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Locomotor activity of *Phalerisida maculata* Kulzer (Coleoptera, Tenebrionidae) on Chilean sandy beaches

Actividad locomotora de *Phalerisida maculata* Kulzer (Coleoptera, Tenebrionidae) en playas arenosas chilenas

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ABSTRACT

The locomotor activity of the beetle *Phalerisida maculata* Kulzer (Coleoptera Tenebrionidae) was studied on the surface of the substrate in two sandy beaches of the Chilean coast: one in north central (ca. 29°S) and the other in south central Chile (ca.39°S). During the summer period of 1991 the circadian locomotor activity was studied in the southern beach, while during that of 1997 in both beaches. To analyze the activity, pitfall traps were used which were ordered along two transects extended between the upper beach and the resurgence zone. The traps were checked (i.e. collection of captured insects) every two hours for a total period of 26 hours. The results showed that the adults of *P. maculata* were mostly active during the night hours, whereas the larvae were active during both, the day and night. Studies carried out in the beach located in south central Chile show that differences in the tidal range (neap vs. spring tides) do not affect the activity patterns. During the locomotor activity, adult and larvae move to lower intertidal levels than those usually occupied while buried. Results of laboratory experiments using actographs under conditions of darkness and constant temperature, suggest that adults and larvae of *P. maculata* presented a circadian rhythm similar to that observed in the field experiments. It is concluded that *P. maculata* presents a behaviour that appear to be under control of an endogenous rhythm, without showing differences in the circadian rhythm of activity when beaches located at different latitudes are compared.

Key words: sandy beaches, Insecta, Coleoptera, locomotor activity.

RESUMEN

Se estudió la actividad locomotriz del escarabajo *Phalerisida maculata* Kulzer (Coleoptera, Tenebrionidae) sobre la superficie del sustrato de dos playas arenosas de la costa de Chile: una en el centro norte (ca. 29°S) y otra en el centro sur (ca. 39°S). Durante el período estival de 1991 se estudió la actividad locomotriz circadiana en la playa del centro sur y durante el de 1997 en ambas playas. Para analizar dicha actividad, se usaron trampas ordenadas a lo largo de dos transectos extendidos entre el borde superior de la playa y la zona de resurgencia. Las trampas se revisaron (i.e. recolección de insectos capturados) cada dos horas por un período total de 26 horas. Los resultados mostraron que los adultos de *P. maculata* fueron activos mayoritariamente durante las horas de oscuridad, mientras que las larvas fueron activas durante el día y la noche. Estudios llevados a cabo en la playa localizada en el centro sur de Chile, mostraron que las diferencias en el rango mareal (período de sicigia vs. cuadratura) no afectan los patrones de actividad. Durante la actividad locomotriz, adultos y larvas se desplazan a niveles ms bajos de los que ocupan habitualmente cuando están enterrados. Los resultados de experimentos de laboratorio realizados con actógrafos bajo condiciones de oscuridad y temperatura constante, sugieren que adultos y larvas de *P. maculata* presentan un ritmo circadiano similar al observado en los experimentos de terreno. Se concluye entonces que *P. maculata* presenta un comportamiento de actividad que pareciera estar bajo control endógeno, no presentando diferencias en el ritmo circadiano de actividad cuando se comparan playas ubicadas en diferentes latitudes.

Palabras clave: playas arenosas, Insecta, Coleoptera, actividad locomotriz.

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INTRODUCTION

The intertidal macroinfauna of exposed sandy beaches along the Chilean coast is usually zoned in three faunal belts: an upper belt, whose taxonomic composition varies according to latitude, and in which ocypodid crabs, talitrid amphipods, coleopteran insects, tylid and cirolanid isopods are represented; a middle belt dominated by cirolanid isopods, and a lower one, in which anomuran decapods, polychaetes and bivalves are the most common taxa (Jaramillo 1987, 1994). This zonation pattern, and other similar patterns elsewhere (see review by McLachlan & Jaramillo 1995), are derived from surveys of burrowed infauna during low tide.

