



Locomotor activity and zonation of upper shore arthropods in a sandy beach of north central Chile

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Abstract

The tenebrionid beetle *Phalerisida maculata* Kulzer, the talitrid amphipod *Orchestoidea tuberculata* Nicolet and the oniscid isopod *Tylos spinulosus* Dana are semi-terrestrial burrowing species, which coexist on sandy beaches of north central Chile (28–30°S). During the night, these scavengers emerge to make downshore migrations. Given the similarity in niches of these three species (all are known to include macroalgal detritus in their diet) and their relatively high abundance on that beaches, there is the potential for some degree of interaction, both inter- and intraspecific. Field studies were carried out to examine zonation of these burrowing organisms and eventual time and/or space partitioning of locomotor activity during night hours. Locomotor activity on the beach surface was analyzed over 12 h periods during spring and neap tides of September and December 2000, and March 2001. Scavengers moving over the beach surface were captured using pitfall traps buried with their rims flush with the beach surface along a transect extended from the foot of the dunes to the highest levels reached by the swashes. Every 1 h the captured animals in the traps were collected. Locomotor activity was also studied in the laboratory with chambers equipped with infrared recording systems (actographs). Data downloaded from the actographs were graphed to obtain a display of locomotor activity per 15 min interval during the course of the 7 day experiments. Results show space partitioning of burrowed organisms and time partitioning in the locomotor activity of *O. tuberculata*, *T. spinulosus* and *P. maculata* over the beach surface. Circular statistics showed that usually the activity peaks of *O. tuberculata* were more different from those of *P. maculata* and *T. spinulosus* than those of the last two species when compared with each other. Intraspecific differences were also found in the surface locomotor activity, primarily between juveniles and adults of *O. tuberculata*. Interseasonal comparisons of capture figures show that the highest locomotor activity occurred during early summer (December 2000). Moon phases apparently affect locomotor activity (i.e. *T. spinulosus* and *P. maculata* had higher locomotor activity during neap tides as compared with that observed during spring tide samplings carried out with full moon). Periodograms resulting from the locomotor activity of adults of *O. tuberculata*, *T. spinulosus* and *P. maculata* studied with actographs and total darkness show evidence of a circadian endogenous component close to 23–25 h. Activity peaks close to 11–14 h were also found that probably represents a circatidal component in the locomotor activity. Results of actograph experiments under constant light show that the circadian rhythm of locomotor activity of *O. tuberculata* was the only one maintained throughout the experiment and phased with the subjective night. Analyses of contour distributional maps and mean hourly zonations show that the locomotor activity of the studied species also differed, specially that of *O. tuberculata* versus that of *T. spinulosus* and *P. maculata*. Results of coexistence experiments showed no evidence of intraspecific interactions. Similar experiments evidenced interspecific interactions: those species with similarities in locomotor activity (that is *T. spinulosus* and *P. maculata*) showed no interactions between them, while both of them had negative interactions with *O. tuberculata*, the species which separated more in time and hourly zonation of locomotor activity. Thus, differences in time/space partitioning of surface locomotor activity can be interpreted as a means to avoid detrimental interactions in this guild of scavengers. That partitioning would allow coexistence of interacting scavenger species and provides evidence that biological interactions are indeed important in community structure of sandy beach macroinfauna.

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1. Introduction

The assumption that physical processes play the primary role in influencing community structure and

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organization of the intertidal macroinfauna of exposed sandy beaches has dominated discussions on the ecology of these coastal habitats for the past decade or more (see review by Brown & McLachlan, 1990). In the last few years it has been shown worldwide that the community structure of sandy beach macroinfauna is closely related to beach morphodynamics, i.e. the interaction between wave climates and sediment type which results in reflective, intermediate and dissipative beaches (sensu Short, 1996). Thus, species richness, abundance and biomass of the intertidal macroinfauna generally increase from reflective to dissipative beaches (Jaramillo & McLachlan, 1993; McLachlan, De Ruyck, & Hacking, 1996; McLachlan, Fisher, Al-Habsi, Al-Shukairi, & Al-Habsi, 1998; McLachlan, Jaramillo, Donn, & Wessels, 1993).

The sandy beaches of Chile harbour very abundant macroinfaunal communities (up to 600,000 individuals m^{-1} , Jaramillo, 2001). Despite evidence from earlier studies for some regions (see earlier discussion), more recent studies carried out along the Chilean coast have shown that community structure of the macroinfauna is not consistently related to beach morphodynamics (Jaramillo, 2001; Jaramillo, Contreras, Duarte, & Quijón, 2001). Thus, other factors may be the cause of that result, among them, biological interactions. In other coastal habitats where physical processes play a key role in community organization (e.g. Connell, 1978; Sousa, 1979), biological processes such as competition and predation are also important to community structure (e.g. Connell, 1961; Lubchenco, 1978; Paine, 1966). For sandy beaches, however, such processes have not been thoroughly explored. One of the few examples is that of Croker and Hatfield (1980), which demonstrated significant interactions between haustoriid amphipod species on a sandy beach of Maine, USA. They concluded that competitive interactions explained the seasonal variability in space partitioning of these amphipod species. Some less direct evidence of inter- and intraspecific interactions exists. For example, Defeo (1996) found that experimental closure of the fishing season of the bivalve *Mesodesma mactroides* (Deshayes) on sandy beaches of Uruguay resulted in decreased abundance of recruits, a result which suggested that intraspecific interactions between adults and recruits had occurred. Also, Dugan and Hubbard (1996) based upon significant correlations between some life history characteristics and population abundances of the sand crab *Emerita analoga* (Stimpson) suggested that intraspecific interactions could influence populations of this species, i.e. high abundances of this species may result in lower growth rates. Thus, despite the fact that few studies have addressed the role of biological interactions in community organization of sandy beach macroinfauna, there is some evidence which suggests such interactions could be important and should be investigated more explicitly.

Space does not generally appear to be limiting in the three dimensional soft sediment environment of sandy beaches, but other resources such as food availability could be potentially limiting at least on some temporal or spatial scales. For example, it is well known that many sandy beaches support a scavenger assemblage of arthropods that are mainly active at night. When burrowed, these organisms (including tenebrionid beetles, talitrid amphipods and tyloid isopods) inhabit characteristic zones in the upper beach levels (McLachlan & Jaramillo, 1995). When active, they move over most of the beach surface scavenging mainly on organic debris (primarily macroalgal drift). Little is known concerning the possible extent of competitive or other interactions either within or between scavenger species in this situation. However, there are some lines of evidence to suggest that behavioural patterns have evolved that minimize negative interactions by spatial or temporal partitioning. For example, Fallaci et al. (1999) found differences in the zone of locomotor activity of *Talitrus saltator* (Montagu) in the French coast, i.e. the juveniles presented a more landward distribution compared with adults and compared with another sympatric talitrid (*Talorchestia brito*, Stebbing) which was always closer to the sea. Kennedy, Naylor, and Jaramillo (2000) suggested that differences in the timing of locomotor activity between juveniles and adults of the talitrid amphipod *Orchestoidea tuberculata* Nicolet could be the outcome of biological interactions.

Sandy beaches located at the coast of north central Chile (28–30°S) harbour unusually high abundances of the talitrid amphipod *Orchestoidea tuberculata* Nicolet, the oniscid isopod *Tylos spinulosus* Dana and the tenebrionid beetle *Phalerisida maculata* Kulzer. These species can be classified as downshore migrants, semi-terrestrial species, which burrow on the upper shore, commonly close to the high tide or drift line and emerge to make downshore migrations. All are known to include macroalgal detritus in their diet. Given the similarity in niches of these three species and their relatively high abundance on the beaches of the region, there is the potential for some degree of competition, interference or even predation, both inter- and intraspecific. A study that attempts to record simultaneously their surface locomotor activity, both in the field and under constant conditions in the laboratory, could make significant progress in elucidating the role of biological interactions in shaping the behaviour and community organization of these downshore migrant species. Thus, field and laboratory studies were carried out at the coast of north central Chile to address the following questions: (1) is there evidence of time and/or space partitioning of locomotor activity during night hours in different species or age groups (juveniles versus adults) of *O. tuberculata*, *T. spinulosus* and *P. maculata*? and (2) is there any evidence of intraspecific and/or interspecific interactions in that species? The across shore distribution of

burrowed organisms was also studied to analyze eventual space partition while these species are inactive (i.e. under the beach surface).

2. Material and methods

2.1. Study area

Field studies were carried out at the beach of El Apollillado (29°10'S, 71°29'W), included in the Peruvian or Transition Zoogeographic Zone of the Chilean coast (Dell, 1971; Knox, 1960; Marincovich, 1973). This beach is located at the semi-arid coast of Chile with an annual rainfall close to 110 mm (Brattström & Johanssen, 1983). The length of the beach is close to 1.5 km and is backed by dunes of 5–6 m height. Morphodynamically, El Apollillado is an intermediate type of beach (sensu Short & Wright, 1983). Tides are semi-diurnal with an approximate range of 1.4 m.

2.2. Field studies

Zonation of burrowed organisms was studied during surveys carried out during 12 September 2000 (spring tide), 20 September 2000 (neap tide), 10 December 2000 (spring tide), 16 December 2000 (neap tide), 10 March 2001 (spring tide), 16 March 2001 (neap tide), August 2001 (spring tide) and August 2001 (neap tide). In those surveys, cores (0.03 m², 30 cm deep) were collected with cylinders at 10 equally spaced levels along three transects (separated by 1 m) extending from above the drift line to the swash zone, i.e. the uppermost station was located above the drift line, the second on the drift line and the last at the lowest limit of the swash zone (indicated by bore collapse). The sediment was sieved through a 1 mm mesh and the organisms collected were stored in 5% formalin until sorting. Surface (about 5 mm) samples were collected for grain size analyses with a settling tube (Emery, 1938). The morphology of the beach (i.e. beach face slope at the site of one transect randomly selected from the three ones) was determined by Emery's profiling technique (Emery, 1961).

Locomotor activity on the beach surface was studied over the period when the three species studied are active over the beach surface, i.e. primarily night hours. Thus, those studies lasted 12 h from 20:00 to 07:00 hours. Sampling dates were 12–13 September 2000 (spring tide), 20–21 September 2000 (neap tide), 10–11 December 2000 (spring tide), 16–17 December 2000 (neap tide), 10–11 March 2001 (spring tide) and 16–17 March 2001 (neap tides). Samplings carried out during spring tides corresponded to full moon, while those of neap tides were carried out during the last quarter of the moon. Scavengers moving over the beach surface were captured using pitfall traps, which were plastic jars (120 mm

height, 50 mm diameter) buried with their rims flush to the beach surface. Traps were located at 3 m intervals along a transect extended from the foot of the dunes (dry zone) to the highest levels reached by the swashes. They were removed and replaced according to the variability in the extent of the beach exposed by the tide. Each trap contained about 5 cm of seawater–formalin (10%) to prevent the escape of captured animals. Every 1 h the captured animals in the traps were emptied into plastic bags, and the seawater–formalin solution replaced.

