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Differences in Behavioural Strategies between Two Sympatric Talitrids (Amphipoda) Inhabiting an Exposed Sandy Beach of the French Atlantic Coast

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A study on the surface activity and zonation of *Talorchestia brito* and of two age classes of *Talitrus saltator* was done along the French Atlantic coast. Samples were taken with a transect of pitfall traps and climatic data were recorded. The data were collected during two periods of 48 hours, one around spring tide and the other around neap tide. Activity patterns, mean hours of activity, total and hourly mean zonations and hourly orientation indices were calculated in daily and tidal hours at both spring and neap tides. Simple correlation analysis was used to compare between species and within age classes both the trends of the distributions of the activity patterns and those of the hourly mean zonations. Multiple regression analysis was employed to correlate surface activity and hourly mean zonation with environmental factors. The results indicate that both species were nocturnal and that most activity occurred on the ebbing tide. Total mean zonations changed between the two synodic phases with a landward shift at spring tide. Also, the hourly mean zonations varied during the activity period according to the tides and synodic phases. Juveniles of *T. saltator* presented a more landward distribution compared with adults and compared with *T. brito* which was always found closer to the sea. Zonation patterns seem to be related in a complex way to the environmental variables such as air relative humidity, sand temperature and moisture, atmospheric pressure and tidal elevation. Furthermore it was emphasized that for certain aspects the behavioural strategies of adult *T. saltator* differed from those of the juveniles and of *T. brito*. On the whole this work shows the behavioural plasticity of littoral talitrids and the different strategies of two sympatric species in the use of space and time.

Keywords: activity patterns; zonation; environmental factors; sympatric sandhoppers; French Atlantic coast

Introduction

Sandy beach arthropods include species with wide geographical distributions. A general feature of these species is behavioural plasticity, which has been considered a key factor in the survival and evolution of the macrofauna on exposed sandy beaches (Brown, 1996). Previous studies have demonstrated that different populations of the same species from Atlantic and Mediterranean sandy beaches modulated their behavioural strategies in relation to environmental factors characteristic of the inhabited area (Colombini *et al.*, 1994, 1996; Colombini & Chelazzi, 1996; Fallaci *et al.*, 1996). Two sympatric talitrid species, *Talitrus saltator* (Montagu) and *Talorchestia brito* Stebbing, have been selected for comparative study of their behaviour along the French Atlantic coast. Behavioural and physiological adaptation to different environmental conditions has been studied extensively in *T. saltator* both in the field (Geppetti & Tongiorgi, 1967; Rüppel, 1967; Karlbrink, 1969; Williams, 1983*a*; Scapini *et al.*, 1992; Williams, 1995) and under laboratory conditions (Williamson, 1951; Bregazzi, 1972; Bregazzi & Naylor, 1972; Ercolini & Scapini, 1974; Williams, 1980; Morritt, 1987, 1988; Scapini *et al.*, 1988, 1993). In contrast for *T. brito*, although brief notes on its biology and ecology were given by Lagardère (1966) and Vader (1970), no in-depth eco-ethological study has been done for this species. Rüppel (1967) made observations on a field community of talitrids, but the two species, *T. saltator* and *T. brito*, were not distinguished from each other. Williams (1983*a*) has analysed the locomotor activity rhythm of three different amphipod species, including *T. saltator*, on a beach with wide tidal excursions associated to a steep slope, whereas Geppetti and Tongiorgi (1967) and Scapini *et al.* (1992) have studied the behaviour of *T. saltator* on a flat sandy beach with minimal tidal fluctuations. The importance of beach morphodynamic features for the macrofaunal community was pointed out by McLachlan (1980), who proposed a classification of beaches into reflective, intermediate and dissipative.

The intention here was to compare the adaptation of two sympatric talitrid populations inhabiting a wide and flat sandy beach subjected to medium tidal fluctuations with other populations previously studied. The aim of this work was to contribute to the knowledge of behavioural adaptations of *T. brito* and *T. saltator* giving special attention to the relations between surface activity and environmental conditions (beach morphology, tidal and synodic phases, climate). The behaviour of the adults and juveniles of *T. saltator* was compared to illuminate phenotypic plasticity.

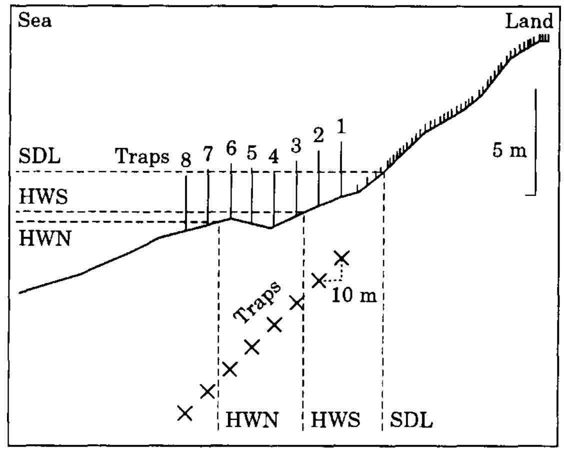

FIGURE 1. Study area: cross-section of the beach-dune system (top) and trapping system of tetradirectional pitfall traps (bottom). SDL=storm drift line, HWS=high water of spring, HWN=high water of neap.

Materials and methods

The study was done on a sandy beach along the Atlantic coast of France at Truc Vert (44°41′33″N; 1°14′42″W), a locality immediately north of the Basin of Arcachon (Bordeaux, France). This dissipative and exposed beach was north–south oriented, with a slope of 3%, mean grain size of 366 μm and was backed by a dune (about 25 m in height), covered by *Ammophila arenaria* (L.) Link. The data were collected during two periods of 48 h, one during a spring tide and the other during the consecutive neap tide period between 23 June and 2 July 1994. Dawn was at 04.20h and sunset at 19.45h. At spring tide, low tide occurred at 23.08h and 23.56h during the first and second night whereas at neap tide, high tide times were 22.18 and 23.24h and with low tide at 04.26 and 05.26h during the two nights of study. The chosen season was one in which talitrids showed the highest activity and juveniles were present allowing comparisons between adults and juveniles and between species.

