

Environmental factors influencing the surface activity of *Eurynebria complanata* (Coleoptera, Carabidae)

Factores ambientales que influyen la actividad de superficie
de *Eurynebria complanata* (Coleoptera, Carabidae)

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ABSTRACT

In the past few years several studies have been conducted on the eco-ethology of different populations of *Eurynebria complanata* (Linnaeus, 1767) living along the Atlantic shores of France and on the Tyrrhenian sandy beaches of Italy. It was demonstrated that Mediterranean populations differed from Atlantic ones in their life cycles as they presented summer aestivation and shorter pre-imaginal phases. Moreover, differences in morphology were found between the two populations and these were related to differences in life cycles and to different adaptations due to climatic conditions. The aim of present study was to analyse the surface activity of *E. complanata* in relation to the most important environmental factors in order to understand which ecological constraints influence the behavioural adaptations of Atlantic and Mediterranean populations. Being a strictly nocturnal species, both in France and in Italy, night surveys were carried out on the field. Standard trapping methods (directional pitfall traps) were used. Simultaneously, environmental factors (air temperature, relative humidity, pressure, wind speed and direction, sand temperature and moisture, tidal level, light intensity) and prey presence (*Talitrus saltator*) were registered each hour. Zonation patterns and migrations perpendicular to the shoreline to and from the trophic zone were analysed both in daily and tidal hours. Movements parallel to the shoreline were also recorded. Mean hour of activity, hourly mean zonations and orientation indexes were calculated. To study the correlations between surface activity, hourly mean zonations and the different environmental factors multiple regression analysis was employed. The results indicate that both populations present daily variations in their activity patterns related to changes in the microclimatic conditions and to other environmental factors such as prey activity and tidal level. For the Italian population variations in the mean zonation of the beetle's activity showed a more seaward zonation at the beginning of the period of activity and a more landward one at the end of such period. For the French population different results were obtained according to the synodic phases and seasons of the year. Furthermore in this species diel rhythms were predominant over tidal ones. The results indicate that *E. complanata* is a highly specialized beetle and presents a great plasticity in its behavioural adaptations.

Key words: Coleoptera, sandy beach, diel and tidal activity, zonation.

RESUMEN

En los últimos años se han realizado varios estudios sobre la eco-etología de diferentes poblaciones de *Eurynebria complanata* (Linnaeus, 1767) en la costa Atlántica de Francia y en playas arenosas italianas del Mar Tirreno. Se demostró que las poblaciones del Mediterráneo difieren de las del Atlántico en sus ciclos de vida por presentar estivación de verano y fases pre-imago más cortas. Más aún, se han encontrado diferencias morfológicas entre esas dos poblaciones y éstas se relacionan a diferencias en ciclos de vida y a diferentes adaptaciones debidas a condiciones climáticas. El objetivo del presente estudio fue analizar la actividad sobre la superficie de la playa de *E. complanata*, en relación a los factores ambientales más importantes a fin de entender que restricciones ecológicas influyen las adaptaciones conductuales de las poblaciones atlánticas y mediterráneas. Siendo una especie estrictamente nocturna tanto en Francia como en Italia, se llevaron a cabo muestreos nocturnos de terreno. Se usaron métodos estándar de captura (trampas direccionales). Simultáneamente se registraron en forma horaria factores ambientales (temperatura del aire, humedad relativa, presión, velocidad y dirección del viento, temperatura y humedad de la arena, nivel mareal, intensidad de la luz) y presencia de presa (*Talitrus saltator*). Se analizaron los patrones de zonación y migraciones perpendiculares a la línea de costa, hacia y desde la zona trófica. También se registraron los movimientos paralelos a la línea de costa. Se calculó actividad horaria promedio, zonación horaria promedio e índices de orientación. Se utilizaron análisis de regresión múltiple para estudiar las correlaciones entre actividad sobre la superficie de la playa y los diferentes factores ambientales. Los resultados indican que ambas poblaciones presentan variaciones diarias en sus patrones de actividad relacionados a cambios en las condiciones microclimáticas y a otros factores tales como actividad de la presa y nivel mareal. La población italiana mostró una zonación más cercana al mar al principio del período de actividad y una zonación más continental al final de ese período. Para la población francesa se obtuvieron resultados diferentes de acuerdo a las fases sinódicas y estaciones del año. Aún más, los ritmos diarios predominaron sobre los mareales. Los resultados indican que *E. complanata* es un escarabajo altamente especializado presentando una gran plasticidad en sus adaptaciones conductuales.