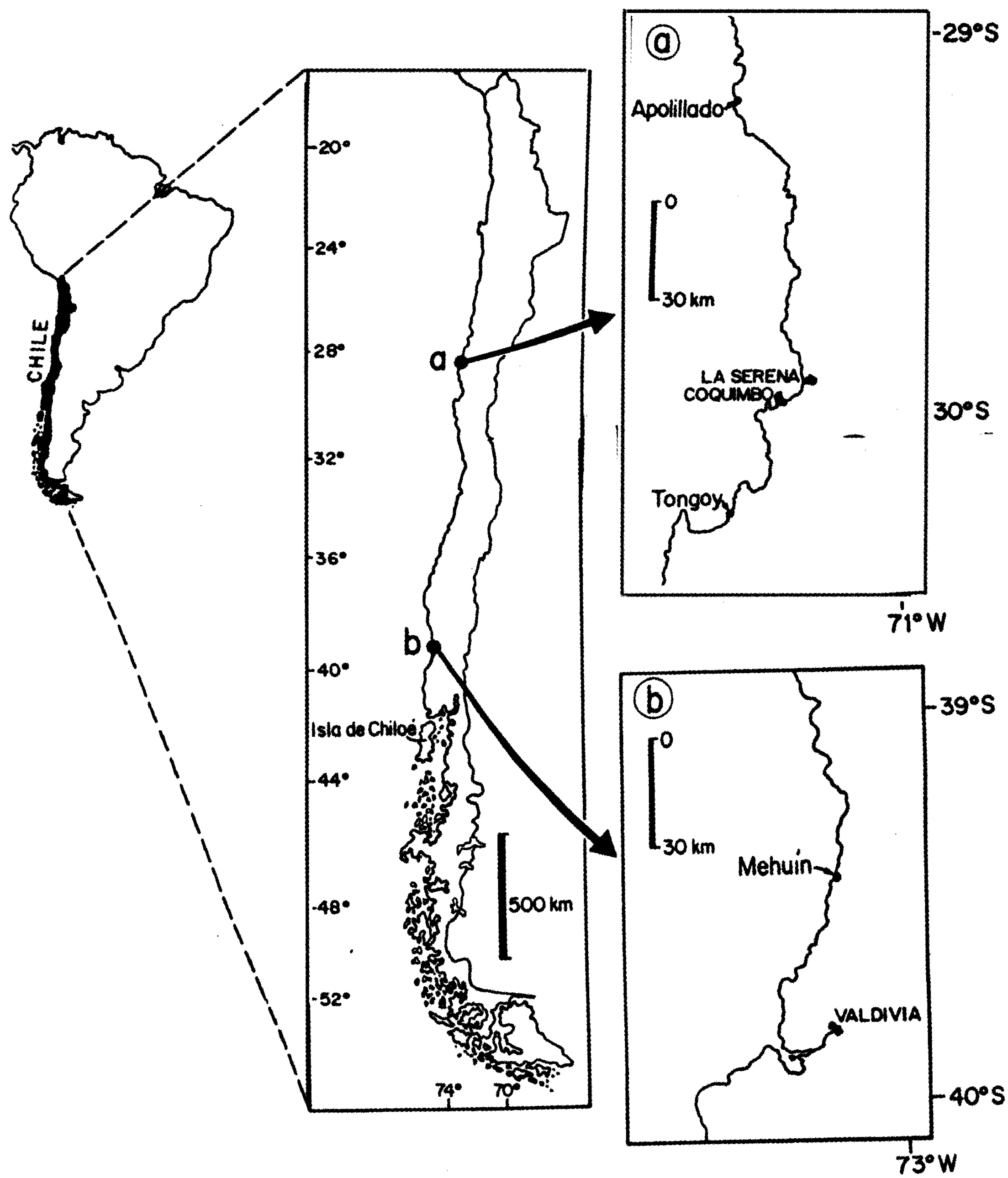

Fig. 1. Location of Apolillado (a) and Mehuín (b), at the coast of north central and south central Chile; ca. 29 and 39 ° S, respectively.

Ubicación de Apolillado (a) y Mehuín (b), en la costa del centro norte y centro sur de Chile; cerca de 29 y 39° S, respectivamente.

However, many of these organisms have active phases, either on the beach surface or in the surf during high tides (Jones & Hobbins 1985, Colombini & Chelazzi 1996, Naylor & Rejeki 1996).

Species of talitrid amphipods, tylid isopods and coleopteran insects are among the most common organisms which are active over the beach surface. During low tide, and primarily during the night, they move around the beach surface in search of stranded wrack (mainly seaweeds) or other organic debris which represent their food source (e.g., Duarte 1974, Stenton-Dozey & Griffiths 1983, Almeida et al. 1993). The nocturnal activity patterns of these organisms have been studied by Williamson (1954), Craig (1970, 1973), Jaramillo et al. (1980), Scapini et al. (1992) and Kennedy (1997) who have related their results to the environmental conditions and the need to escape from predators.

The talitrid amphipod *Orchestoidea* tuberculata Nicolet and the beetle *Phalerisidia maculata* Kulzer typically burrow at the uppermost beach levels of sandy beaches along the Chilean coast from about 29 to 42°S (Jaramillo 1987, 1994, Jaramillo et al. 1998). While the circadian activity of *O. tuberculata* has been analyzed by comparing field and laboratory studies (Jaramillo et al. 1980, Kennedy 1997), no similar analyses have been previously published for *P. maculata.*

Since the geographic distribution of *P. maculata* spans over a relatively long coastal range, it is worthwhile evaluating differences in the locomotor activity of this species at different sites along this latitudinal range. Thus the locomotor activity of *P. maculata* was studied at two sandy beaches of the Chilean coast separated by about 1300 km: one located on the coast of north central Chile and the other in south central Chile. Simple field experiments were designed to describe the temporal and spatial variability in surface locomotor activity in *P. maculata*, including any effects of the tidal cycle on surface locomotor activity. Laboratory experiments were intended to reveal the presence and periodicity of any endogenous components in the activity rhythm.

MATERIALS AND METHODS

Study Area

The study sites were Playa Apolillado (29° 10' S, 71° 29' W) and Playa Universitaria de Mehuín (Mehuín hereafter) (39 ° 26' S, 73° 13' W) (Fig. 1), which are separated by approximately 1300 km. The intertidal width of these beaches is similar (50 - 60 m), and the mean sediment grain size at each beach is also similar (250 - 320 microns) (EJ, unpublished data). The beach at Mehuín is backed by a cliff (metamorphic rock) of about 10 m height, while that of Apolillado is backed by dunes 5 - 6 m height.

Spatial distribution of the locomotor activity of Ph. maculata *on the beach surface*

The field studies comparing the locomotor activity of *Ph. maculata* at both areas were carried out during the summer of 1997 (Mehuín: 22-23 February, Apolillado: 26-27 March). The effect of tidal variability during neap and spring tides was studied during field experiments in the summer of 1991 (spring tide: 14-15 February, neap tide: 21-22 February). During both studies, sampling was carried out over 26 h to analyze quantitative variability of daily locomotor activity. Pitfall traps (glass jars, 120 mm height, 50 mm diameter), were buried with their rims flush with the beach surface, and filled with seawater to prevent the escape of captured beetles. The traps were located at 3 m intervals during 1997 and 2 m during 1991. The traps were arranged along two transects (2 m apart) extending between the supralittoral zone of the beach and the resurgence zone. The traps were checked and emptied every two hours and captured individuals were fixed in a 10% solution of formalin in seawater. The number of captured beetles at both transect were averaged and used to deduce locomotor activity over the beach surface (cf. Colombini et al. 1994, Craig 1973, Fallaci et al. 1996, Williams 1983).