Tetradirectional pitfall traps (Scapini *et al.*, 1992), in this case with intercepting strips 5 m long, were placed at regular distances in the eulittoral along a transect starting from the base of the dune (storm drift line) to the shoreline limits (Figure 1). The centre of the first trap was 20 m from the dune's base, followed by a second placed seawards at 10 m from the centre of the previous trap, but displaced by 10 m parallel to the shoreline. Other traps were placed with the same pattern and their number varied from 3 to 8 according to the tidal elevations. The system of traps separately intercepted the surface-active amphipods walking or jumping from four directions: from land, sea, and from the two directions parallel to the shoreline (north and south). The traps were visited at an hourly frequency and individuals were collected, preserved in 75% ethanol and then counted. Adults of *T. saltator* and *T. brito* were distinguished and considered separately from the juveniles (length <4 mm). The males of *T. brito* were easily recognized by the second gnathopod; the females, the subadults and the juveniles on the basis of the body morphology e.g. the greater lateral flattening of the body of *T. brito* with respect to *T. saltator*. Males and females were not considered separately because of the great proportion of subadults, damaged individuals and possibly intersexes. Since few juveniles of *T. brito* were counted, statistical comparisons with adults was not attempted. For *T. saltator*, however, juveniles were analysed separately from adults because of their high abundance.

A series of environmental factors (air temperature, relative humidity, atmospheric pressure, tidal elevation) were recorded each hour along with faunal data. Sand surface temperatures (1 cm from the surface) were recorded at two different points of the beach, corresponding to trap 1 (near the dune's base) and 3 (20 m more towards sea). In the same positions standard samples of sand, taken from the surface, were collected to determine the moisture content. Substrate temperature and moisture were not measured because talitrids burrowed in the surface layers. Prior to the spring tide observations heavy rains had occurred.

Circular statistical tests were used to analyse the diel and tidal components of talitrid activity, estimated from the number of individuals captured (mean hours of activity) (Batschelet, 1981). The Rayleigh test was used to determine whether the population showed a significant preference for a certain hour of the day or of the tidal cycle. Confidence intervals (95%) for the mean hour of activity were calculated with parametric standard error (Fisher, 1993). The V test was used to assess whether activity was concentrated around the expected hour of activity (for nocturnal species 24.00h; low tide for the tidal cycle when most of the beach is at the sandhopper's disposal).

Simple linear regression analysis was used to compare the trends of the capture frequencies and the mean zonations in daily and tidal hours. Multiple regression analysis, through the backward elimination method, was used to correlate the surface activity and hourly mean zonation of the amphipods with the environmental variables (Bliss, 1970; Zar, 1984). To examine the zonation of the surface activity patterns the number of captured talitrids (weight) was included in the regression analysis. For this analysis the statistical package Statgraphics Version 4.0, 1989 (STSC Inc.) was used.

To test the direction of migration, capture frequencies were analysed in the four directions (sea, land, north, south). The V test was used to test whether captures were concentrated in the expected direction (sea or land according to the daily and tidal hours). The parameter u of the V test was used as an orientation index. The orientation indices for the sea–land axis were calculated by keeping separate the capture frequencies of the more landward traps (traps 1, 2) from those of the central (traps 3–6) and seaward traps (traps 7, 8). These indices were calculated both for daily and tidal hours.

Mean zonations were calculated through one-sample analysis methodology (Zar, 1984) with confidence limits of 95%.

To analyse the capture frequency and zonation in tidal hours, taking into account the alternating high and low tides, the time between two successive high tides was subdivided in 12 equal segments (tidal hours). Equivalent time segments (relative to the tidal cycles) were then combined and a total tidal cycle was constructed that was independent from the actual length of the high tide–low tide time, which varies from day to day throughout the synodic cycle.

For the means and relative confidence limits (95%) and for circular statistic analysis only data with captures of five or more individuals were considered. The significance level of $P<0.05$ was used.

Results

Temporal component of surface activity

Surface activity of both species was limited to night time with an outburst of activity in the first and second part of the night during spring and neap tides, respectively [Figure 2(a–c)] and this occurred always during ebbing tide [Figure 2(d–f)].

No significant correlations were obtained when comparisons were made between the distributions of the capture frequencies at spring and neap tide for either species in daily and tidal hours (Table 1, activity). Furthermore no correlations were found in tidal hours when comparisons were made at spring tide between the two age classes of *T. saltator* and *T. brito*. The same occurred at neap tide between the juveniles and *T. brito*. In all other cases positive and highly significant correlations were obtained. Circular distributions in daily and tidal hours (Table 2) were significantly non-random (see Rayleigh test) and mean hours of activity were significantly concentrated around midnight and around low tide (see V Test), except for *T. brito* at spring tide and juvenile *T. saltator* at neap tide (in tidal hours). Mean hours of activity were always significantly different from each other when comparisons were made between adult and juvenile *T. saltator* and the two species (see confidence limits). In *T. brito*, mean hours of activity anticipated at spring tide and were delayed at neap tide when compared with *T. saltator*. Furthermore, juvenile *T. saltator* mean hours of activity anticipated that of the adults in both synodic periods (Table 2).

Spatial component of surface activity

From the total mean zonation (obtained considering all hourly samples) in the two synodic phases it is evident that *T. brito* lived downshore of *T. saltator*, and *T. saltator* adults were significantly seawards of juveniles [Figure 3(a)]. During spring tide, mean zonations of both species were between the high water of neap and the high water of spring whereas at neap tide the talitrids were restricted to a zone about 16 m (horizontally) around the high water of neap. Juveniles of *T. saltator* showed the greatest shift between spring and neap tide periods [Figure 3(b)].