2.3. Laboratory studies

2.3.1. Locomotor activity

The locomotor activity of amphipods, isopods and beetles was studied in chambers equipped with infrared recording systems (actographs) during September and December 2000, and January and March 2001. The actographs were designed and constructed at the School of Ocean Sciences, University of Wales, UK (Warman, unpublished data). Animals for use in actographs were collected by hand from their burrowing zone during daylight hours 24 h before the start of the experiments. These animals were placed in plastic jars containing damp sand (10–12% water content) collected from the very same depth where the animals were collected; pieces of algal wrack collected from the collection site were also added to the jars. After transport to the laboratory, the animals were transferred to glass containers with damp sand. These containers were kept under conditions of continuous darkness and room temperature (15 °C). After an acclimatization period of 48 h from the time of collection, the actograph experiments were initiated. These experiments were performed in glass containers with dimensions of 250 mm length, 150 mm height and 70 mm width. The glass containers were filled to a level of 60 mm with damp sand from the burrowing site of the experimental animals. A Perspex platform of 80 mm length and 70 mm width was placed in the mid section of the glass container. This provided a flat, horizontal surface upon which locomotor activity could be recorded. Surface locomotor activity was registered by interruption of two infrared beams across each container for each species, the beams arranged to pass over the surface of the Perspex platform in the glass containers. We had two actographs for each specific container to avoid the eventual possibility of data loss due to failure of the equipment. After a predetermined download interval of 15 min, the data were downloaded to computer. During the experiments (7 days), the containers were kept in a light-tight enclosure within the constant temperature room (15 °C). A group of 30, 20 and 15 adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata*, respectively, were placed in each container for each experimental trial. Group of animals rather than single specimens were

used to examine population responses rather than individual ones. None of these animals died during the experiments. The ranges in cephalothorax length of *O. tuberculata* and *T. spinulosus* used in the actographs were 14–18 and 16–22 mm, respectively, while the range in body size (from the anterior tip of the head to the posterior tip of the abdomen) of *P. maculata* was 4–6 mm. The experiments carried out during September and December 2000, and March 2001 were performed in darkness, while those carried out during January 2001 were done with constant light.

2.3.2. Coexistence experiments

Adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* were collected from their burrowing zones and kept in damp sand for 24 h before initiating the experiments. The ranges in cephalothorax length and body size of that experimental animals were the same as used in the actograph experiments (see earlier discussion). The experimental design proposed by Underwood (1986) to evaluate intra- and interspecific interactions was employed to investigate the effects of population density on survival of these species. The experiments were run from 14 to 17 August 2001. The animals were placed in plastic bowls measuring 12 cm in diameter and 11 cm in height, and covered with a plastic lid with small holes to allow air exchange. Each bowl was filled to a depth of 3 cm with damp sand (10–12% water content) from the burrowing zone. The experimental treatments were as presented in Table 1. Six replicated bowls were used for each treatment. Experiments were run at ambient room temperatures (16–18 °C) in constant darkness. No food was provided during the experiments. During the morning of August 17, the number of dead animals in each experimental bowl was recorded.

2.4. Data analysis

The trapped specimens of *Phalerisida maculata* were sorted into larvae and adults, while those of *Orches-*

toidea tuberculata and *Tylos spinulosus* were sorted in juveniles and adults. For the last two species, the juveniles were those animals with body lengths (apex of cephalon to distal tip of telson) of <12 mm, while adults were those individuals with body lengths >12 mm. The individuals of the second groups were classified as adults because of different developments of sexual characters, such as chelipeds in males of amphipods, brood plates in females of amphipods and isopods, etc. The catch data per time interval were used in circular statistics (Zar, 1999) to analyze the eventual periodicity in locomotor activity. The average angle (i.e. the mean hour) was calculated and the dispersion of the data (r) around this angle (based on the frequency allocation obtained by the Rayleigh Test (z)) was used to calculate the probability (P) to see whether the studied population presented a circular uniform distribution (or whether larvae and adults of *P. maculata* and juveniles and adults of *O. tuberculata* and *T. spinulosus* showed a significant concentration of locomotor activity during some hour of the night). Values of angles were doubled or tripled when the distributions had more than a mode (Zar, 1999). For circular statistical analysis only data with captures of more than five individuals per sampling period were used (Zar, 1999).

Data downloaded from the actographs were graphed to get a display of locomotor activity per 15 min interval during the course of the 7 day experiments. That data were then used in a periodogram analysis performed by the program 'Perio' (Aagard, 1993). The output of this program is a periodogram showing a graphical display of possible period lengths within a user specified range plotted against standard deviations (s-units). Ninety-five percent confidence intervals calculated for the same data in randomized order are superimposed on that graphical display. Periodogram peaks exceeding the upper 95% confidence limit were taken as statistically significant and indicative of periodicity in the locomotor activity.

Table 1

Experimental design to test for eventual intraspecific and interspecific interactions in *Orchestoidea tuberculata* (Ot), *Tylos spinulosus* (Ts) and *Phalerisida maculata* (Pm). Each treatment (T) had six replicates (see text)

T number	Number of animals	T number	Number of animals	T number	Number of animals	Comparisons of:	Effects of:	Interaction
1	10 Ot	4	20 Ot	10	30 Ot	T 1–T 4–T 10	Ot on Ot	Intraspecific
2	10 Ts	5	20 Ts	11	30 Ts	T 2–T 5–T 11	Ts on Ts	Intraspecific
3	10 Pm	6	20 Pm	12	30 Pm	T 3–T 6–T 12	Pm on Pm	Intraspecific
		7	10 Ot + 10 Ts	13	10 Ot + 20 Ts	T 1–T 7–T 13	Ts on Ot	Interspecific
		8	10 Ot + 10 Pm	14	10 Ot + 20 Pm	T 1–T 8–T 14	Pm on Ot	Interspecific
		9	10 Ts + 10 Pm	15	10 Ts + 20 Pm	T 2–T 9–T 15	Pm on Ts	Interspecific
				16	10 Ts + 20 Ot	T 2–T 7–T 16	Ot on Ts	Interspecific
				17	10 Pm + 20 Ot	T 3–T 8–T 17	Ot on Pm	Interspecific
				18	10 Pm + 20 Ts	T 3–T 9–T 18	Ts on Pm	Interspecific

The spatial distribution of juveniles and adults of *Orchestoidea tuberculata* and *Tylos spinulosus*, and that of larvae and adults of *Phalerisida maculata* during the neap tide samplings was analyzed through the examination of contour distributional maps and calculations of mean hourly zonations. The maps were made with the software SURFER (using Krigging interpolation) and were based upon the number of captured organisms per trap and per hourly sampling period. No such displays were prepared for the spring tide samplings due to the low captures of amphipods, isopods and beetles during that samplings. Mean hourly zonations were estimated through the following steps: (i) multiplication of the number of animals captured at each trap by the distance from that trap to the starting point (zero m); (ii) sum of all the former values; and (iii) division of that sum by all the animals captured during each hourly sampling. The confidence limits of 95% were estimated through the critical value of a *T* distribution with $n - 1$ degrees of freedom (n = number of individuals captured at each hour) multiplied by the standard error. That values were added to and subtracted from the mean to obtain the upper and lower confidence limits (cf. Sokal & Rohlf, 1995). Only data with five or more individuals captured were considered.

The results of the coexistence experiments (mortality in percentage) were analyzed with ANOVA on arcsin transformed data and the a posteriori test, Tukey's Honest-Significant-Difference or HSD (Sokal & Rohlf, 1995).

3. Results

3.1. Beach characteristics

Table 2 shows that during the spring and neap tides of September and December 2000, beach face slopes were similar; on the other hand, during March 2001 the beach face slope was flatter (1/29, i.e. 1 m of difference in height per 29 m of horizontal distance) during the spring and steeper (1/19) during neap tide. Means and range size of sands showed that coarser grains occurred during late winter (September) and late spring (December) than during late summer (March).

3.2. Zonation of the buried organisms

Fig. 1 shows that during the spring tide of September, the only species found buried under the sand surface was *Orchestoidea tuberculata*. During the neap tide of that month and during the samplings carried out in December, that amphipod was the most abundant species followed by *Tylos spinulosus* and *Phalerisida maculata*. On the other hand, during March the most

Table 2

Beach face slopes and sand characteristics of the beach of El Apollillado during day low tides. s.d. is the standard deviation

		Beach face slope	Sand characteristics in microns	
			Mean size (s.d.)	Range sizes
September 2000	Spring tide	1/23	313 (61)	232–426
	Neap tide	1/21	314 (32)	245–359
December 2000	Spring tide	1/27	319 (49)	250–404
	Neap tide	1/25	241 (34)	216–299
March 2001	Spring tide	1/29	255 (37)	211–311
	Neap tide	1/19	247 (26)	220–295

abundant species was the isopod *T. spinulosus*. Fig. 1 shows a habitat partitioning of *O. tuberculata*, *T. spinulosus* and *P. maculata* when burrowed under the surface; usually the population modes of the amphipod were located at lower shore levels than those of the isopod and the insect.

3.3. Locomotor activity over the beach surface

Fig. 2 shows the locomotor activity of juveniles and adults of *Orchestoidea tuberculata* and *Tylos spinulosus* and larvae and adults of *Phalerisida maculata* deduced from catch data or the number of animals captured on the pitfall traps. During September, most of the captured specimens were juveniles of *O. tuberculata* which were active most of the night. During the neap tide of that month, pitfall traps captured juveniles and adults of *O. tuberculata* and *T. spinulosus* and only adults of *P. maculata*. While the locomotor activity of adults of *O. tuberculata* and *T. spinulosus* peaked at slightly different times, that of juveniles peaked at totally opposed times (Fig. 2). During this sampling, adults of *P. maculata* peaked at the beginning of the night. During the spring tide sampling of December, *O. tuberculata* was represented over the beach surface by juveniles and adults; the first ones peaked at different times of the night, while adults were more active after midnight (Fig. 2). *Tylos spinulosus* and *P. maculata* were represented by juveniles and adults, respectively; both of them being more active at the end of the night (Fig. 2). During the neap tide sampling of December, pitfall traps captured juveniles and adults of *O. tuberculata* and *T. spinulosus*, while just adults of *P. maculata*. While the locomotor activity of juvenile and adults of *O. tuberculata* peaked at different times, that of juveniles and adults of *T. spinulosus* peaked at similar times (Fig. 2). During the spring and neap tide samplings of March, most of the captured organisms were juveniles. During the spring tide samplings, they appeared and disappeared from the beach surface, while during the neap tide samplings they were active most of the night (Fig. 2).