Locomotor activity of Ph. maculata *in laboratory conditions*

In order to study the occurrence of spontaneous surface locomotor activity of adults and larvae of *P. maculata* in the laboratory, beetles were collected from both beaches and transferred to glass containers with damp sand from the collection sites. These containers were kept under conditions of constant light, humidity and temperature (15°C), in a room at Instituto de Zoología, Universidad Austral de Chile, Valdivia. After an acclimitization period of at least 24 hours from the time of collection, the actograph experiments were initiated (March 1997).

All actograph experiments were performed in glass containers with dimensions of 250 mm lenght, 150 mm height and 70 mcm width. These glass containers were filled to a level of 60 mm with damp sand from the burrowing zone at the collection site (Apolillado or Mehuín), already containing the experimental individuals. 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. During experiments, the containers were kept in a light-tight enclosure within the constant temperature room. The temperarture was maintained at 15°C throughout the course of the experiment. Typically 30 adults of *P. maculata* were placed in each container for each xperimental trial. In

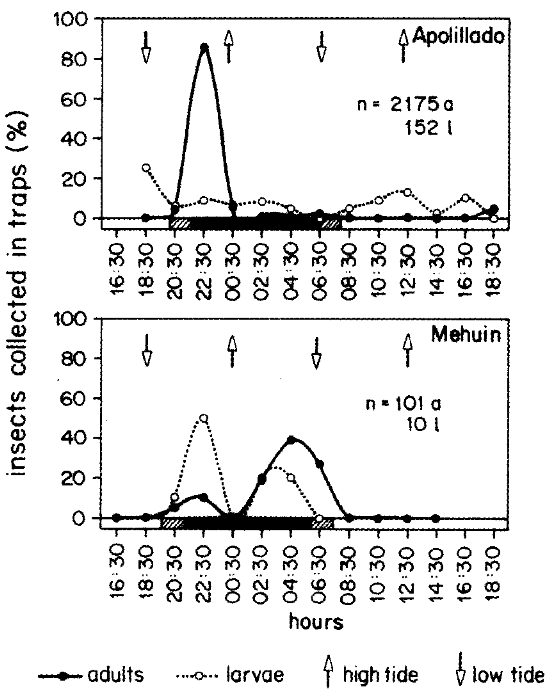

Fig. 2. Temporal distribution of the locomotor activity of adults and larvae of *P. maculata* over the beach surface at Apolillado and Mehuín during the summer of 1997. The dark bars show the hours of darkness (night), while the gray ones show the approximate time of sunset and sunrise. The hours indicated on the X-axis represent the hours at which the captured animals were collected from traps. Total number of collected adults (a) and larvae (l) are indicated.

Distribución temporal de la actividad locomotriz de adultos y larvas de *P. maculata* sobre la superficie de la playa en Apolillado y Mehuín durante el verano de 1997. Las barras negras indican las horas de oscuridad (noche), las grises señalan el tiempo aproximado del atardecer y amanecer. Las horas que se indican en el eje X representan las horas en las cuales los animales capturados se retiraron de las trampas. Se indica el número total de adultos (a) y larvas (l) recolectados.

experiments with larvae, 50 individuals were used in each experiment, as they are less easily detected by the actographs owing to their smaller size.

The actograph apparatus was designed and constructed at the School of Ocean Sciences, University of Wales, UK. Detailed circuit diagrams are available in Warman (1990). The apparatus consists of a series of transmitters of infrared light and a series of receivers. The infrared light beam was arranged to pass just above the perspex platform so an individual moving across the surface of the perspex platform would interrupt the infrared beam. When the receiver failed to receive the infrared light from the transmitter, a digital signal was sent to a BBC model B computer running a specially designed event recording program. The output from each receiver was recorded in the computer as a separate channel. After a predetermined download interval (15 min), the data in each channel were downloaded to magnetic cassette. Thus at the end of an experiment (72 h) the results showed the number of beam interruptions in each of the 15 min intervals throughout the experiment.

The program Perio (Aagaard 1993) was used for statistical analyses. This program provides a display of all possible period lengths within a user-defined range, plotted against standard deviation. The higher the standard deviation at a particular period length, the more significant the rhythmicity at that period. The statistical significance of the standard deviation values was assessed by comparing them with the upper 95% confidence interval derived from the same activity data in randomized form. Thus, any standard deviation value exceeding the 95 % confidence interval was taken to indicate a statistically significant periodicity.

RESULTS

The locomotor activity over the beach surface of Apolillado and Mehuín

Figure 2 shows the frequency of collected insects on the beaches at Apolillado and Mehuín during the summer of 1997. In Apolillado, the adults were mostly active during the hours of darkness, although some individuals were collected around the time of sunset, when they began to be active over the beach surface (collecting time: 20:30 pm). Adult *P. maculata* had disappeared from the beach surface by sunrise, at about 7:00 am. Most of the adults (90 %) were collected early in the night (collecting time: 22:30 pm), just before high tide. Following this initial activity peak, there was a sharp reduction in numbers trapped throughout the night (Fig. 2). In contrast to the pattern shown by adults, *P. maculata* larvae at Apolillado were active during most of the sampling period and no reduction of locomotor activity during high tides was observed. Although locomotor activity was relatively evenly distributed throughout the study period, larvae showed a peak of activity late in the afternoon of the first sampling day (collecting time: 18:30 pm) (Fig. 2).