During the two synodic periods significant variations in the hourly mean zonations of each species, both in diel and tidal hours, occurred during the night (Figure 4). At each hour talitrids were highly aggregated, except for *T. brito* during spring tide [Figure 4(a,d)]. During the spring tide the hourly mean zonation of *T. brito* and of the two age classes of *T. saltator*, in daily hours, had similar trends of the distribution of the capture frequencies as shown by the simple regression analysis (Table 1). The distribution of the hourly mean zonations of the juveniles at spring tide was positively correlated with that at neap tide. Furthermore, at neap tide positive correlations were found between the distribution of the adults of

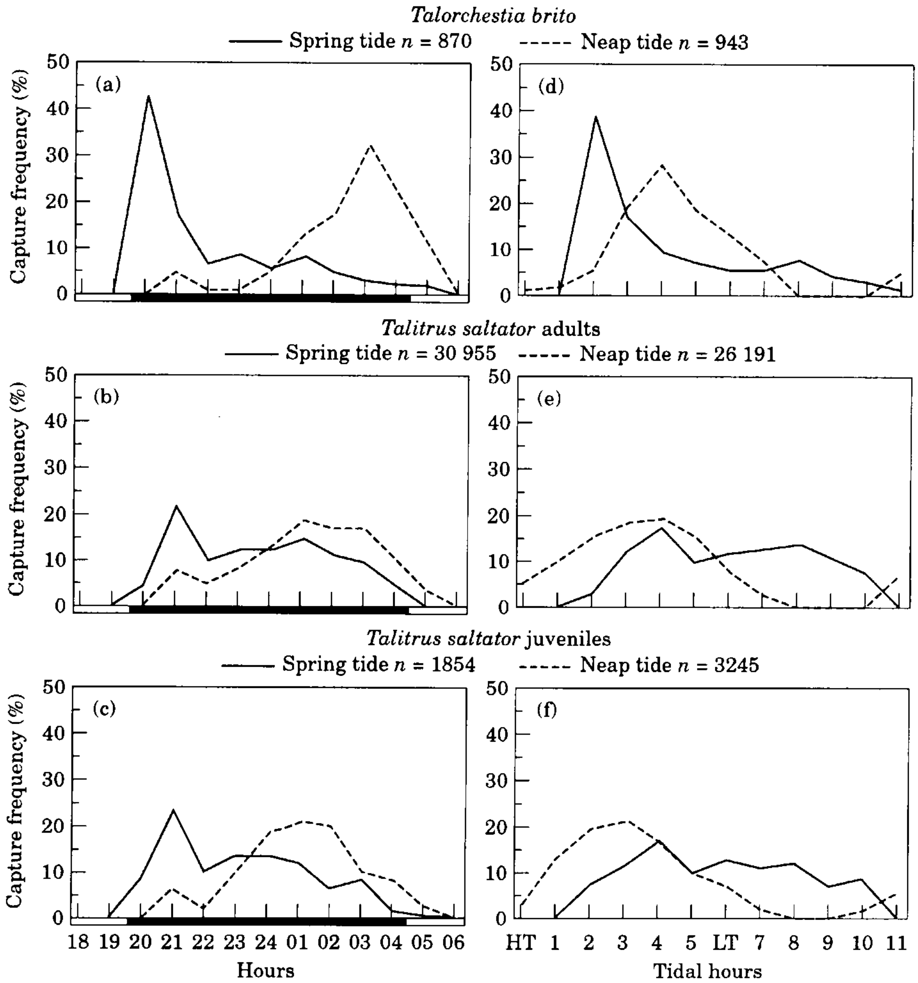

FIGURE 2. Capture frequency of *Talorchestia brito* and of the two age classes of *Talitrus saltator* with tetradirectional pitfall traps in daily (a–c) and in tidal hours (d–f), shown in both phases of the synodic period. HT=high tide, LT=low tide.

T. saltator and that of *T. brito*. In tidal hours at spring tide the distribution of the mean zonations of the adults of *T. saltator* was positively correlated with those of the juveniles and *T. brito*. In the latter species positive correlations were found between the distributions at spring and neap tides. A negative correlation was obtained for the juveniles *T. saltator* when the distribution of spring tide was compared with that of neap tide (Table 1).

Direction of orientated movements

The orientation indices calculated in daily hours shows that at spring tide [Figure 5(a–c)] significant orientated movements (V test) during nocturnal surface activity were exclusively towards the sea in all traps except for the adults of *T. saltator* in the central traps (3–6 at 03.00 and 04.00h in which landward movements were registered. *T. brito* was advanced more towards the sea with respect to *T. saltator* and was only sporadically captured in the landward traps (1–2) (n=10 at spring tide and n=0 at neap tide). During neap tide, *T. brito* [Figure 5(d)] showed a seaward tendency throughout the night but no significant movements were recorded around high tide (around 23.00h). Only before dawn was a significant landward movement registered for the seaward traps. Similar movements towards sea at the beginning of the activity period were observed in both age classes of *T. saltator* [Figure 5(e,f)]. These movements were followed by landward ones around high tide. As the tide ebbed movements of *T. saltator* were again towards the sea.

When orientation indices were calculated in tidal hours at spring tide for *T. brito* and for the juveniles of *T. saltator*, movements were always seawards both on

TABLE 1. Outputs from simple regression analyses to compare the trends of the distribution of the capture frequencies and hourly mean zonation of *Talorchestia brito* and the two age classes of *Talitrus saltator*

		Talorchestia brito		*Talitrus saltator* adult		*Talitrus saltator* adult		*Talitrus saltator* juvenile	
		Spring		Spring		Neap		Neap	
		Daily	Tidal	Daily	Tidal	Daily	Tidal	Daily	Tidal
Talorchestia brito Spring	Activity	—	—	0·398 $P<0·005$	NS	—	—	—	—
	Zonation	—	—	0·927 $P=0·001$	0·896 $P=0·001$	—	—	—	—
Talitrus saltator juvenile Spring	Activity	0·483 $P<0·001$	NS	0·771 $P<0·001$	0·936 $P<0·001$	—	—	NS	NS
	Zonation	0·779 $P<0·008$	NS	0·869 $P<0·002$	0·758 $P<0·007$	—	—	0·909 $P<0·003$	− 0·636 $P<0·05$
Talorchestia brito Neap	Activity	NS	NS	—	—	0·769 $P<0·001$	0·790 $P<0·004$	0·645 $P<0·001$	NS
	Zonation	NS	0·882 $P<0·004$	—	—	0·692 $P<0·04$	NS	NS	NS
Talitrus saltator adult Neap	Activity	—	—	NS	NS	—	—	0·957 $P<0·001$	0·923 $P<0·001$
	Zonation	—	—	0·927 $P<0·001$	0·896 $P<0·001$	—	—	—	—

Comparisons were made in the two phases of the synodic period both in daily and tidal hours. Correlation coefficients and probabilities are shown. NS=not significant, dashes=comparisons not made.