Palabras clave: Coleoptera, playas arenosas, actividad diaria y mareal, zonación.

INTRODUCTION

It is already well known that sandy coastlines are unstable and dynamic environments due to the interactions between wind, sand and wave action. These cause continuous changes in the physical and chemical gradients which impose very special adaptations to the resident organisms (Hesp 1991, Brown & McLachlan 1990, McLachlan 1991). These are expressed not only through morphological and physiological adaptations (Marcuzzi 1960, Koch 1961, Brun 1970, Edney 1971, Wharton 1980, Coineau et al. 1982, Seely et al. 1983, Zachariassen et al. 1987a,b, Naidu & Hattingh 1988, Abushama & Al-Salameen 1989, Parmenter et al. 1989, Abushama & Al-Salameen 1991) but especially through sophisticated behavioural strategies (Pardi 1956, Tongiorgi 1969, Chelazzi et al. 1983, Chelazzi & Colombini 1989, Colombini et al. 1994).

Many beach Coleoptera are capable of varying their activity in time and space in relation to predictable and/or unpredictable climatic changes (Chelazzi et al. 1983, Ronchetti et al. 1986, Chelazzi & Colombini 1989, Colombini et al. 1994) generally associated with tidal variations and/or sudden sea storms. In particular, the spatial variations to and from the feeding areas and resting grounds are modulated by oriented movements perpendicular and parallel to the shoreline. These movements are regulated not only by astronomical orientation (Papi 1955, Pardi 1956, 1958, Colombini et al. 1994) but also by different tactical responses (scototaxis, fototaxis, anemotaxis, halotaxis, psammotaxis etc.) generally exhibited under non-stressful conditions. In this dynamic environment upper shore terrestrial arthropods represent interesting study material to understand the ecological constraints influencing the different adaptations.

Quite a few authors have analysed these problems on many Coleoptera [Staphylinidea (Craig 1970, Richards 1982, Chelazzi et al. 1983, Richards 1983, 1984), Carabidae (Evans 1988), Tenebrionidae (Colombini et al. 1994)] but few studies have dealt with the different adaptations that a given species can exhibit when living on sandy beaches of different geographical areas. To this purpose

the Coleoptera Carabidae *Eurynebria complanata* (Linnaeus 1767) was chosen because it inhabits Mediterranean sandy shores including North African beaches and the Atlantic ones from Morocco to Great Britain (Rüdolph 1970, King & Stabins 1971, Dachy 1987). This beetle was chosen also because it has a very specialized diet feeding on talitrids both during the larval (Gautier 1967, Spence & Sutcliffe 1982) and adult phases (Colombini 1989). Moreover, being an extremely fast runner (Evans & Forsythe 1984) this species has a high mobility that together with its relatively large size has permitted the study of its surface activity not only at a population level but also individually. Differences in the life cycles and in body size have already been reported for the Atlantic and the Mediterranean populations (Colombini & Chelazzi 1991). The aim of this work was to ascertain whether different behavioural strategies were employed in the use of space and time under different ecological conditions on the same beach (synodic and tidal phases) or on different shores with presence or absence of large tidal excursions.

MATERIAL AND METHODS

Two different populations of *E. complanata* were studied: one inhabiting a Tyrrhenian beach (Mediterranean Sea) near Burano (42° 23' 30" N; 11° 22' 30" E) and the other on the Atlantic sandy beach (Truc Vert 44° 41' 33" N; 1° 14' 42" W) of France near Archachon.