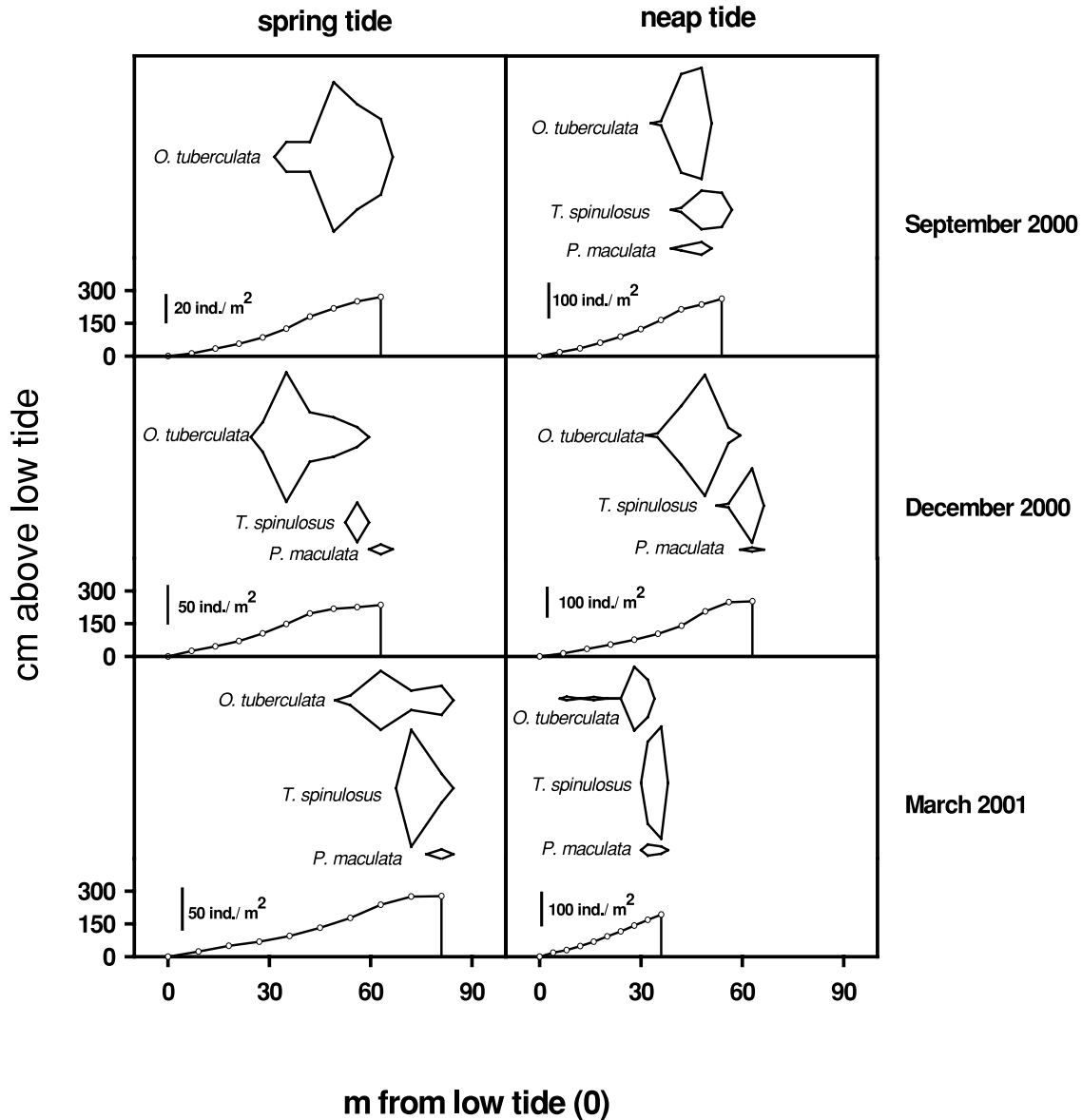


Fig. 1. Intertidal distribution of buried specimens of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings at the beach of El Apollillado. Note changes of scales for population abundances.

The results of circular statistics applied to the nocturnal locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* are shown in Table 3. While during the spring tides, the locomotor activity of the three species occurred at different times of the night, during neap tide most of that activity occurred during the first part of the sampling period (i.e. before 02:00 hours) (Table 3). Juveniles and adults of the three species presented locomotor activity significantly concentrated around the estimated mean hour ($P \leq 0.01$); the exceptions were juveniles of *T. spinulosus*, which during the spring tide of September presented a locomotor activity uniformly distributed along the sampling period ($P = 0.076$). During September and December, the locomotor activity was concen-

trated in a single mean activity hour. On the other hand, during the spring tide of March, juveniles of *O. tuberculata* had their surface locomotor activity concentrated around two mean hours (19:48 and 03:21 hours), while those of *T. spinulosus* had their activity concentrated around three mean hours (21:40, 03:40 and 06:06 hours) (Table 3). Similarly, during the neap tide of March, the locomotor activity of larvae of *P. maculata* was concentrated around two mean hours (22:08 and 05:06 hours) (Table 3). Interspecific comparisons show that the mean hour of locomotor activity differed among species, while intraspecific comparisons show that juveniles and adults of *O. tuberculata* differed more between themselves, than juveniles and adults of *T. spinulosus* and larvae and adults of *P. maculata* (Table 3).

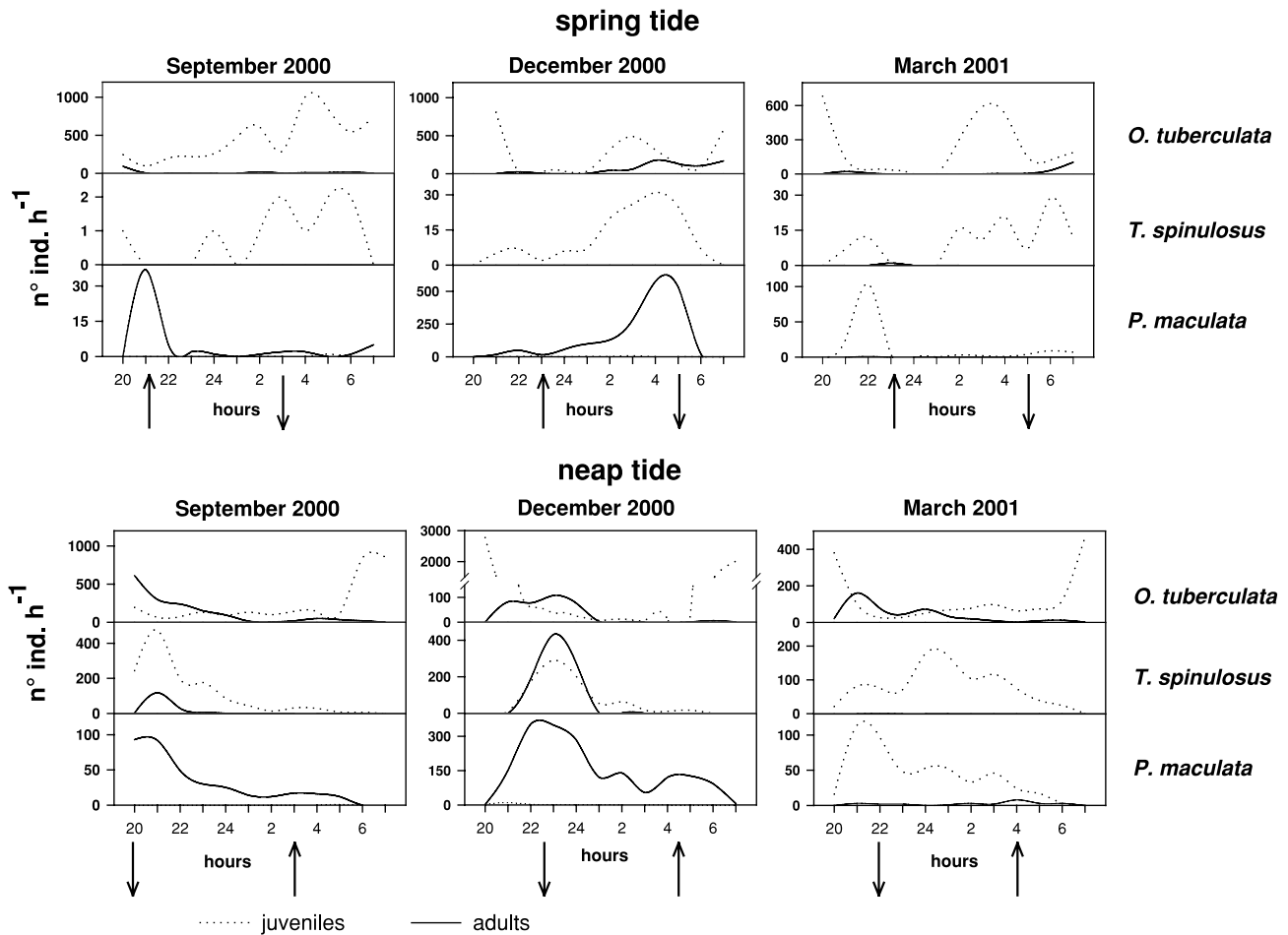


Fig. 2. Temporal distribution of the locomotor activity of juveniles and adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings. Locomotor activity deduced from number of captured organisms in pitfall traps along the transect (see Section 2). Upward arrows, approximate time of observed high tide; downward arrows, approximate time of observed low tide.

3.4. Locomotor activity in laboratory conditions

The locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* under free running conditions and continuous darkness is shown in Figs. 3–5. Interseasonal comparisons show that the activity records for *O. tuberculata* were higher during September and March, and lower during the experiments carried out during December. On the other hand, the activity records for *T. spinulosus* were higher during December and lower during March and September, while those of *P. maculata* peaked during December and March.

For each sampling period, the locomotor activity of *Orchestoidea tuberculata* and *Tylos spinulosus* was primarily restricted to the hours of subjective night, while that of *Phalerisida maculata* occurred throughout most of the time. During the experiments carried out during December (Fig. 4) and March (Fig. 5), the activity of *P. maculata* tended to be lower during the subjective day. The results collected from the actographs also show that usually the locomotor activity of *T.*

spinulosus begins and finishes earlier than that of *O. tuberculata*. This is clearly seen during the experiments carried out in September and December (Figs. 3 and 4, respectively).