TABLE 2. Mean hours of activity calculated in daily and tidal hours in both phases of the synodic period

	Talorchestia brito				*Talitrus saltator* adults				*Talitrus saltator* juveniles			
	Spring tide n=870		Neap tide n=943		Spring tide n=30955		Neap tide n=26191		Spring tide n=1854		Neap tide n=3245	
	Daily	Tidal	Daily	Tidal	Daily	Tidal	Daily	Tidal	Daily	Tidal	Daily	Tidal
Mean hour	21·49	3·07	02·27	4·14	23·40	6·00	01·13	3·08	23·10	5·38	01·03	2·51
c.l.	± 00·10	± 0·09	± 00·07	± 0·06	± 00·02	± 0·02	± 00·02	± 0·02	± 00·06	± 0·10	± 00·04	± 0·05
r	0·814	0·451	0·895	0·676	0·831	0·420	0·859	0·550	0·835	0·382	0·884	0·609
z	576·874	176·977	755·241	431·211	21371·647	5467·769	19346·952	7918·503	1293·646	270·921	2534·232	1204·873
	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001
u	28·568	1·127	31·103	17·701	205·930	104·573	186·887	8·521	49·646	22·848	68·524	− 3·638
	P<0·001	NS	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	P<0·001	NS

Means are calculated starting from 24.00h and high tide, for daily and tidal hours, respectively. Probability levels are reported. NS=not significant, n=sample size, r=mean vector length, z=Rayleigh test, u=V test, c.l.=confidence limits.

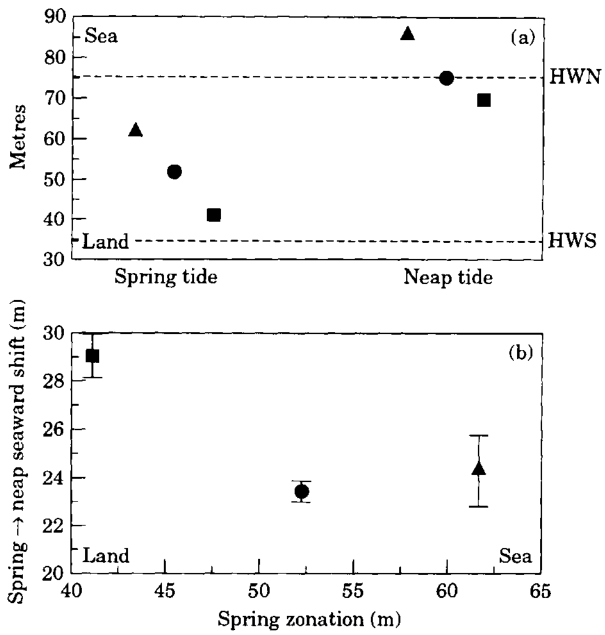

FIGURE 3. (a) Total mean zonation of surface-active amphipods during spring and neap tides; (b) extent of the synodic shift in the zonation of each species in relation to their zonation during spring tide. For each species confidence limits (95%) are shown. HWS=high water spring, HWN=high water neap. *Talorchestia brito*=triangles; *Talitrus saltator*; adults=circles, juveniles=squares.

ebbing and rising tides [Figures 6(a,c)]. By contrast, landwards-oriented movements of adult *T. saltator* were found in the central and seaward traps during rising tide [Figure 6(b)]. At neap tide for *T. brito* significant landwards movements were registered before and at low tide [Figure 6(d)]. The two age classes of *T. saltator* showed landward movements at the beginning of the ebbing tide and seawards immediately before low tide [Figure 6(e,f)].

Multiple regression analysis

At spring tide for *T. brito* the only variable that correlated significantly with surface activity was tidal elevation, but it only explained 28% of the variability (see R^2) (Table 3). Surface activity of the two age classes of *T. saltator* gave similar correlations with the environmental factors especially at neap tide. Instead, at spring tide negative correlations were found with air temperature and sand moisture whereas positive correlations were obtained with atmospheric pressure and for the juveniles with sand temperature near land. At neap tide for *T. brito* only atmospheric pressure showed a significant correlation and explained 46% of the variability (Table 3). In this case the constant was significantly correlated. In this synodic period, surface activity of the two age classes of *T. saltator* was positively correlated with air temperature and negatively with sand temperature and moisture near land.

At spring tide (Table 4), the hourly mean zonations of *T. brito* presented a positive correlation with relative humidity and atmospheric pressure and a negative one with sand moisture. The two age classes of *T. saltator* were negatively correlated with tidal elevations, showing that as the tide ebbed, the mean zonation, starting from the base of the dune, increased and sandhoppers moved towards the sea. The hourly mean zonations of the adults and juveniles were positively correlated with sand temperatures recorded near sea and near land, respectively. Positive and negative correlations were obtained, respectively, for the adults and juveniles with atmospheric pressure. During neap tide (Table 4) the hourly mean zonation of *T. brito* was positively correlated with the relative humidity of the air and sand temperatures near sea and negatively with tidal elevations. The hourly mean zonation of adult *T. saltator* was found to be negatively correlated with atmospheric pressure. For the juveniles positive correlation was obtained with the sand temperature near the sea and the tidal elevations, and a negative one with sand temperature and moisture near land with atmospheric pressure.

