al. 2003). We found that temporal segregation was much more important in niche partitioning of surface-active beach crustaceans than differences in spatial distribution (Table 5). Essentially, all species feed in the lower to middle part of the beach where swash deposits food material. The feeding position is therefore largely dictated by swash regimes and there appears to be little opportunity to segregate niches across the dune-swash gradient. Nevertheless, *T. brito* feeds lower on the beach than *T. saltator* and *T. europeaus*, and its spatial distribution is significantly different from that of the other species. In contrast to the moderate to weak spatial separation, species activity was strongly disjoint in time, especially the strong separation of *T. brito*.

In conclusion, the present study analysed for first time the rhythms of activity of three coexistent supratidal crustaceans in a mesotidal exposed beach of the Atlantic coast of Spain. Some relevant ecological results, such as differences between synodic phases in activity and position across the beach face, the variability in the effect of the environmental variables or the spatio-temporal segregation of niches were obtained. These patterns suggested that supratidal species of sandy beaches, besides coping with a highly variable physical environment, might adjust their behaviour to avoid intra and interspecific competition for space or food or both.

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