Adult *P. maculata* at Mehuín, like those at Apolillado, were inactive during daylight hours (Fig. 2), a pattern also shown by larvae. In both adults and larvae, locomotor activity began on the beach surface during sunset (collecting time: 20:30 pm) and had ceased by sunrise (around 7:00 am). While the maximum locomotor activity of adults occurred during the low tide (around 4:00 am), that of larvae peaked just before the high tide (which occurred around 0:30 am) (Fig. 2). As was the case in Apolillado, the locomotor activity of adults on the beach surface dropped to zero during the night high tide, a situation also observed for larvae (Fig. 2).

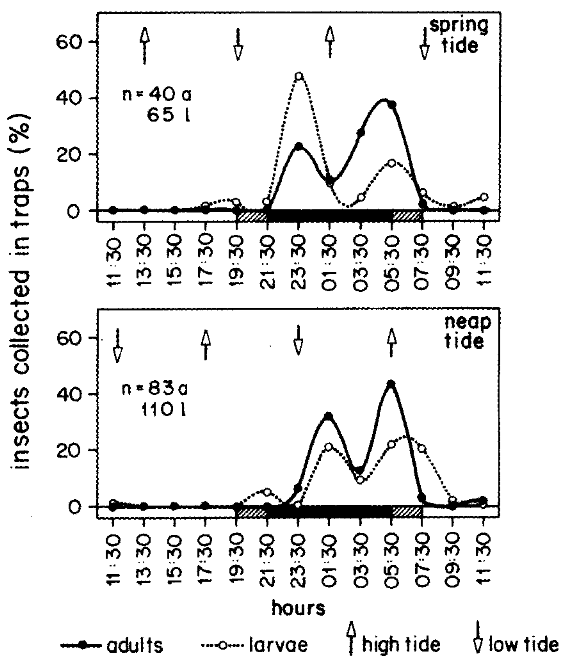

Fig. 3. Temporal distribution of locomotor activity of adults and larvae of *P. maculata* over the beach surface at Mehuín, during spring and neap tide (summer of 1991). The dark bars show the hours of darkness (night), while the gray ones show the hours of sunset and sunrise. The hours indicated on the X-axis represent the hours at which the captured animals were collected from traps. Total number of collected adults (a) and larvae (l) are indicated.

Distribución temporal de la actividad locomotriz de adultos y larvas de *P. maculata* sobre la superficie de la playa en Mehuín, durante marea de sicigia y cuadratura (verano de 1991). Las barras negras indican las horas de oscuridad (noche), las grises señalan el tiempo aproximado del atardecer y amanecer. Las horas que se indican en el eje X representan las horas en las cuales los animales capturados se retiraron de las trampas. Se indica el número total de adultos (a) y larvas (l) recolectados.

Locomotor activity over the beach surface of Mehuín during spring and neap tides

Figure 3 shows the frequency distribution of collected insects on the beach at Mehuín during spring and neap tides in summer 1991. During both samplings, the adults were mostly active during the nocturnal hours, although some individuals were also collected at sunrise or even during daylight hours. Larvae were active during both the night and the day (before and during sunset, or early in the morning). Adults and larvae showed two peaks of locomotor activity (Fig. 3); those of the spring tide were clearly separated by the time of high tide. During both sampling periods, adult activity peaked during the end of the night, just before the low tide during spring tide and just before the high tide during neap tide. While during spring tide the larvae peaked early in the night (collecting time: 23:30 pm), during neap tide similar peaks of activity were observed around mid night and late in the night, just before sunrise (collecting times: 1:30 am and 5:30 am, respectively) (Fig. 3).

Spatial distribution of the locomotor activity over the beach surface

Figure 4 shows the spatial and temporal distribution of trapped *P. maculata* at Apolillado and Mehuín during the summer of 1997. It can be seen that far more organisms were collected at Apolillado than Mehuín, primarily from 20:30 to 22:30 pm Larvae and adult beetles were active over the uppermost beach levels, independent of the width of exposed beach at each sampling period. These levels correspond to the drift line and retention zone of Salvat (1964); beetles were not active on the beach levels where the water content of the sands is higher (i.e., the resurgence zone). Figure 4 shows that the activity band of *P. maculata* at Apolillado was broader than that

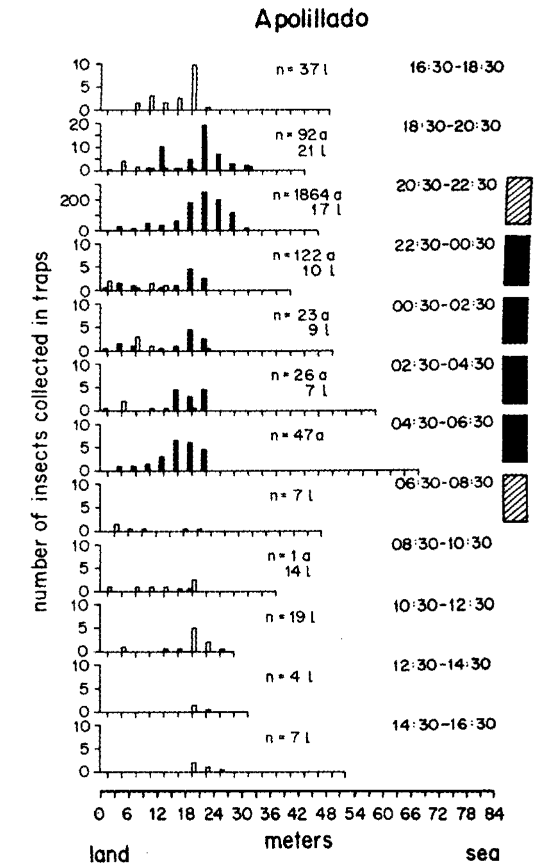

Fig. 4. Zonation of the locomotor activity of adults (black columns) and larvae (white columns) of *P. maculata* on the beach surface at Apolillado during the summer of 1997. Length of X - axis changes throughout the study period showing the variability in intertidal width due to tidal variability (i.e., a shorter X - axis means a high tide period and viceversa). The dark bars at the right of each graphic, show the hours of darkness (night), while the gray ones show the approximate time of sunset and sunrise. Inserted numbers represent the total number of adult (a) and larvae (l) of *P. maculata* collected at both transects.