Discussion

At spring tide, the more intense activity and earlier emergence of *T. brito*, compared with *T. saltator*, can be seen in relation to the species' foraging area which is definitively further seaward. Its slower movement due to crawling and its less efficient jumping behaviour (personal observation) also may necessitate earlier activity. Food, represented by Cyanophyceae and Diatomeae (Vader, 1970), is found in the surf zone supporting the idea that *T. brito* can resist temporary submersion better than *T. saltator*, which is a poor swimmer (Dahl, 1946) and feeds on fresh strandline debris higher up the beach. The decrease in surface activity of *T. brito*, registered at low tide and as the tide rose after midnight, was probably due to more limited movements when feeding. During neap tide, movements of *T. brito* were again extremely concentrated in time as the tide ebbed, showing a preference for this phase (Lagardère, 1966). Also for *T. saltator* most captures (60% of the adults, 70% of the juveniles) were obtained before midnight during spring tide, and again there was a decrease at low tide. In contrast to *T. brito*, here the decrease was more gradual. At neap tide after dusk a small amount of activity was recorded in *T. saltator* but, high tide being

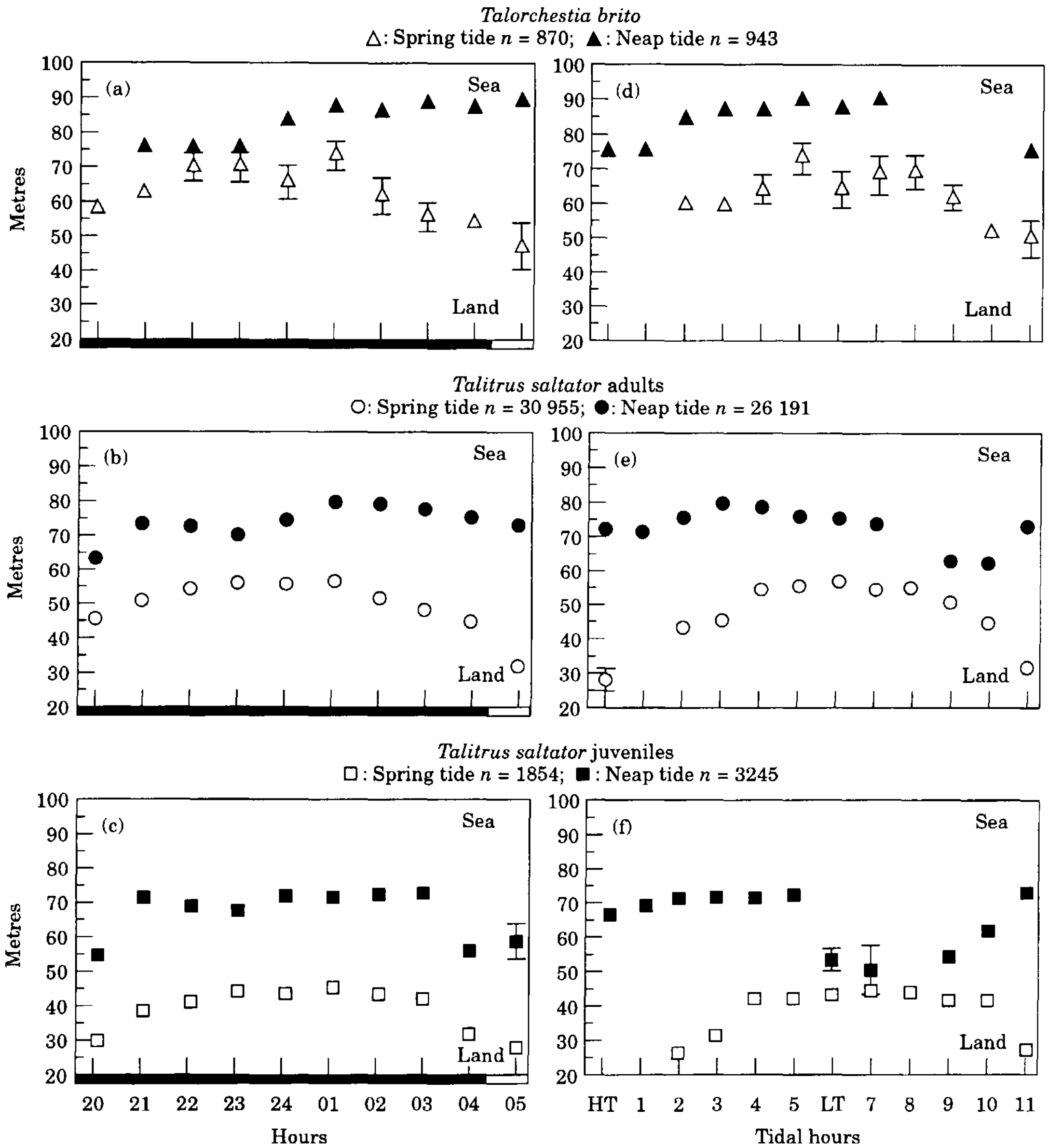

FIGURE 4. Daily (a–c) and tidal (d–f) hourly mean zonations of surface-active amphipods shown in both phases of the synodic period. Confidence limits (95%) are shown. HT=high tide, LT=low tide.

near midnight, most individuals emerged in the second part of the night. For this species there was a preference to move when the tide ebbed. Williams (1983*a*), in a study on the nocturnal surface activity of *T. saltator, Talorchestia deshayesi* (Audouin) and *Orchestia gammarella* (Pallas) at Derbyhaven, Isle of Man, showed that for *T. saltator* emergence was uninfluenced by the nocturnal high tide. For all three species there were movements upshore, with some reduction in the activity at high tide, followed by downshore movements as the tide ebbed. For the juveniles of *T. saltator*, Williams (1983*a*) found that emergence occurred 2–3 h prior to adults and that they remained active for 1 h longer. On the French Atlantic coast this difference between adults and juveniles was not found (see simultaneous activity peaks) even if the juveniles presented a mean hour of activity significantly earlier than to the adults. No diurnal activity was recorded for the juveniles after sunrise as was demonstrated in the Tyrrhenian population of *T. saltator* during the months of April and October (Scapini *et al.*, 1992). Both on the Isle of