Standard trapping methods (Scapini et al. 1992) were used to gain information on the temporal and spatial patterns of the beetle's activity. Tetradirectional pitfall traps, with intercepting strips 5 m long, were placed at regular distances on the eulittoral and supralittoral along a transect from the base of the dune to the shoreline limits. On the Atlantic shore the first trap was at 20 m from the dune's base, followed by the second one placed towards sea at 10 m from the center of the previous trap and shifted 10 m parallel to the shoreline (orientated N-S). Other traps were placed with the same scheme and their number (1-8) varied according to the tidal levels. On the Italian beach several transects

were placed along the sea-land axis. The traps were spaced every 5 m and their number was considerably smaller (1-3) due to the narrower eulittoral resulting from coast morphology and a reduced tidal range. The pitfall traps were placed so as to intercept separately the beetles coming from four different directions: land, sea and the two directions parallel to the shoreline (from N and S and for Burano's beach NW, SE). Traps were visited each hour and the beetles were counted and immediately released in the opposite direction from which they were caught. Simultaneously environmental factors such as air temperature, relative humidity (R.H.) and prey presence (talitrids) were recorded. On some occasions other factors such as atmospheric pressure, wind speed, sand temperature (one towards land and one towards sea corresponding to traps 1 and 3 respectively), sand moisture (taken at the surface), tidal level, temperature of the beetle's resting sites, were also registered.

To analyse the diel components of the activity patterns circular statistic analysis (Batshelet 1981) was used. Rayleigh test (z) was employed to test if the frequency distribution was significantly concentrated in a certain hour of the day (r is the mean vector length). Confidence limits (95%) for the mean hour of activity were calculated through graphic interpolation (Fig. 5.2.1 Batshelet 1981). Note that the curve for $n = 200$ was used even when the number of specimens captured were higher than 200. V test (u) was applied to verify whether the resulting mean hour of activity was significantly clustered around the expected hour of activity (24:00 h for nocturnal animals).

Multiple regression analysis (Bliss 1970, Zar 1984) through the Backward Elimination Method was employed to correlate the activity and zonation of *E. complanata* with the different environmental parameters. For this analysis the direction of the wind was split in the two components along the sea-land and S-N axes. The direction of the wind, considered in polar co-ordinates, was transformed into Cartesian components (sine - cosine of the angle) and positioning the x semi-axis in the N (NW at Burano) direction and y semi-axis with the landward direction (E and at Burano NE).

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

From the capture frequency obtained in the four directions (sea, land, N,S and for Burano's beach NW, SE) orientation indexes (R) were calculated through circular statistic analysis. V test was used to test if the resultant vector was significantly clustered in the theoretical expected direction (TED = towards sea or land according to the hour of the day). Hourly and total mean zonations, with relative confidence limits (95%), were calculated through one-sample analysis methods using the statistical programme "Statgraphic's Version 4.0". For the latter and for circular statistic analysis only data with captures greater or equal to 5 were considered. Significant levels of $p < 0.05$ were used.