Zonación de la actividad locomotriz de adultos (columnas negras) y larvas (columnas blancas) de *P. maculata* sobre la superficie de la playa en Apolillado durante el verano de 1997. La longitud del eje X cambia a través del período de estudio mostrando la variabilidad en el ancho del intermareal debido a variabilidad mareal (un eje X más corto representa un período de marea alta y viceversa). Las barras negras al costado derecho de cada gráfico indican las horas de oscuridad (noche), mientras que las grises señalan el tiempo aproximado de atardecer y amanecer. Los números insertados en los gráficos representan el número total de adultos (a) y larvas (l) de *P. maculata* recolectados en ambos transectos.

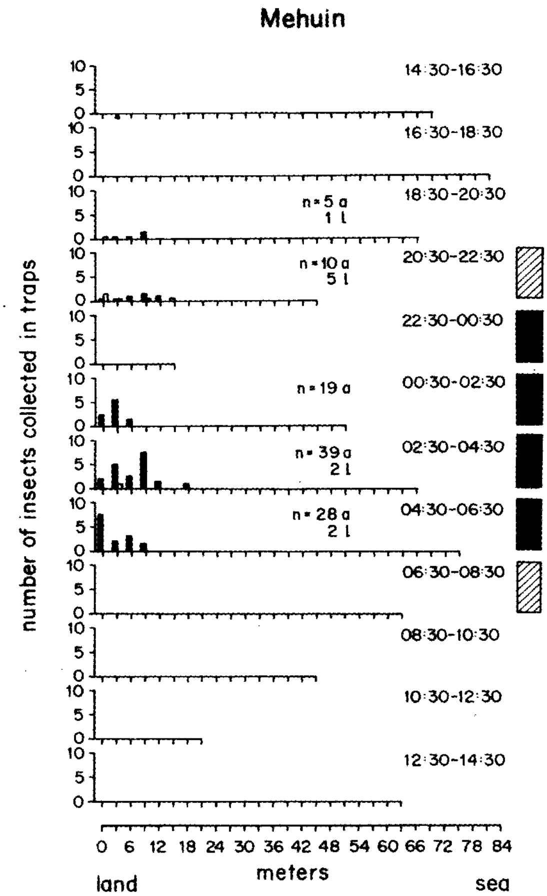

Fig. 5. Zonation of the locomotor activity of adults (black columns) and larvae (white columns) of *P. maculata* on the beach surface at Mehuín during the summer of 1997. Length of X - axis changes throughout the study period showing the variability in intertidal width due to tidal variability (i.e., a shorter X - axis means a high tide period and viceversa). The dark bars at the right of each graphic, show the hours of darkness (night), while the gray ones show the approximate time of sunset and sunrise. Inserted numbers represent the total number of adult (a) and larvae (l) of *P. maculata* collected at both transects.

Zonación de la actividad locomotriz de adultos (columnas negras) y larvas (columnas blancas) de *P. maculata* sobre la superficie de la playa en Mehuín durante el verano de 1997. La longitud del eje X cambia a través del período de estudio mostrando la variabilidad en el ancho del intermareal debido a variabilidad mareal (un eje X más corto representa un período de marea alta y viceversa). Las barras negras al costado derecho de cada gráfico indican las horas de oscuridad (noche), mientras que las grises señalan el tiempo aproximado de atardecer y amanecer. Los números insertados en los gráficos representan el número total de adultos (a) y larvas (l) de *P. maculata* recolectados en ambos transectos.

observed at Mehuín (Fig. 5). The same figure also shows that at Apolillado, the adult beetles moved to lower beach levels than larvae; the data from Mehuín suggest a similar pattern (Fig. 5).

Figure 6 shows the daily activity of adults and larvae during the spring and neap tide samplings carried out at Mehuín during the summer of 1991.The spatial distribution of activity did not appear to be affected by the differing tidal ranges during the two samplings. In adults the highest catches occurred in the lower levels of the activity fringe (26 to 36 m during spring tide and 26 to 38 m during neap tide). The distribution of larval activity was more uniform within the activity fringe during both samplings. During the spring tide sampling, adults and larvae moved downshore to the lowest beach levels and were captured as low as at the uppermost extent of the swash zone (Fig. 6).