During the first 2 days of September, the locomotor activity of *Orchestoidea tuberculata* started after the expected time of high tide (Fig. 3). Later on, that activity seems to be not affected by the expected high tide. During December, the maximum locomotor activity occurred after the expected time of high tide (Fig. 4), while during March the locomotor activity of this amphipod occurred exclusively after the expected times of high tides (Fig. 5). In other words, that activity occurred during low tide periods. During September, the locomotor activity of *Tylos spinulosus* showed a similar trend to that of *O. tuberculata*, i.e. at the beginning of the experiments the activity started after the expected time of high tide; later on, that activity was lower but not affected by the expected time of high tide (Fig. 3). During December, the locomotor activity of this isopod was concentrated during the first 4 days of the experiments, and usually after the expected time of high tide

Table 3

Mean hours of surface locomotor activity of juveniles or larvae and adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings

	Spring tide						Neap tide					
	<i>O. tuberculata</i>		<i>T. spinulosus</i>		<i>P. maculata</i>		<i>O. tuberculata</i>		<i>T. spinulosus</i>		<i>P. maculata</i>	
	Juveniles	Adults	Juveniles	Adults	Larvae	Adults	Juveniles	Adults	Juveniles	Adults	Larvae	Adults
<i>September 2000</i>												
<i>n</i>	5545	164	10	0	1	56	2873	1532	1309	159	2	306
Mean hour	04:26	19:22	04:20		05:00	20:58	06:26	20:58	21:30	21:14	22:00	21:18
<i>r</i>	0.341	0.515	0.504		(*)	0.719	0.515	0.667	0.675	0.943	(*)	0.495
<i>z</i>	645.254	43.471	2.539			28.91	760.553	682.360	597.014	141.409		88.068
<i>P</i>	0.000	0.000	0.076			0.000	0.000	0.000	0.000	0.000		0.000
<i>December 2000</i>												
<i>n</i>	7760	727	136	0	19	1778	6931	357	838	901	20	1803
Mean hour	06:48	04:26	03:26		02:54	06:06	19:24	22:32	23:26	23:06	21:26	23:22
<i>r</i>	0.680	0.640	0.559		0.539	0.706	0.865	0.804	0.748	0.929	0.805	0.393
<i>z</i>	3585.11	298.181	42.468		5.529	886.913	5188.75	230.974	469.350	778.422	12.960	278.060
<i>P</i>	0.000	0.000	0.000		0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>March 2001</i>												
<i>n</i>	2771	179	116	1	15	160	1548	465	956	1	27	503
Mean hour	19:48	07:02	21:40	23:00	21:46	21:38	19:06	22:10	00:50	22:00	22:08	22:56
	03:21		03:40								05:06	
			06:06									
<i>r</i>	0.452	0.811	0.72		0.784	0.751	0.481	0.578	0.431		0.407	0.393
<i>z</i>	564.927	117.598	60.112		11.808	903.124	357.964	155.124	177.261		4.481	197.698
<i>P</i>	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000		0.010	0.000

n, number of arthropods collected in traps; *r*, mean vector length; *z*, Rayleigh test; *P*, probability level; and *, no enough data for statistical analysis.

(Fig. 4). During March, *T. spinulosus* was mostly active after the expected times of high tide (Fig. 5). The locomotor activity of *Phalerisida maculata* did not show a clear pattern, even when in some cases the peaks in locomotor activity occurred after the expected times of high tides (e.g. Figs. 3 and 4).

The periodograms derived from the actograph data show significant peaks (i.e. values above the 95% confidence interval) at a period length of ~24–25 h. These peaks were more pronounced for *Orchestoidea tuberculata* and *Tylos spinulosus*, as compared with *Phalerisida maculata*. Barely significant peaks at ~11–12 h were also observed for *O. tuberculata* and *T. spinulosus*, but not for *P. maculata* (Figs. 3–5).

Fig. 6 shows the results of the free running experiments under continuous light. Even under those experimental conditions, the adults of *Orchestoidea tuberculata* maintained a circadian rhythm of locomotor activity phased with the periods of subjective night. In general, the maximum locomotor activity occurred after the expected time of high tide. The periodogram of that activity shows again a circadian and circatidal endogenous rhythm with significant peaks at 24:08 and 11:31 hours, respectively. On the other hand, *Tylos spinulosus* was inactive during most of the experiment, with the exception of a single register. *Phalerisida maculata* showed an erratic pattern of locomotor activity without

any phasing with the time of subjective night or expected high tide (Fig. 6).

3.5. Spatial distribution of the locomotor activity over the beach surface

Examination of the contour distribution maps, based upon the capture figures of juveniles for the neap tide samplings of September, December and March, shows aggregation of the locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* at different areas of the intertidal (Fig. 7). In other words, position, shape and intensity of aggregations differ for the juveniles of these three species. The contour maps for adults showed a clearer pattern in the distribution of amphipods, isopods and beetles across the intertidal (Fig. 8), i.e. the locomotor activity of *O. tuberculata* was concentrated in lower beach levels than those in which the activity of *T. spinulosus* and *P. maculata* was higher. Due to the low abundances of captured individuals during the spring tides, no contour maps are presented for those samplings (cf. Fig. 2).

The examination of the hourly variation in the mean zonation of surface locomotor activity shows that most of the time, juveniles and adults of *Orchestoidea tuberculata* moved closer to the low tide level than *Tylos spinulosus* and *Phalerisida maculata* (Figs. 9–11).

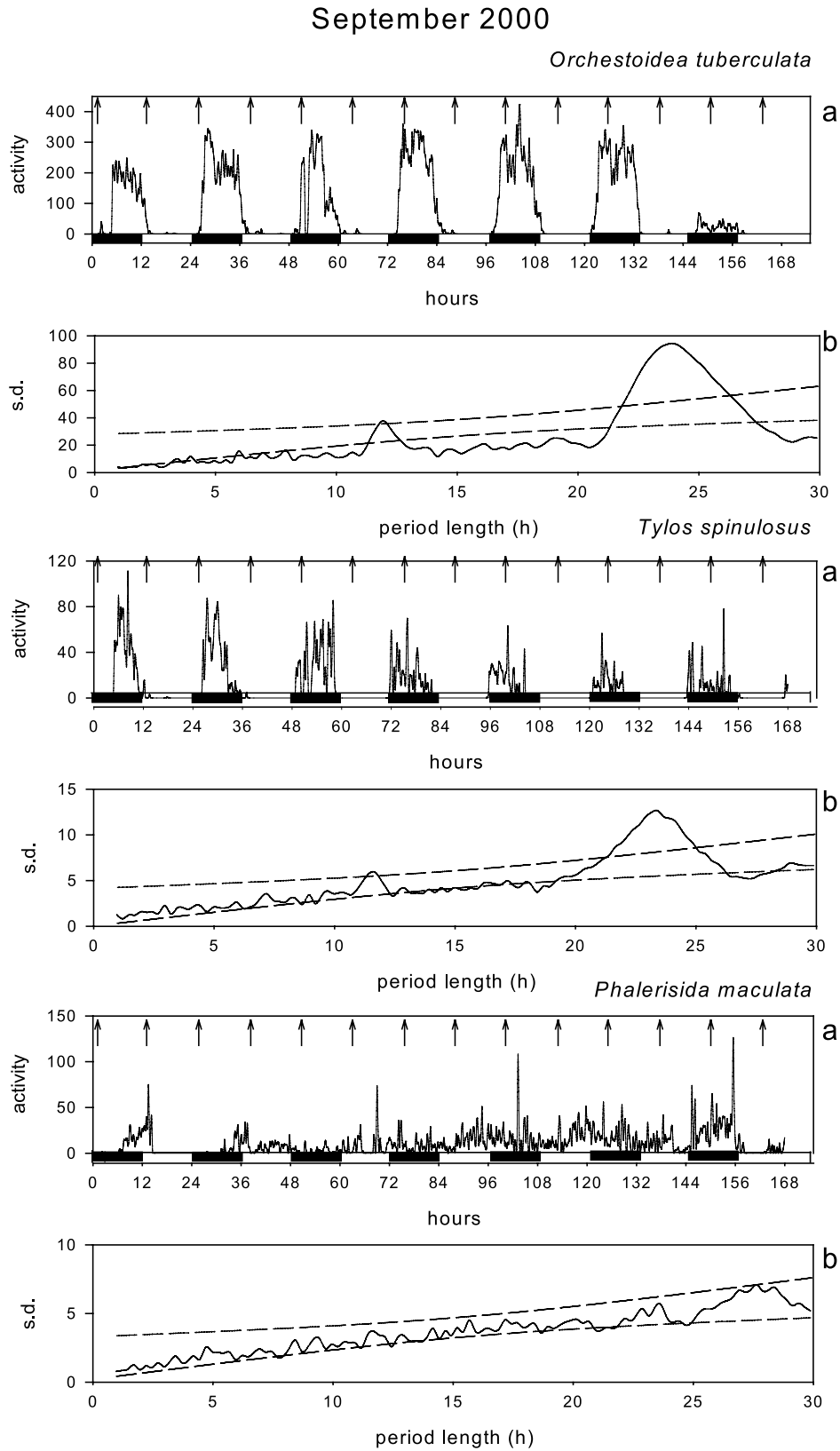


Fig. 3. Locomotor activity (beam breaks in 15 min) of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* in laboratory conditions (actographs) and darkness during the experiments carried out in September 2000. (a) The dark bars in the X-axis show the corresponding dark periods (subjective night) in the field. The upward arrows indicate the approximate time of high tides according to tidal tables. (b) Periodogram of data shown in graph (a). The dotted lines show the 95% confidence intervals. s.d., Standard deviation.

December 2000

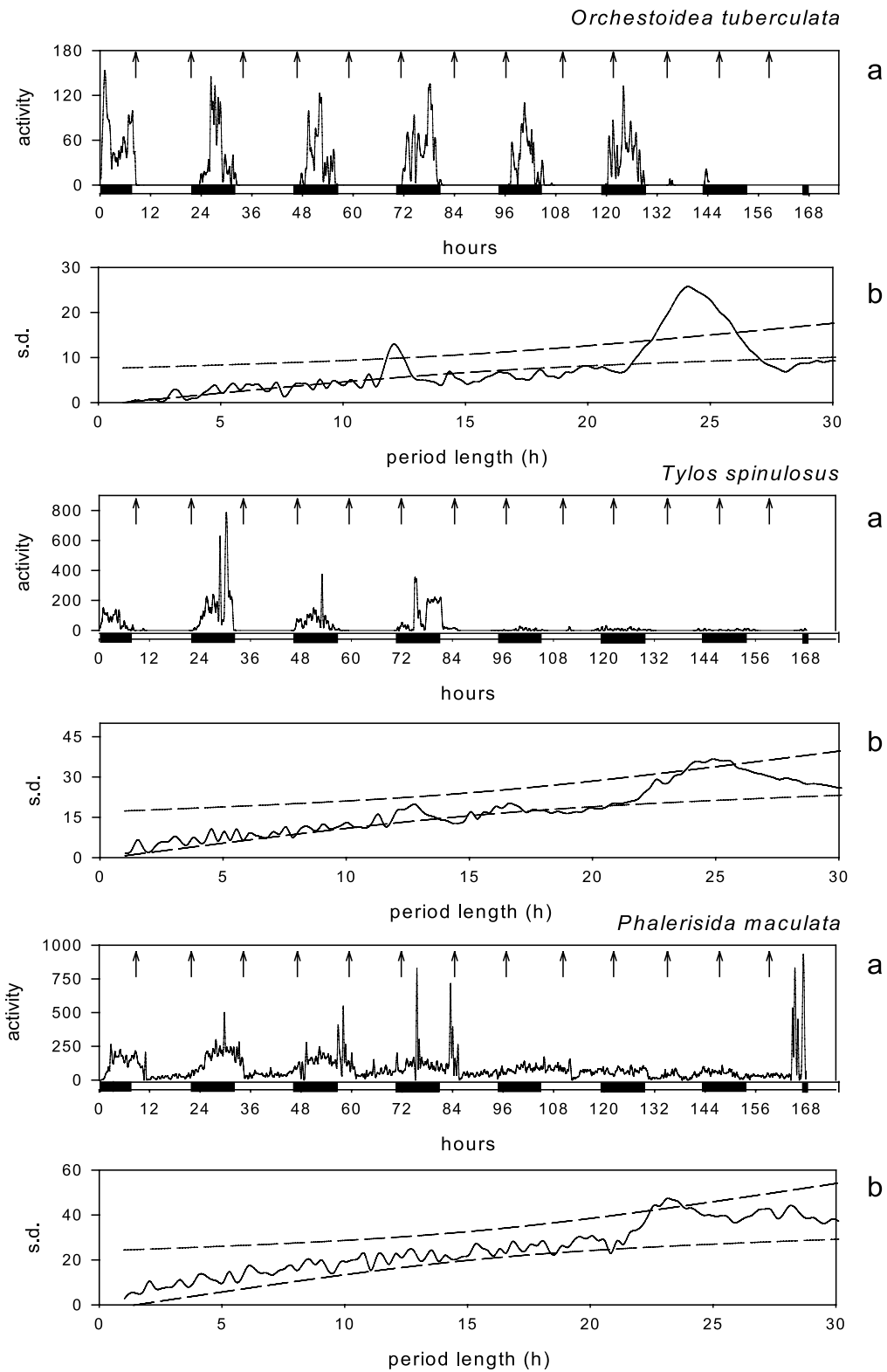


Fig. 4. Locomotor activity (beam breaks in 15 min) of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* in laboratory conditions (actographs) and darkness during the experiments carried out in December 2000. (a) The dark bars in the X-axis show the corresponding dark periods (subjective night) in the field. The upward arrows indicate the approximate time of high tides according to tidal tables. (b) Periodogram of data shown in graph (a). The dotted lines show the 95% confidence intervals. s.d., Standard deviation.