RESULTS

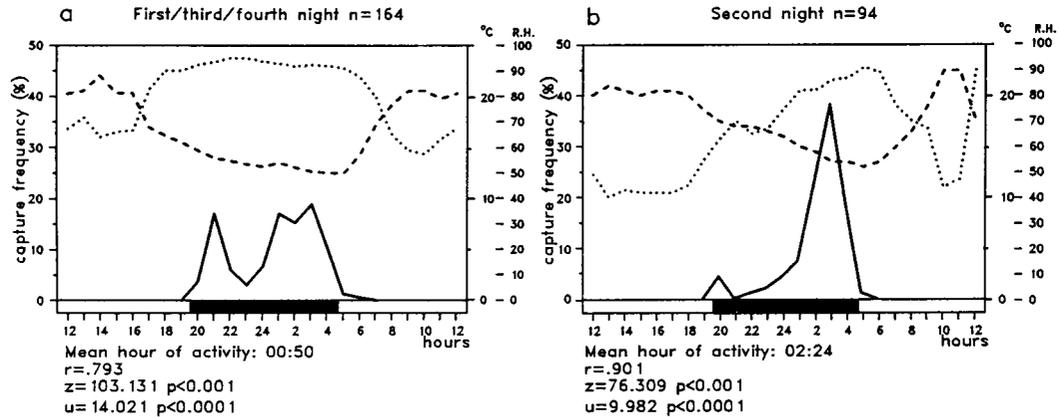
THE ITALIAN POPULATION

Daily surface activity

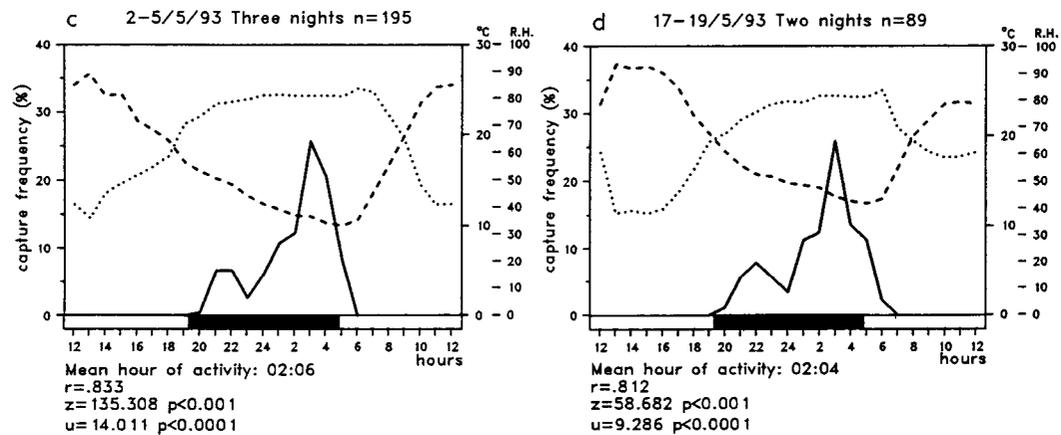
For the Italian population all field experiments were conducted during spring months in three different years (1989, 1993, 1994). The results indicate that the beetle's surface activity is strictly nocturnal with an onset immediately after sunset. Surface activity ceases after sunrise when *E. complanata* retreats to a suitable resting site to spend the day hours. The results indicate that the distribution of the capture frequencies can vary between nights. For example the activity rhythm can present two peaks, one in the first and the other in the second part of the night (Fig. 1a).

In some cases the first peak of activity can be depressed (Fig. 1c, d) or almost totally suppressed (Fig. 1b, f), while in another case (Fig. 1e) the second peak of activity can be

Experiments 15-19 May 1989



Experiments May 1993



Experiments April-June 1994

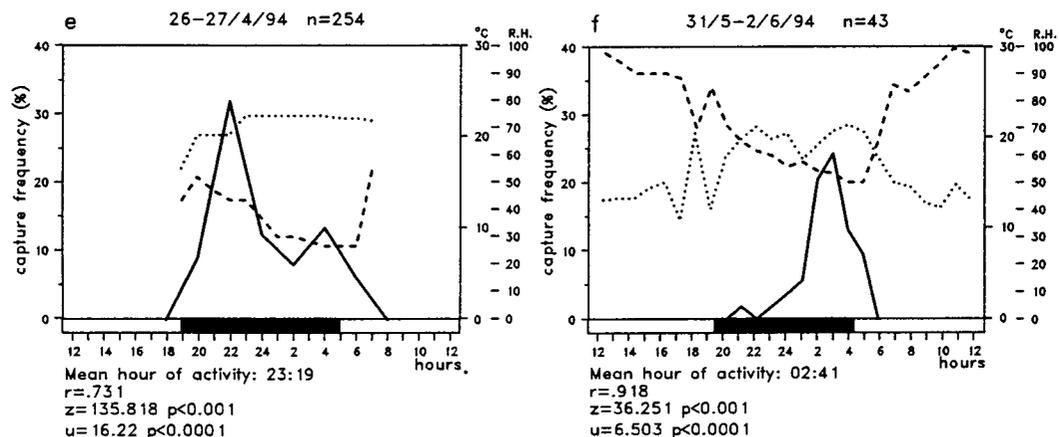


Fig. 1: Surface activity of the Italian population of *E. complanata* (continuous lines) in three different years. Air temperature (dashed lines) and relative humidity (dotted lines) are also shown. For each set of field experiments the values of circular statistic analysis are reported (Rayleigh test and V test).