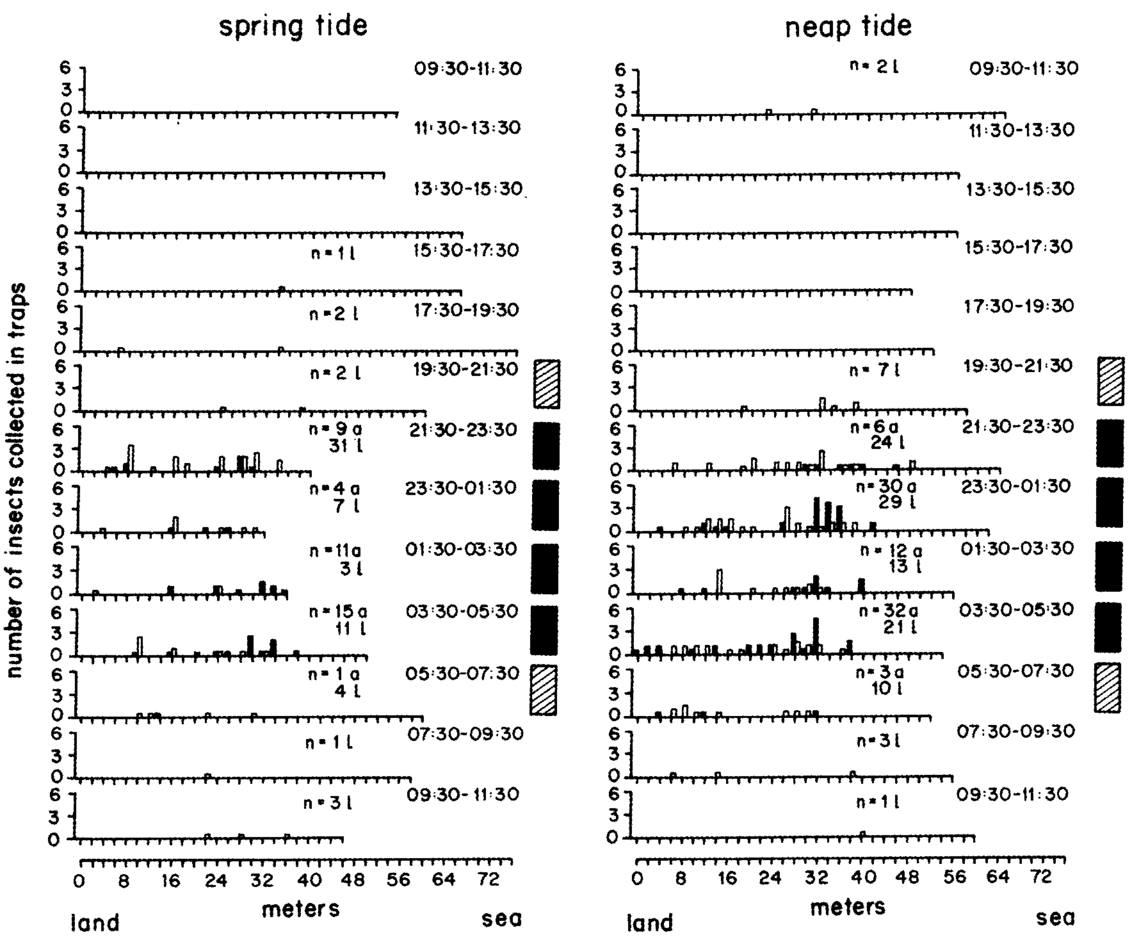

Fig. 6. Zonation of the locomotor activity of adults (black columns) and larvae (white columns) of *P. maculata* on the beach surface at Mehuín during the spring and neap tide (summer 1991). Length of X - axis changes throughout the study period showing the variability in intertidal width due to tidal variability (i.e., a shorter X - axis means a high tide period and viceversa). The dark bars at the right of each graphic, show the hours of darkness (night), while the gray ones show the approximate time of sunset and sunrise. Inserted numbers represent the total number of adult (a) and larvae (l) of *P. maculata* collected at both transects.

Zonación de la actividad locomotriz de adultos (columnas negras) y larvas (columnas blancas) de *P. maculata* sobre la superficie de la playa en Mehuín durante la marea de sicigia y cuadratura (verano de 1991). La longitud del eje X cambia a través del período de estudio mostrando la variabilidad en el ancho del intermareal debido a variabilidad mareal (un eje X más corto representa un período de marea alta y viceversa). Las barras negras al costado derecho de cada gráfico indican las horas de oscuridad (noche), mientras que las grises señalan el tiempo aproximado de atardecer y amanecer. Los números insertados en los gráficos representan el número total de adultos (a) y larvas (l) de *P. maculata* recolectados en ar.:bos transectos.

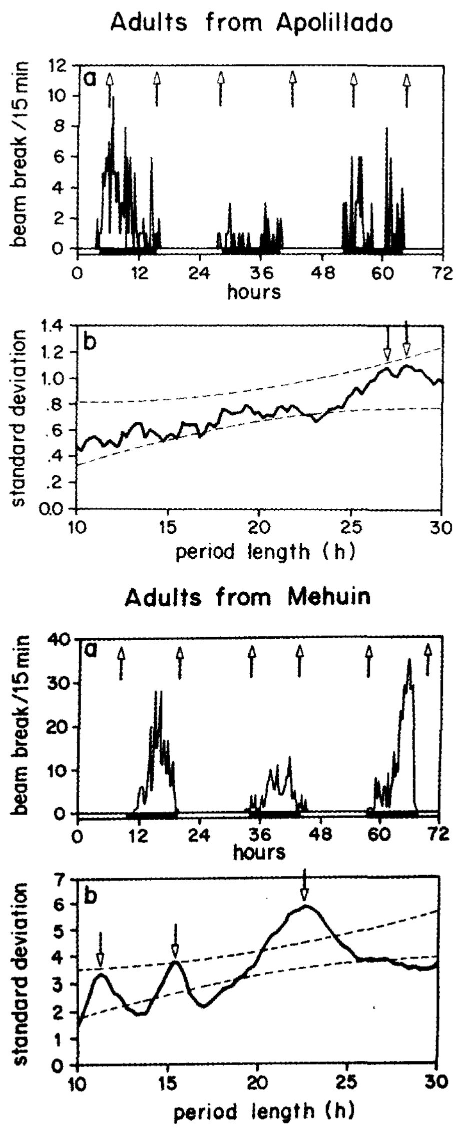

Fig. 7. Locomotor activity in laboratory conditions (actographs) of adults of *P. maculata* collected at the beaches Apolillado and Mehuín. a) The dark bars in the X - axis show the corresponding dark periods (night) in the field. The arrows the high tide hours according to tidal tables. b) Periodogram of data shown in graph a. The dotted lines show the 95% confidence intervals. The arrows show the significant activity peaks and that close to the 95% confidence interval line.