March 2001

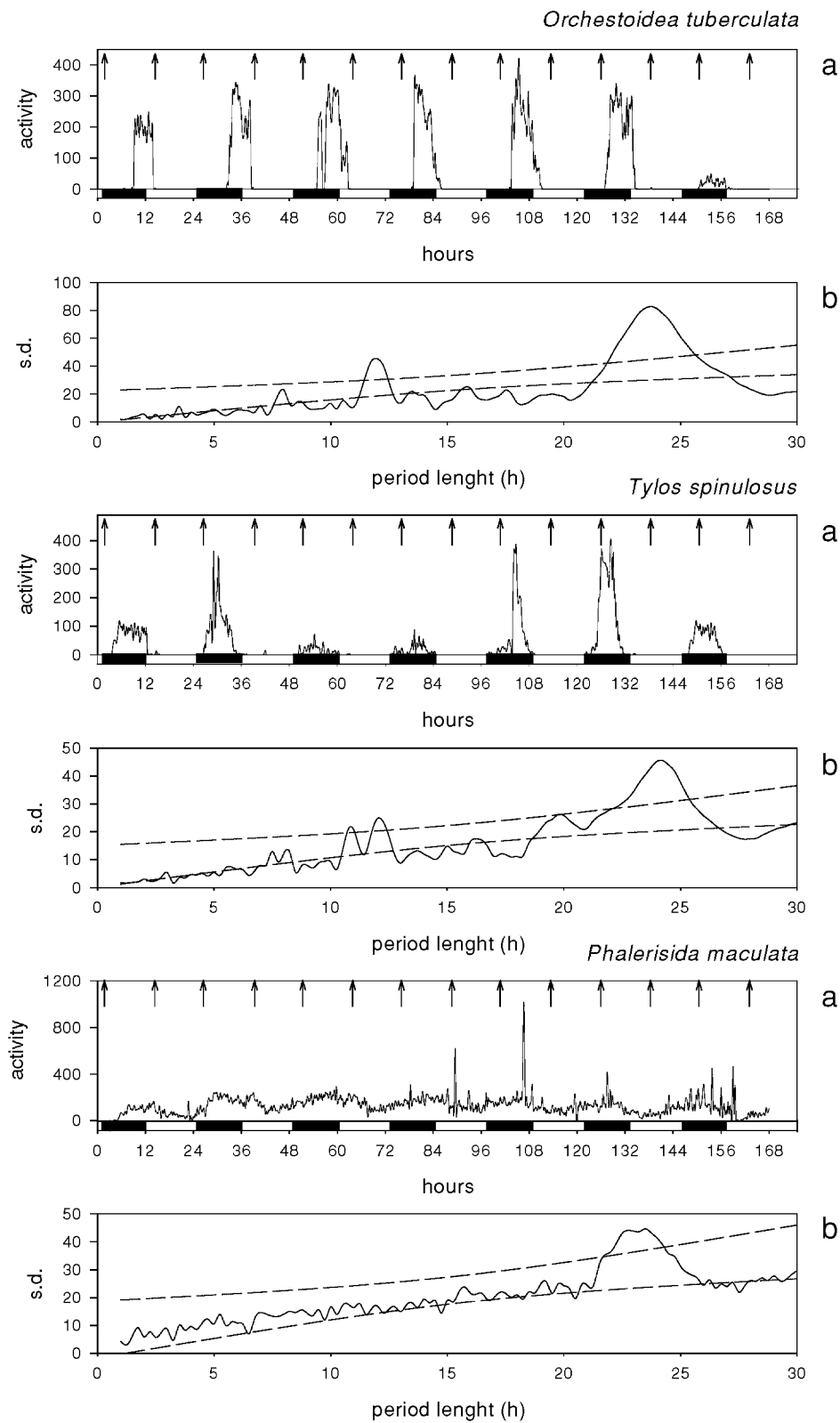


Fig. 5. Locomotor activity (beam breaks in 15 min) of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* in laboratory conditions (actographs) and darkness during the experiments carried out in March 2001. (a) The dark bars in the X-axis show the corresponding dark periods (subjective night) in the field. The upward arrows indicate the approximate time of high tides according to tidal tables. (b) Periodogram of data shown in graph (a). The dotted lines show the 95% confidence intervals. s.d., Standard deviation.

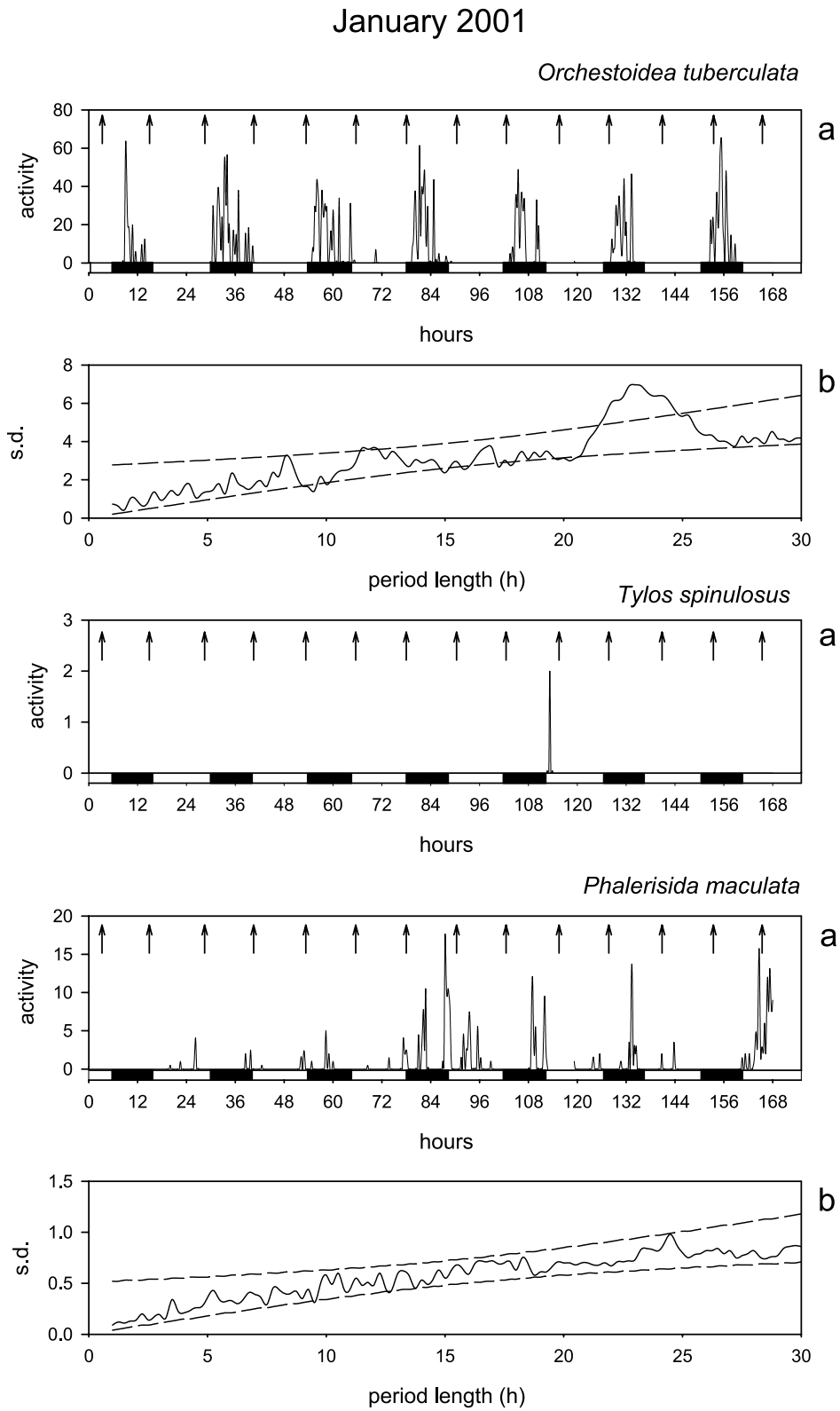


Fig. 6. Locomotor activity (beam breaks in 15 min) of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* in laboratory conditions (actographs) and continuous light during the experiments carried out in January 2001. (a) The dark bars in the X-axis show the corresponding dark periods (subjective night) in the field. The upward arrows indicate the approximate time of high tides according to tidal tables. (b) Periodogram of data shown in graph (a). The dotted lines show the 95% confidence intervals. s.d., Standard deviation.