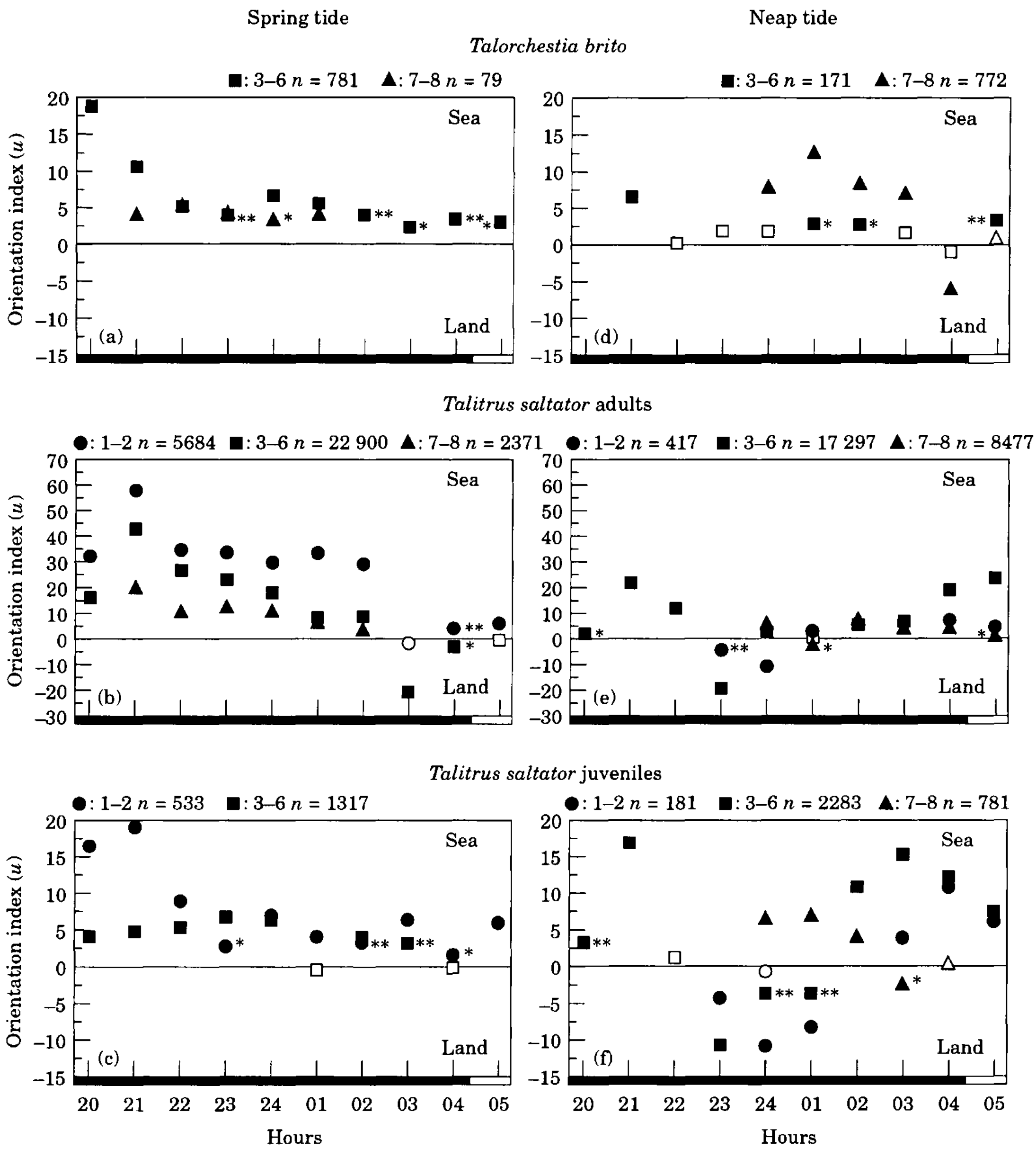

FIGURE 5. Variation of orientation index (u) of *Talorchestia brito* and of the two age classes of *Talitrus saltator* in daily hours during spring (a–c) and neap (d–f) tides. Seaward and landward movements are shown in the three groups of traps. Non-significant levels of P are indicated as open symbols, $^{*}P<0{\cdot}05$, $^{**}P<0{\cdot}001$, $P<0{\cdot}0001$ closed symbols without asterisks.

Man (Williams, 1995) and in the Mediterranean (Scapini *et al.*, 1992), juveniles burrowed lower down on the shore compared with the adults in an area where the risk of dehydration was low. In these two cases beach morphology played an important role. Williams' (1995) beach was characterized by a small width (about 20 m), an average slope of 36% and large tidal excursions (10 m), whereas the Mediterranean beach of Scapini *et al.* (1992) had a slightly greater width (about 40 m), an average slope of 6% and a low tidal excursion (30 cm). By contrast, on the French Atlantic coast juvenile *T. saltator* burrowed higher up the beach compared with the adults in an area above the high water of spring. This can be related to a greater beach width (about 100 m from the dune's base to the mean tidal level), to a smaller slope (3%) and a relatively large tidal excursion (4·5 m). The combination of these three variables, together with beach exposure and grain size (McLachlan, 1991), probably generated the differences found in the