Actividad locomotriz en condiciones de laboratorio (actógrafos) de adultos de *P. maculata* colectados en las playas de Apolillado y Mehuín. a) las barras negras en el eje X indican los períodos correspondientes de oscuridad (noche) en terreno. Las flechas indican las horas de marea alta en el ambiente natural, de acuerdo a tablas de marea. b) periodograma de los datos que se muestran en el gráfico a. Las líneas punteadas indican los límites de confianza para el 95%. Las flechas indican los máximos significativos de actividad y aquellos cercanos a la línea del 95% del intervalo de confianza.

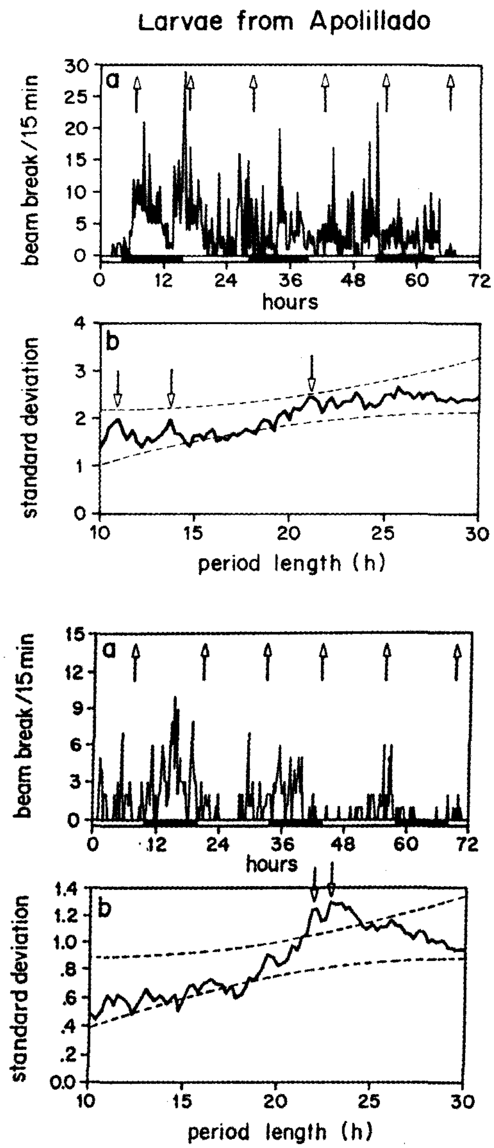

Fig. 8. Locomotor activity in laboratory conditions (actographs) of larvae of *P. maculata* collected at the beaches Apolillado and Mehuín. a) The dark bars in the X - axis show the corresponding dark periods (night) in the field. The arrows show the high tide hours according to tidal tables. b) Periodogram of data shown in graph a. The dotted line shows the 95% confidence intervals. The arrows show the significant activity peaks and that close to the 95% confidence interval line.

Actividad locomotriz en condiciones de laboratorio (actógrafos) de larvas de *P. maculata* colectados en las playas de Apolillado y Mehuín. a) las barras negras en el eje X indican los períodos correspondientes de oscuridad (noche) en terreno. Las flechas indican las horas de marea alta en el ambiente natural, de acuerdo a tablas de marea. b) periodograma de los datos que se muestran en el gráfico a. Las líneas punteadas indican los límites de confianza para el 95%. Las flechas indican los máximos significativos de actividad y aquellos cercanos a la línea del 95% del intervalo de confianza.

Locomotor activity in laboratory conditions

Figures 7 and 8 show the locomotor activity of *P. maculata* in laboratory conditions. Both adults and larvae collected at Apolillado and Mehuín had similar patterns of locomotor activity to those found in the field; i.e., adult insects collected at both beaches were active during continuous darkness (Fig. 7), while larvae showed locomotor activity throughout the experiments (72 h) (Fig. 8). However, the larvae from Apolillado and Mehuín showed a reduction in activity during some hours (cf. Fig. 8). The periodograms of the activity of adults showed activity peaks at 27 and 28 hour for Apolillado and 11.5, 15.5 and 22.5 hours for Mehuín. However, the only significant value was that for the adults from Mehuín (22.5 h) (i.e. value above the 95% confidence interval) (Fig. 7). The periodogram of activity of larvae collected at Apolillado does show three non significant activity peaks (11, 14 and 21 hours), but close to the 95% confidence interval line. The larvae from Mehuín, however, show a significant periodicity at 21.5 - 23 hours (Fig. 8).

DISCUSSION

The analyses of the locomotor activity of *P. maculata* during the summers of 1991 and 1997 showed that adults became active at sunset, they moved over the beach surface during the night, and then disappeared from the beach surface at sunrise. Larvae were trapped both diurnally and nocturnally, the diurnal activity being most marked during the sampling carried out at Apolillado. The absence of larvae during the daylight hours of the sampling carried at Mehuín during 1997 may be due to the very low overall number of larvae collected during that sampling period. Field observations carried out at Mehuín during summer months, confirmed the presence of active *P. maculata* larvae during the day.