juveniles - neap tide

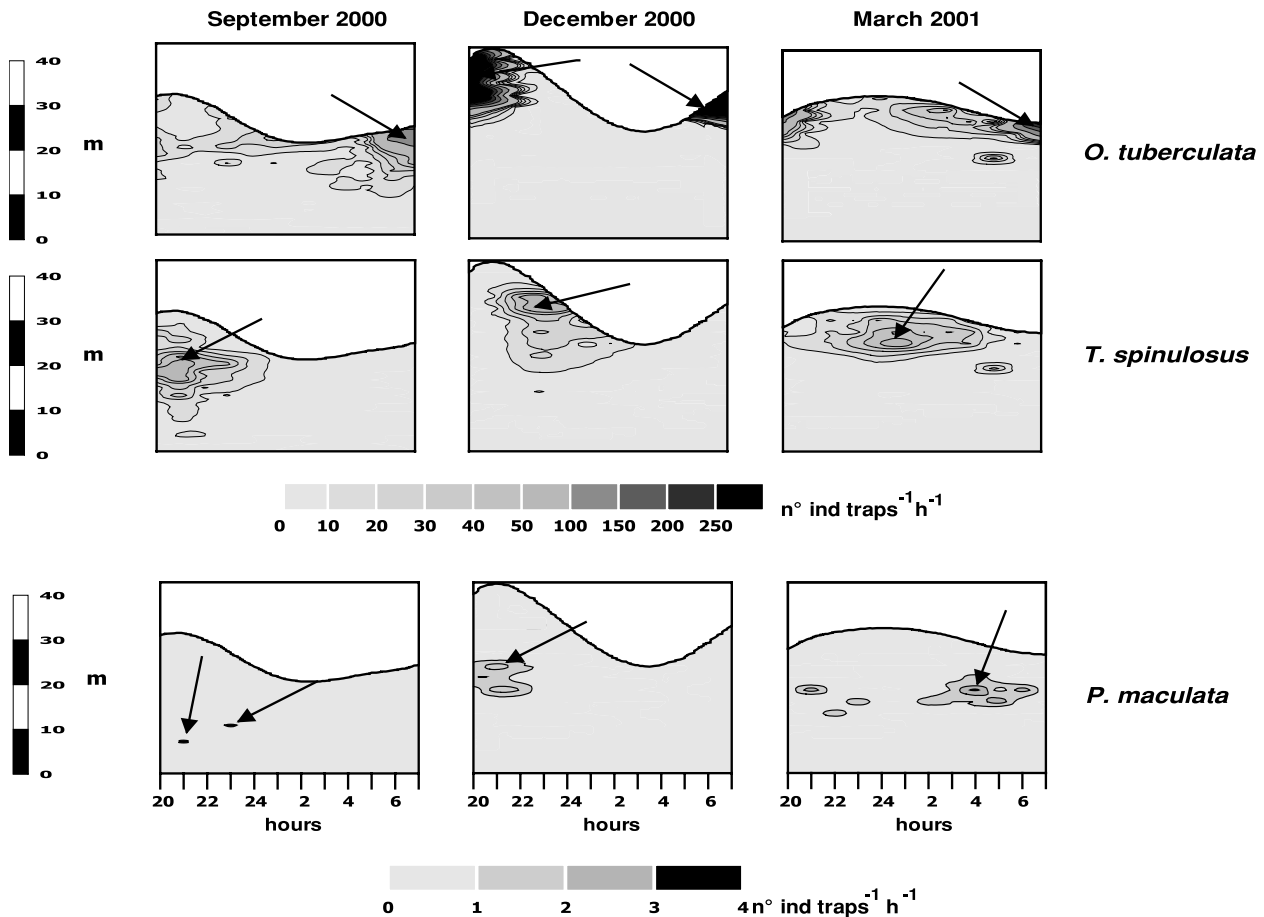


Fig. 7. Contour distribution maps of the locomotor activity of juveniles of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the neap tide samplings. The arrows indicate the areas with the highest concentration of locomotor activity. Note the different scales for *P. maculata*.

That juveniles and adults, also had a greater magnitude in hourly changes of mean zonation, a pattern which is particularly seen from the high to low tide hour of the spring tide samplings of December and March (Figs. 10 and 11). Results of ANOVA carried out to test for eventual differences in the mean zonation of the three species (Table 4) show that usually the mean zonation of adults and juveniles of *O. tuberculata* differed significantly from the mean zonation of the other species. On the other hand, the only significant difference between the mean zonations of active *T. spinulosus* and *P. maculata* was that found between adults and juveniles of *T. spinulosus* during the neap tide of September (Table 4).

3.6. Coexistence experiments

Table 5 shows the results of the coexistence experiments aimed to evaluate intraspecific interactions. Mean percentage mortality of *Orchestoidea tuberculata* varied

between 0.8 and 5.0% without significant differences ($P > 0.05$) among densities (10, 20 and 30 individuals). Mean percentage mortality of *Tylos spinulosus* tended to be higher at higher population densities, while that of *Phalerisida maculata* was zero at different densities of beetles (Table 5).

The results aimed to test interspecific interactions are shown in Table 6. Mean percentage mortality of *Orchestoidea tuberculata* did not differ significantly ($P < 0.05$) when kept alone, as compared with the treatments having 10 and 20 *Tylos spinulosus*. Mortality of this amphipod was zero when coexisting with 10 *Phalerisida maculata*; however, it increased significantly to 25% when the density of *P. maculata* increased to 20 individuals. Mean percentage mortality of *T. spinulosus* was similar when kept alone or with 10 *O. tuberculata*; however, it increased significantly to 26.7% when maintained with 20 *O. tuberculata*. On the other hand, the mean percentage mortality of *T. spinulosus* did not differ significantly when kept alone or with 10 and 20

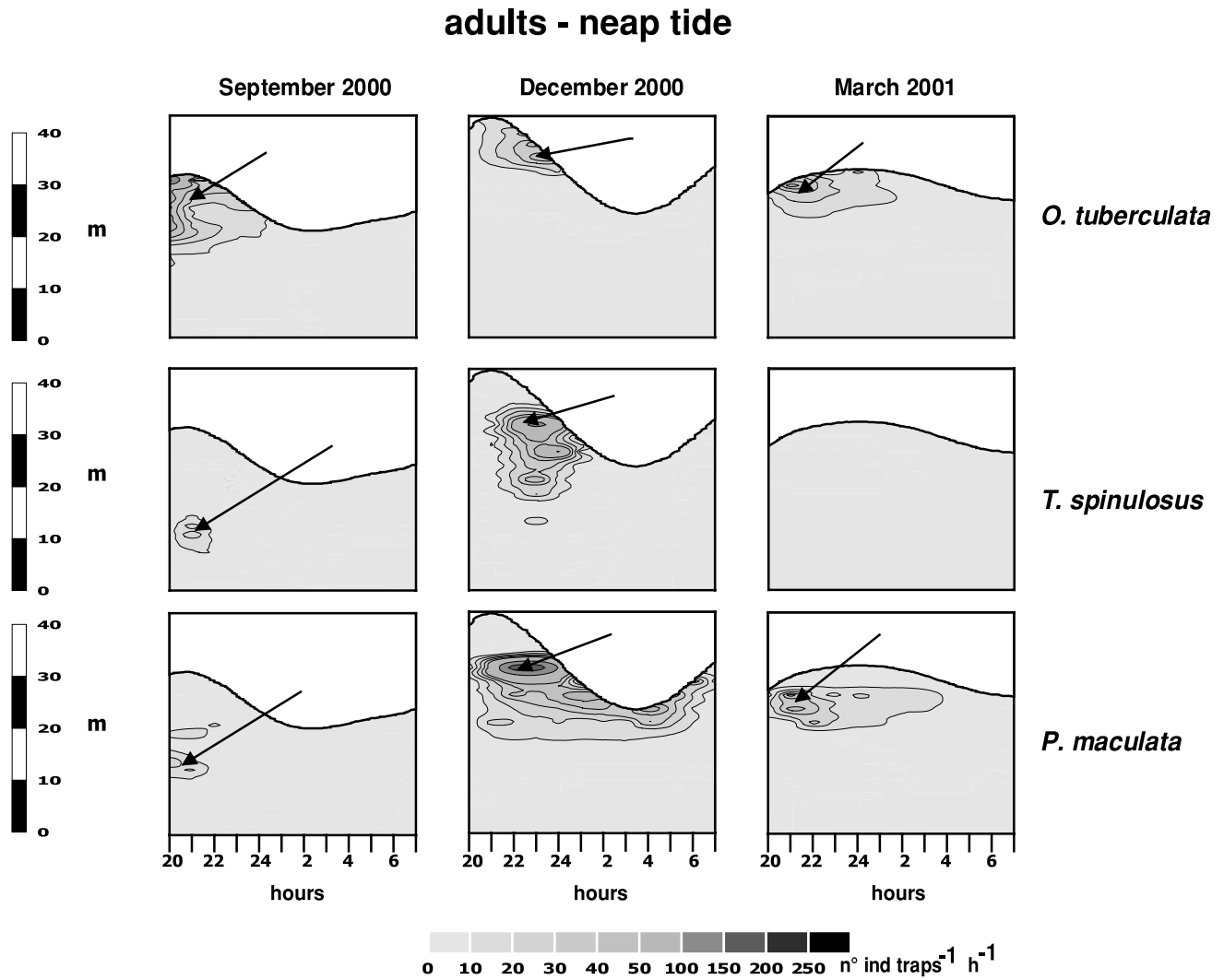


Fig. 8. Contour distribution maps of the locomotor activity of adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the neap tide samplings. The arrows indicate the areas with the highest concentration of locomotor activity.

P. maculata. Mean percentage mortality of *P. maculata* was zero when kept together with *O. tuberculata* at two different densities (10 and 20 individuals). Similarly, mortality was zero or very low when maintained together with 10 and 20 *T. spinulosus* (Table 6).

4. Discussion

The results of this study show that a time partitioning in the locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* exists over the beach surface. Circular statistics applied to that locomotor activity showed that the mean hours of surface locomotor activity varied among experiments. In some cases, the peak in the locomotor activity of *O. tuberculata* occurred before or later than the peak of the other species. For example, during the neap tide of September, the juveniles of *O. tuberculata* peaked during

early morning, while adults peaked during the early night and before than the other two species. On the other hand, during the spring tide of March, the adults of *O. tuberculata* peaked during early morning, while the juveniles peaked during the late evening and in the middle of the night. Colombini, Chelazzi, Falacci, and Palesse (1994) also found differences in the sequence of the mean hours of surface locomotor activity of 14 coexisting species of tenebrionid beetles. Intraspecific differences were also found in the surface locomotor activity, primarily between juveniles and adults of *O. tuberculata*, a pattern also found by Kennedy et al. (2000) in a sandy beach of south central Chile (ca. 39°S). Similarly, Fallaci et al. (1999) found in a sandy beach of France differences in locomotor activity of juveniles and adults of the amphipod *Talitrus saltator*; thus, the mean hour of activity of juveniles usually occurred earlier than that of adults. These authors also found interspecific differences; during spring tide, the adults of