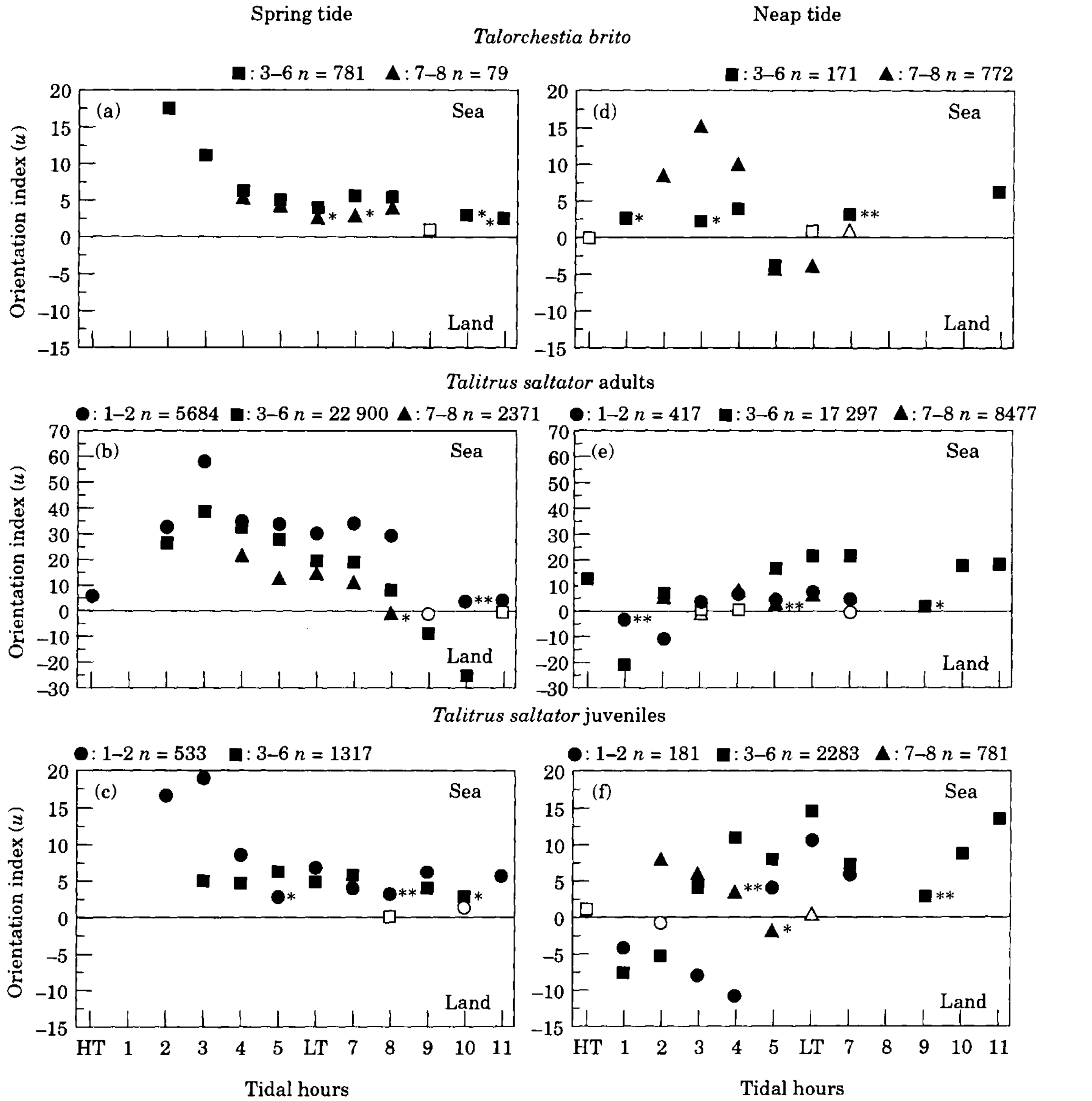

FIGURE 6. Variation of orientation index (u) of *Talorchestia brito* and of the two age classes of *Talitrus saltator* in tidal hours during spring (a–c) and neap (d–f) tides. HT=high tide, LT=low tide. For further information see Figure 5

burrowing distribution of the two age classes of *T. saltator* in the different geographical areas.

The analysis of the activity patterns in tidal hours shows that most talitrid activity occurred on the ebbing tide and that the mean hours of activity were significantly concentrated at low tide, except for *T. brito* at spring tide and the juveniles of *T. saltator* at neap tide. The differences found in the mean hours of activity between spring and neap tides for both species indicate that the synodic phases definitively influence the activity period. In fact the capture frequencies varied according to when the high tide and low tide fell during the night. It should be stressed that this does not necessarily mean that the species exhibit an endogenous tidal rhythm. The absence of this kind of rhythm, in *T. saltator* was demonstrated by experiments in constant conditions (Bregazzi & Naylor, 1972; Williams, 1980). However Pardi *et al.* (1974) found an endogenous tidal rhythm, in *Talorchestia martensii* Weber on a Somalian sandy shore. In the case of the French Atlantic coast the tides are suggested to influence the behaviour of the amphipods inducing upshore or downshore movements with consequent changes in zonation.

TABLE 3. Multiple regression of surface activity with environmental factors (air temperature and relative humidity, sand temperatures and moistures, atmospheric pressure, tidal elevation)

	Constant	Air temperature (°C)	Air relative humidity (%)	Sand temperature Sea (°C)	Sand temperature Land (°C)	Sand moisture Sea (%)	Sand moisture Land (%)	Atmospheric pressure (mmHg)	Tidal elevation (m)	R^2
Spring tide										
Talorchestia brito	NS	NS	NS	NS	NS	NS	NS	NS	14·6004 *P*<0·02	0·276
Talitrus saltator adults	NS	− 166·1910 *P*<0·004	NS	NS	NS	− 314·9254 *P*<0·005	− 380·8938 *P*<0·03	8·6338 *P*<0·001	NS	0·846
Talitrus saltator juveniles	NS	− 41·0819 *P*<0·04	NS	NS	29·7506 *P*<0·03	− 27·7782 *P*<0·002	NS	0·7100 *P*<0·02	NS	0·809
Neap tide										
Talorchestia brito	41179·3480 *P*<0·001	NS	NS	NS	NS	NS	NS	− 54·2749 *P*<0·001	NS	0·457
Talitrus saltator adults	NS	961·2643 *P*<0·009	NS	NS	− 927·2093 *P*<0·03	NS	− 2117·9920 *P*<0·007	NS	NS	0·727
Talitrus saltator juveniles	NS	118·0103 *P*<0·03	NS	NS	− 113·3118 *P*<0·05	NS	− 266·0124 *P*<0·014	NS	NS	0·667

Significant regression coefficients and their probabilities are shown. The constant of the multiple regression equation and the coefficient of multiple determination (R^2) are also reported.