The different patterns of locomotor activity shown by the adults and juveniles of *P. maculata* have been observed also in the isopod *Tylos granulatus* Krauss (Imafuku 1976), and in the amphipods *Talitrus saltator* (Montagnu) (Williams 1980, Scapini et al. 1992), *Orchestoidea tuberculata* (Jaramillo et al. 1980, Kennedy 1997) and *Orchestoidea corniculata* Stout (Bowers 1964). In most of these studies, it was suggested that the threat of predation by birds could be the cause of absence of adults on the surface of the beach during daylight hours, as they would easily be preyed upon. It has also been suggested that physical factors, such as air or sediment temperature, relative humidity and rain may explain the differences in activity between day and night (Scapini et al. 1992). Craig (1970) mentioned that the beetle *Thinopinus pictus* LeConte emerged on the beach surface solely during low tide at night, so minimizing daytime desiccation as well as avoiding wave action during high tide. Richards (1983) found that the foraging activity of *T. pictus* is determined by the search of food. Bowers (1964) mentioned that along Californian beaches, the interrelations between sand desiccation, environmental temperature, penetrability and particle size can control the locomotor activity of the amphipods *O. corniculata* and *Megalorchestia* (*Orchestoidea*) *californiana* (Brandt). Benson & Lewis (1976) suggested that the locomotor activity of *Talorchestia quoyana* (Milne-Edwards) was controlled by a circadian rhythm with an active nocturnal phase, and by a circatidal rhythm which further inhibited activity during high tide. The two cycles combined would then generate an activity rhythm according to which most of the animals would be active on the beach surface during low tide. According to Benson & Lewis (1976) the combination of these two rhythms is an adaptation of *T. quoyana* to the littoral habitat in which it is highly advantageous to avoid both daytime predation and wave action during high tide, especially during spring tides.

The results collected from the actograph experiments showed an endogenous circadian component in the locomotor activity of both larvae and adults of *P. maculata*. This endogenous component has been also found for other species inhabiting the uppermost levels of sandy beaches (Wildish 1970, Atkinson & Naylor 1973, Benson & Lewis 1976, Imafuku 1976, Williams 1980, 1982, Kennedy 1997). Some authors have suggested that an endogenous component to the activity rhythm is an advantage in the sense that during periods of inactivity, burrowing organisms are to a greater or lesser extent shielded from stimuli which might indicate the state of the diurnal or tidal cycle (e.g. light, temperature humidity, wave action). Hence an endogenous rhythm, or combination of endogenous rhythms allows burrowing organisms to remain in phase with environmental cycles (Bregazzi & Naylor 1972, Williams 1980, 1982).

The endogenous rhythm with a circadian periodicity of 22.5 hours shown by adults of *P. maculata* from Mehuín, was similar to that found in other supralittoral species such as *Orchestia gammarella* (Pallas) (Wildish 1970), *Talitrus saltator* (Williams 1980) and *Orchestoidea tuberculata* (Kennedy 1997). An endogenous circatidal rhythm seemed to be present in adults of Mehuín and larvae of Apolillado, since two activity peaks at 11 and 16 hours for adults and 11 and 14 hours for larvae were close to the significant level. The results of the other experiments (adults of Apolillado and larvae of Mehuín) did not show significant periodicity which could be related to an endogenous rhythm with circatidal periodicity. The lack of evidence for either circadian or circatidal endogenous rhythmicity may not reflect a true absence of an endogenous rhythm, but simply the inadequacy of the particular data set. It is also probable that in the field, endogenous stimuli for the initiation and termination of surface activity are reinforced by exogenous stimuli (such as light and wave action). Thus, it is quite possible, indeed, that different environmental conditions occurring in other days than those studied here may result in different patterns to that reported in this study. Further studies are required to clarify the situation with regard to a circatidal component to the activity rhythm.

The analyses of the zonation of the locomotor activity of *P. maculata* over the beach surface, show that adults and larvae moved to lower shore levels than those occupied when buried (cf. Jaramillo 1987, 1994). These levels correspond to the drift line and retention zone of Salvat (1964). Beetles are not active over the beach levels where water content of sands are highest (i.e., the resurgence zone). Similar patterns have also been observed in other sand beach insects, such as *Cafius* sp. (Chelazzi et al. 1983), *T. pictus* (Richards 1983) and *Eurynebria complanata* (Linneus) (Colombini & Chelazzi 1996), as well as the talitrid amphipods *O. tuberculata* (Jaramillo et al. 1980) and *O. californiana* (Richards 1983).

The spatial distribution of locomotor activity has been discussed by Chelazzi & Colombini (1989) in a *Tyrennian* population of the tenebrionid beetle *Phaleria bimaculata* (Linneus). This species shows several behavioural similarities to *P. maculata* such as a similar zonal distribution (both buried and active), active surface locomotor behaviour, morphologically reduced wings and a habitat on beaches with small tidal variation. Taken in conjunction, these factors would explain the ample range of locomotor activity and the weak or absent tidal rhythm.

The locomotor activity of adults of *P. maculata* at the beach of Apolillado seems to have been affected by moon light. The maximum activity of that beetles occurred just before high tide, while clouds still obscured the full moon (ca. 22:40 pm). After the clouds cleared and during the nocturnal low tide, adult beetles reemerged in high numbers on the beach surface.

In conclusion, the nocturnal locomotor actvity over the beach surface shown by adult *P. maculata* adults in the field, at Mehuín at least, appears to be under the control of an endogenous circadian rhythm, in a similar way to that described for a number of other inhabitants of the supralittoral zone of sandy beaches. In contrast, *P. maculata* larvae appear to be less strictly nocturnal, an ontogenetic difference that also has been described in a number of other supralittoral invertebrates.

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