September 2000

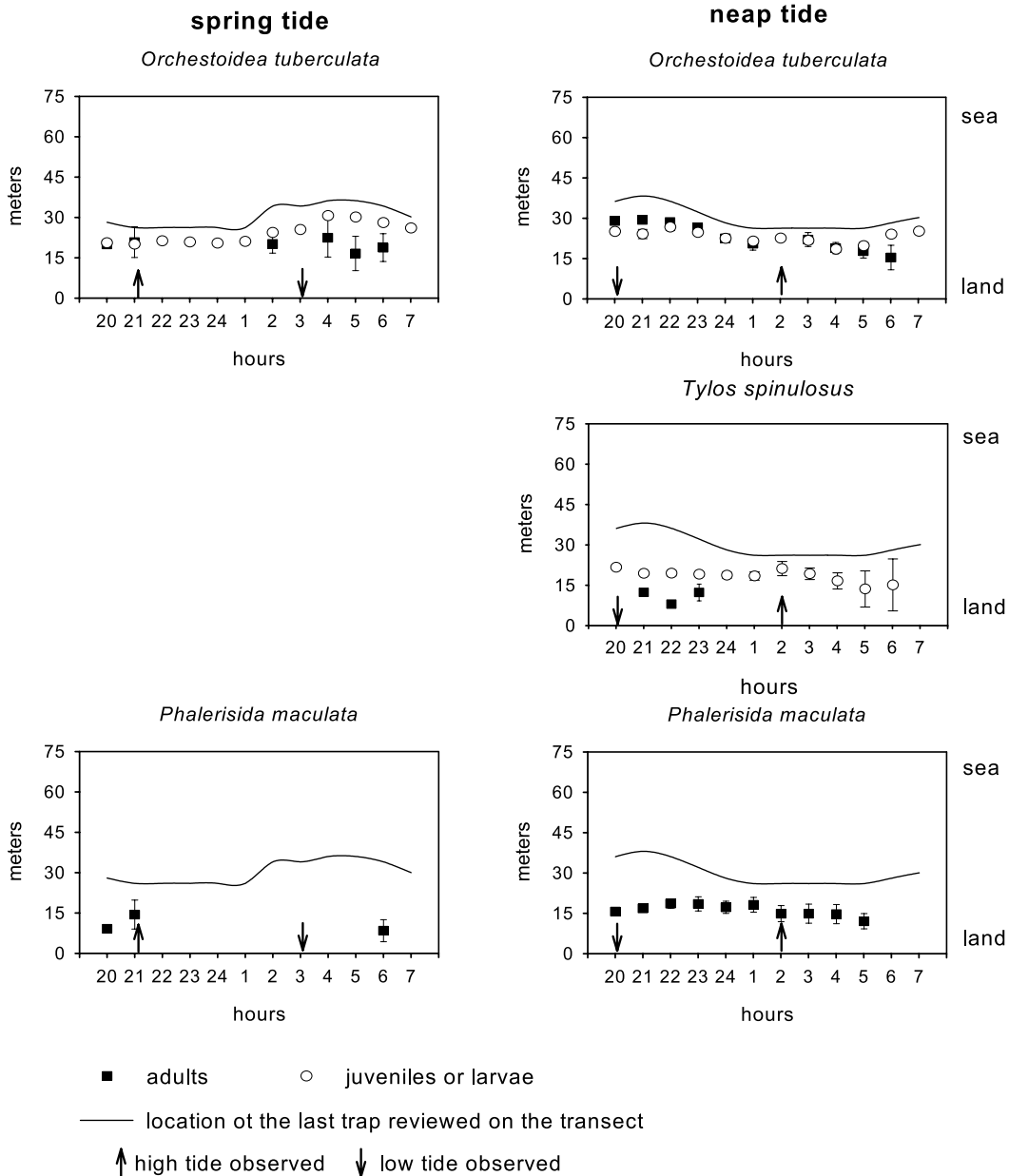


Fig. 9. Mean zonation of surface locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings of September 2000. The values are means with 95% confidence intervals. No graphical display is presented for *T. spinulosus* during the spring tide since the low number of captured specimens precluded the analyses (see Section 2).

the sympatric *Talorchestia brito* had the mean hour of activity before than that of juveniles and adults of *T. saltator*, while during neap tide, the mean hour of activity of adults of *T. brito* was later than that of juveniles and adults of *T. saltator*.

Interseasonal comparisons of capture figures of the three studied species obtained from the pitfall traps show that the highest locomotor activity occurred during early summer (December 2000). Temporal variability in air and sand temperatures and relative humidity have been invoked to influence locomotor activity of talitrid

amphipods, tylid isopods and tenebrionid insects (Colombini et al., 1994; Fallaci, Colombini, Taiti, & Chelazzi, 1996; Scapini, Chelazzi, Colombini, & Fallaci, 1992). Those capture figures also show that moon phases apparently affect locomotor activity over the beach surface. In fact, *Tylos spinulosus* and *Phalerisida maculata* had higher locomotor activity during neap tides (specially the isopod) as compared with that observed during spring tide. The lower locomotor activity shown by these species during spring tides, may well be related to the fact that the spring tide samplings

December 2000

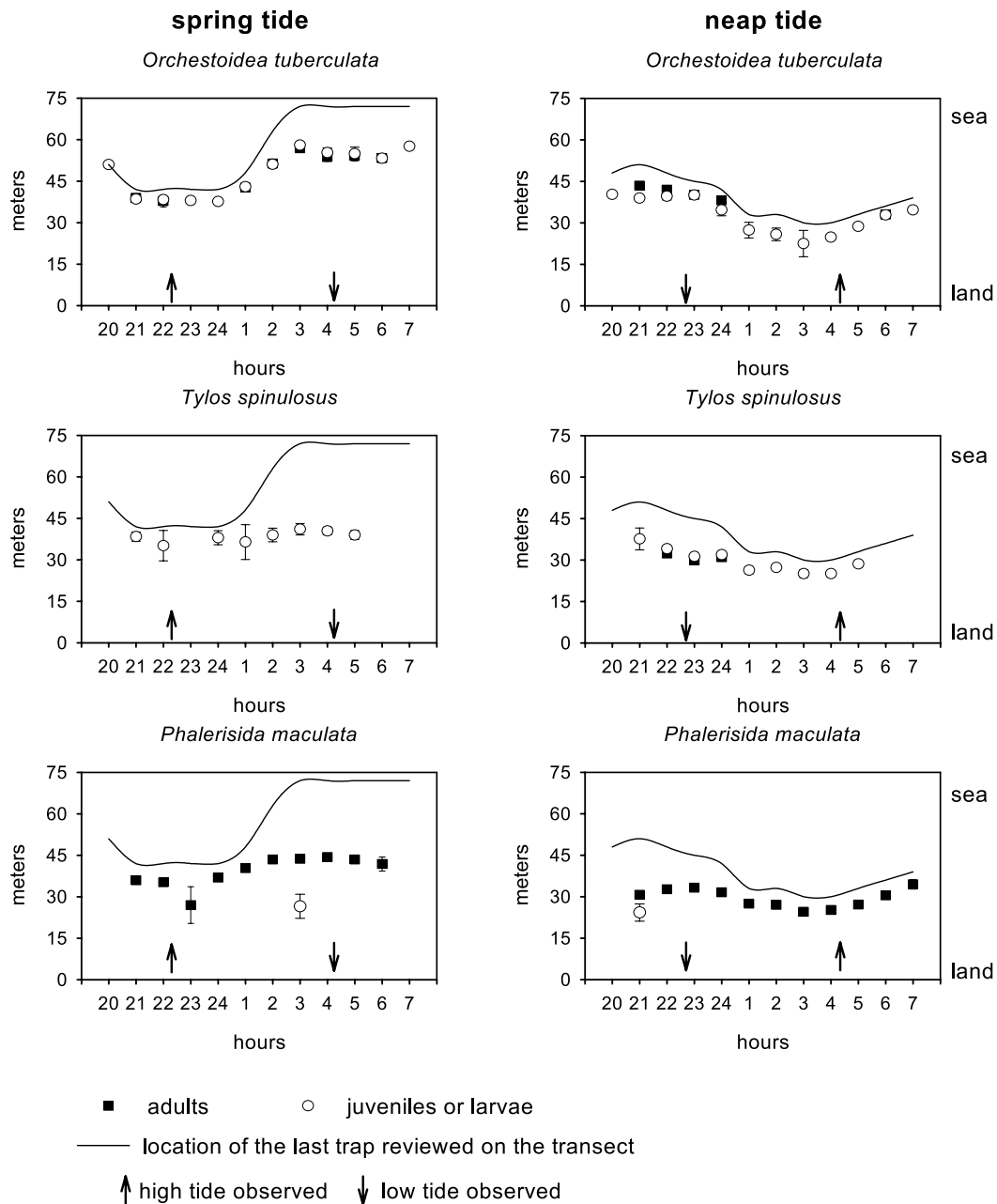


Fig. 10. Mean zonation of surface locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings of December 2000. The values are means with 95% confidence intervals.

were carried out during full moon. As found earlier, moonlight may well be an inhibitor of locomotor activity. For example, during a spring tide sampling carried out at the same beach studied here but during March 1997, the locomotor activity of *P. maculata* occurred just before high tide, while clouds still obscured the full moon; however, after the clouds cleared and during the nocturnal low tide, adult beetles re-emerged in high numbers on the beach surface (Jaramillo, Avellanal, González, & Kennedy, 2000).

The periodograms resulting from the locomotor activity of adults of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* studied with actographs and total darkness show evidence of a circadian endogenous component close to 23–25 h (i.e. every other 23–25 h, a new locomotor activity cycle is initiated). The circadian rhythm of locomotor activity has been observed for several species of the upper shore levels of sandy beaches (Atkinson & Naylor, 1973; Benson & Lewis, 1976; Imafuku, 1976; Wildish, 1970; Williams,

March 2001

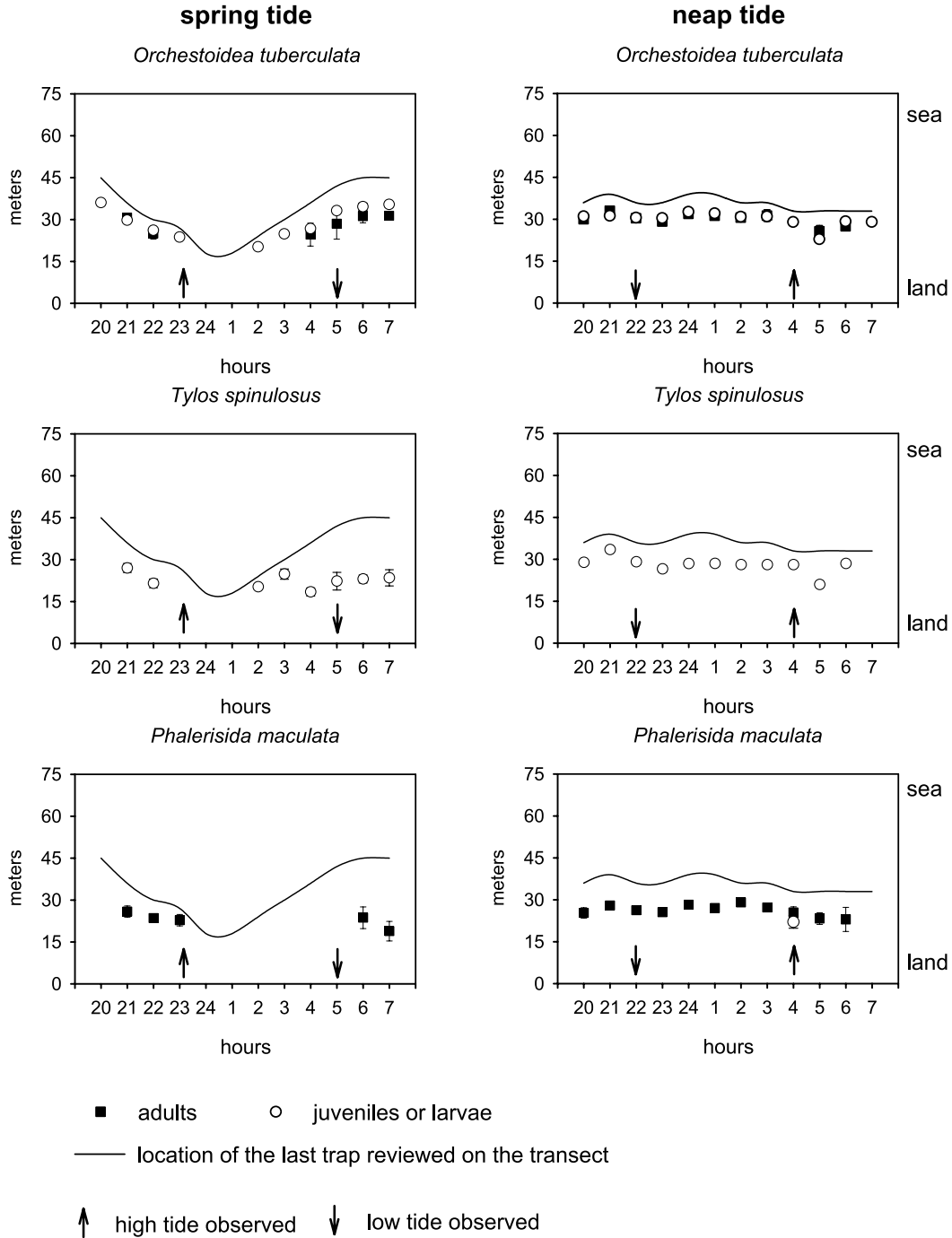


Fig. 11. Mean zonation of surface locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during the spring and neap tide samplings of March 2001. The values are means with 95% confidence intervals.