TABLE 4. Multiple regression of hourly mean zonation of surface-active animals with environmental parameters. For further explanations see Table 3

	Constant	Air temperature (°C)	Air relative humidity (%)	Sand temperature		Sand moisture		Atmospheric pressure (mmHg)	Tidal elevation (m)	R^2
				Land (°C)	Sea (°)	Land (%)	Sea (%)			
Spring tide										
Talorchestia brito	NS	NS	0·8082 $P<0·001$	NS	NS	−4·8841 $P<0·001$	−2·6175 $P<0·05$	0·0295 $P<0·05$	NS	0·995
Talitrus saltator adults	NS	NS	NS	0·4822 $P<0·001$	NS	NS	NS	0·0719 $P<0·001$	−4·1058 $P<0·001$	0·998
Talitrus saltator juveniles	1412·7634 $P=0·01$	NS	NS	NS	0·4393 $P<0·04$	NS	NS	−1·8128 $P<0·02$	−2·6403 $P<0·001$	0·869
Neap tide										
Talorchestia brito	NS	NS	1·0794 $P<0·001$	NS	1·5708 $P<0·001$	NS	NS	NS	−4·7562 $P<0·003$	0·999
Talitrus saltator adults	3022·0360 $P<0·02$	NS	NS	NS	NS	NS	NS	−3·8894 $P<0·02$	NS	0·267
Talitrus saltator juveniles	8805·1920 $P<0·002$	NS	NS	−8·4140 $P<0·03$	8·6155 $P<0·04$	−9·9861 $P<0·04$	NS	−11·5285 $P<0·002$	9·9672 $P<0·001$	0·664

At spring tide the variations in zonation, first towards the sea then towards the land, recorded for *T. brito* and for the two age classes of *T. saltator* during the nocturnal activity period, were not consistent with the orientation indices calculated in daily and tidal hours. The general seaward tendency reflects a massive zonal recovery as a consequence of intense rainfall and winds that had occurred 24 h before sampling. Geppetti and Tongiorgi (1967) and Scapini *et al.* (1992) for *T. saltator* and Pardi *et al.* (1974) for *T. martensii* recorded inland migrations in relation to storms and to the extreme high waters of spring, respectively. Sea winds could have favoured landward movements in relation to a negative anemotaxis, a phenomenon clearly demonstrated by laboratory experiments in *T. saltator* (Scapini *et al.*, 1988). The contemporaneous landward and seaward movements of adult *T. saltator* before dawn, indicate a zonal recovery to a specific area of the beach where resting occurs.

Instead, at neap tide the orientation indices calculated for the two age classes of *T. saltator* in both daily and tidal hours are in accordance with the observed variation in the hourly mean zonations. Movement towards land by adults and juveniles of *T. saltator* was registered at high tide showing an evident avoidance of submersion. These were followed by a seawards-orientated tendency as the tide ebbed. At rising tide inland movements were recorded not only for the two studied species but also for other talitrids such as *Orchestia platensis* (Kröyer), *Talorchestia deshayesii* and *Transkorchestia transkiana* (Stimpson) (Rüppel, 1967; Koch, 1989). These authors considered inundation to be a catastrophic event in that the resulting activity and migration could expose amphipods to predation and to physiologically stressful conditions. In *T. brito* dispersion around high tide was followed by a seaward tendency at ebbing tide. The almost contemporaneous landward and seaward orientation before dawn, showed that during the day amphipods rested in burrows in a restricted beach area. Recovery to a restricted zone was evident also for the juveniles of *T. saltator*. This behaviour was probably related to the necessity to remain over the diurnal high tide in a beach area where the risk of dehydration was limited. In this season during the day sand temperature of 35 °C and a relative humidity of 60% were reached. Williamson (1951) demonstrated that *T. saltator* was more resistant to desiccation than *Talorchestia deshayesii* and *Orchestia gammarellus*. Furthermore Morritt (1987) claims that *T. saltator* exhibits lower water-transpiration rates than *O. gammarellus*. These physiological characteristics together with the differences in feeding behaviour (Vader, 1970; Morritt, 1987) could explain the higher burrowing distribution registered for *T. saltator* compared with *T. brito*. For *T. saltator*, higher upshore distributions with respect to related species *T. deshayesii* and *O. gammarellus* were also found by Williams (1983*b*, 1995) on Derbyhaven Beach, Isle of Man. This suggests that *T. saltator*, and particularly the juveniles, tend to avoid submersion more than *T. brito*. In France at neap tide, the total mean zonation was more seawards and there was an evident dependence of the hourly mean zonation of *T. brito* and the juveniles of *T. saltator* with the same factors: sand temperatures and tidal elevations. This means that the more landward (juveniles) and seaward (*T. brito*) distributed animals were more subjected to environmental stress factors compared with adult *T. saltator* that presented an intermediate mean zonation. Adult *T. saltator* has greater plasticity due to its physiological adaptations (Morritt, 1987) and rapid locomotion all assisted by a greater learning experience (Scapini *et al.*, 1993). Instead, when the distributions of the hourly mean zonations and those of surface activity were correlated with environmental factors a major affinity between adult and juvenile *T. saltator* was found at spring tide and in both synodic phases, respectively. Only tidal elevation seems to be important for the surface activity of *T. brito* at spring tide confirming that this species is more confined to the shoreline than *T. saltator*.

This work has pointed out the differences in the behavioural strategies of two sympatric talitrids inhabiting a beach of the French Atlantic coast subjected to environmental conditions different from those at previously studied localities. These differences were to be expected if biological interactions (competition) are to be avoided. In particular, it was demonstrated that *T. saltator* adopts certain strategies in the use of space in relation to local conditions, confirming its ability to colonize large geographical area. Of interest are the differences found in the distribution patterns of the adults and juveniles. These can be modulated on different beach types showing that behavioural plasticity relates to physiological needs and permits survival in optimal conditions.

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