1980, 1982). When those species are buried into the sediment or when unfavorable environmental conditions do not allow locomotor activity pattern over the beach surface, the endogenous circadian rhythm has an adaptive significance in maintaining that activity phased

with the natural photoperiod (Bregazzi & Naylor, 1972; Williams, 1980, 1982, 1983).

Activity peaks close to 11–14 h were also found that probably represent a circatidal component in the locomotor activity. The locomotor activity of *Orchestoidea*

Table 4

Results of ANOVA carried out to test for eventual differences in the mean zonation of surface locomotor activity of juveniles and adults of *Orchestoidea tuberculata* and *Tylos spinulosus*, and larvae and adults of *Phalerisida maculata* (see text for details)

	Degree of freedom	F-value	P-value	Significant differences between the mean zonation of surface locomotor activity of:
September 2000 (spring tide)	2–18	18.74	0.000	Adults and juveniles of <i>O. tuberculata</i> with adults of <i>P. maculata</i>
September 2000 (neap tide)	4–41	15.13	0.000	Adults and juveniles of <i>O. tuberculata</i> with adults and juveniles of <i>T. spinulosus</i> and adults of <i>P. maculata</i>
December 2000 (spring tide)	4–34	6.52	0.001	Adults of <i>T. spinulosus</i> with juveniles of <i>T. spinulosus</i>
December 2000 (neap tide)	5–35	3.90	0.010	Adults and juveniles of <i>O. tuberculata</i> with juveniles of <i>T. spinulosus</i> and adults and larvae of <i>P. maculata</i>
March 2001 (spring tide)	3–25	5.73	0.000	Adults of <i>O. tuberculata</i> with juveniles of <i>T. spinulosus</i>
March 2001 (neap tide)	4–40	6.57	0	Juveniles of <i>O. tuberculata</i> with juveniles of <i>T. spinulosus</i> and adults of <i>P. maculata</i>
				Adults and juveniles of <i>O. tuberculata</i> with adults and larvae of <i>P. maculata</i>

tuberculata in laboratory conditions and continuous darkness during December and March started right after the predicted times of high tide in most of the 7 experimental days. The corresponding periodograms for December and March were those presenting significant peaks between 11 and 14 h, suggesting that a circatidal component probably exists. On the other hand, during September the locomotor activity of this amphipod (and also that of *Tylos spinulosus* and *Phalerisida maculata*) was inhibited by the tide just during the first 2 or 3 days. Consequently, it is not possible to tell that *O. tuberculata* shows an endogenous circatidal rhythm which would persist. To resolve this situation, it would be necessary to analyze a longer series of data, for example, a series of 15 days (cf. Williams & Naylor, 1978). During December and March, this pattern of tide inhibition was observed for *T. spinulosus*. Consequently, the suggested tidal peaks observed from the periodograms of *O. tuberculata* and *T. spinulosus* during the three laboratory experiments may well have no biological meaning since they are not clearly seen in the free running data (cf. Kennedy et al., 2000; Williams & Naylor, 1978).

The results of the actograph experiments under constant light conditions show that the circadian

rhythm of locomotor activity of *Orchestoidea tuberculata* was the only one maintained throughout the experiment and phased with the subjective night. The noninhibition of the locomotor activity of *O. tuberculata* during the free running experiments carried out with constant light was similar to the findings of Williams (1983); he found that four species of supralittoral peracarids (*Talitrus saltator* (Montagu), *Talorchestia deshayesi* (Audouin), *Orchestia gammarella* (Pallas) and *Ligia oceanica* (Linnaeus)) from the coast of Isle of Man presented locomotor activity under constant light conditions and in some cases during 24 h of the day. The detrimental effect of light on the locomotor activity of *Tylos spinulosus* and *Phalerisida maculata* would explain the higher activity of these two species during the neap tide samplings, as compared with the spring tide samplings carried out during full moon. Similarly, Bregazzi and Naylor (1972) found that the activity of *T. saltator* is partially or totally inhibited under laboratory conditions of total light.

The examination of contour distributional maps and mean hourly zonations show that the locomotor activity of the studied species also differed, specially that of *Orchestoidea tuberculata* versus that of *Tylos spinulosus*

Table 5

Results of experimental trials aimed to evaluate intraspecific interactions in *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata*. T 1, T 4 and T 10, and so on, are treatments (see Table 1 for details). The values are mean percentage mortality with standard deviations in parentheses. Values of *F* (with 2–15 degrees of freedom) and *P* resulting from ANOVA are also given. The formation of treatment groups resulted from Tukey's HSD a posteriori test; *n* is the number of animals

	<i>n</i> = 10	<i>n</i> = 20	<i>n</i> = 30	F-value	P-value	Homogeneous groups
	T 1	T 4	T 10			
<i>O. tuberculata</i>	5.0 (8.4)	0.8 (2.0)	1.1 (1.7)	0.70	0.51	T 1–T 4–T 10
	T 2	T 5	T 11			
<i>T. spinulosus</i>	1.7 (4.1)	9.2 (5.9)	5.5 (5.0)	4.15	0.04	T 2–T 11 and T 5–T 11
	T 3	T 6	T 12			
<i>P. maculata</i>	0	0	0			T 3–T 6–T 12

Table 6

Results of experimental trials aimed to evaluate interspecific interactions between *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata*. T 1, T 7, T 10, and so on, are treatments (see Table 1 for details). The values are mean percentage mortality with standard deviations in parentheses. Values of *F* (2–58 degrees of freedom) and *P* resulting from ANOVA are also given. The formation of groups resulted from Tukey's a posteriori test; *n* is the number of animals

	<i>n</i> = 10	<i>n</i> = 20 (10 + 10)	<i>n</i> = 30 (10 + 20)	<i>F</i> -value	<i>P</i> -value	Homogeneous groups
<i>T. spinulosus</i> on <i>O. tuberculata</i>	T 1 5.0 (8.4)	T 7 3.3 (5.2)	T 13 1.7 (4.1)	0.32	0.73	T 1–T 7–T 13
<i>P. maculata</i> on <i>O. tuberculata</i>	T 1 5.0 (8.4)	T 8 0	T 14 25.0 (8.4)	25.40	0.00	No homogeneous groups
<i>O. tuberculata</i> on <i>T. spinulosus</i>	T 2 1.7 (4.1)	T 7 1.7 (4.9)	T 16 26.7 (17.5)	10.15	0.00	T 2–T 7
<i>P. maculata</i> on <i>T. spinulosus</i>	T 2 1.7 (4.1)	T 9 13.3 (17.5)	T 15 11.7 (14.7)	1.30	0.32	T 2–T 9–T 15
<i>O. tuberculata</i> on <i>P. maculata</i>	T 3 0	T 8 0	T 17 0			T 3–T 8–T 17
<i>T. spinulosus</i> on <i>P. maculata</i>	T 3 0	T 9 0	T 18 0.2 (0.4)			T 3–T 9–T 18

and *Phalerisida maculata*. While the mean hourly zonation of active *O. tuberculata* moved down with the ebbing tide, that of the other two species usually stayed in the same beach levels, independent of tide variability. These results resemble those shown by the laboratory experiments where *O. tuberculata* was the only species whose locomotor activity seemed to present a circatidal component, i.e. that activity was inhibited during the time of the predicted high tide.

The results mentioned earlier show evidence of time and space partitioning of the surface locomotor activity of *Orchestoidea tuberculata*, *Tylos spinulosus* and *Phalerisida maculata* during night hours. Biological interactions have been used to explain similar findings in other areas of the Chilean coast or elsewhere. Even when limited in time and/or replication, the results of the coexistence experiments carried out in this study showed no evidence of intraspecific interactions. However, similar experiments evidenced interspecific interactions while *P. maculata* affected negatively the survival of *O. tuberculata*, this amphipod affected negatively the survival of *T. spinulosus*. On the other hand, no interactions were found between *T. spinulosus* and *P. maculata*. In other words, those species with similarities in locomotor activity (either in peak hours or mean hourly zonation), that is *T. spinulosus* and *P. maculata* showed no interactions between them, while both of them had negative interactions with *O. tuberculata*, the species which separated more in time and hourly zonation of locomotor activity. Thus, differences in time/space partitioning of surface locomotor activity can be interpreted as a means to avoid detrimental

interactions in this guild of scavengers. Similar interpretation was given by Kennedy et al. (2000) who carried out laboratory experiments to test for intraspecific interactions in *O. tuberculata*. These authors found increased mortality of juveniles when kept together with adults as compared with the survival without adults; so, they concluded that the time partitioning in the locomotor activity of adults and juveniles of *O. tuberculata* can be explained in terms of biological interactions between age classes of amphipods. Similarly, Chelazzi, Chellazi, and Focardi (1983) suggest that the coexistence of sympatric staphylinid beetles in a sandy shore of East Africa is due to niche differences, primarily related to different exploitation of space and time. Colombini et al. (1994) found 14 species of tenebrionid beetles in a small sandy beach of a Mediterranean lagoon, some of them with high population abundances. Similar to the arguments of Chelazzi et al. (1983), these authors conclude that the coexistence of that 14 beetles is possible because of differences in locomotor activity and exploitation of different beach zones.

In conclusion, this study has shown important differences in time/space partitioning in surface locomotor activity of three scavenger species inhabiting the upper shore levels of a sandy beach of north central Chile. Space partitioning of organisms burrowed under the sediment surface was also found. That partitioning would allow coexistence of interacting scavenger species and provides evidence that biological interactions are indeed important in community structure of sandy beach macroinfauna. How important are those interactions in affecting population abundances of

Orchestoidea tuberculata, *Tylos spinulosus* and *Phalerisida maculata* is open to question.

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