Actividad sobre la superficie de las poblaciones italianas de *E. complanata* (líneas continuas) en tres años diferentes. Se muestran también la temperatura del aire (líneas de trazos) y la humedad relativa (líneas de puntos). Se entregan los valores de los análisis de estadística circular para cada set de experimentos de terreno (test de Rayleigh y test V).

depressed. The mean hours of activity calculated through circular statistical analysis (Rayleigh test & V test) show that the distribution of the capture frequencies are significantly different from uniform and do not differ significantly from the expected mean hour of activity calculated for nocturnal animals at 24:00 h. In particular the mean hour of activity in Fig. 1a is at 00:50 h and the beetle's activity is significantly concentrated. In Fig. 1c and d the mean hours of activity are at 02:06 h and 02:04 h respectively and again the activity of the beetle is significantly concentrated. In Fig. 1b and f the mean hours of activity are at 02:24 h and 02:41 h whereas in the case of Fig. 1e the mean hour of activity is at 23:19 h. In all cases the distributions of beetle's activity are significantly different from random (see Rayleigh test & V test).

Zonation of the surface activity

The use of pitfall traps regularly placed on the eulittoral gave information on the variation of the beetle's zonation during its period of activity. Considering the hourly mean zonation of *E. complanata* in the experiments conducted in May 1993 in one case (2-5/5/93) (Fig. 2a) no significant differences were registered in the different hours. In the other case (17-19/5/93) (Fig. 2b) the beetles were found in a more seaward zone at the beginning of their activity whereas at dawn their mean zonation (abbreviated mean zon.) was significantly more landwards (22:00 h mean zon. 48.57 m from the dune's base \pm 3.5 m compared with 05:00 h mean zon. 44.44 ± 0.33 m).

Cumulating the hourly mean zonation of the beetles in the 5 nights of experiments (Fig. 2c), the zonation at dawn was significantly more landwards not only with regards to the first hours of the night but also with 01:00 h and 02:00 h (05:00 h mean zon. 41.92 ± 3.03 m compared with 21:00 h mean zon. 48.88 ± 1.6 m, 22:00 h mean zon. 48 ± 1.93 m, 23:00 h mean zon. 48 ± 3.02 m, 01:00 h mean zon. 48.06 ± 1.47 m and 02:00 h mean zon. 47.71 ± 1.61 m). Similar results were obtained in the experiments of April 1994 (Fig. 2d) in which the hourly mean zonation of the beetles during the first part of

the night was significantly more seawards than that found in the second part of the night (20:00 h mean zon. 7.85 m from the sealine limits \pm 1.44 m and 21:00 h mean zon. 7.64 ± 0.71 m compared with 23:00 h mean zon. 10.52 ± 1.78 m, 24:00 h mean zon. 12 ± 1.41 m, 01:00 h mean zon. 11.31 ± 2.1 m and 04:00 h mean zon. 11.51 ± 1.09 m). No significant variations were found in the hourly mean zonation of *E. complanata* in the experiments conducted during the two nights of May-June 1994 (Fig. 2e).

Table 1 shows the mean hour of activity of *E. complanata* on the total of nights in the experiments of May 1993. The mean hour of activity was calculated separately for each of the three series of traps placed on the eulittoral. The traps nearest to the sea intercepted the beetles before the central and landward traps. The mean hours of activity calculated through the capture frequency for each trap were: seaward traps 01:44 h, central traps 02:40 h and landward traps 03:26 h. Significant differences were found only between the seaward (upper confidence limit 02:04 h) and the central traps (lower confidence limit 02:17 h). The mean hour of activity of the landward traps was not significantly different from the others probably because of the small number of animals ($n = 13$) caught by these traps.

Similar results were obtained in the experiments of April 1994 (Table 1). Differences in the mean hour of activity of *E. complanata* calculated for each series of traps were significant in all cases (seaward traps 22:38 h, upper confidence limit 23:10 h; central traps 23:45 h, lower confidence limit 23:13 h; landward traps 01:43 h, lower confidence limit 01:03 h).

Directional variation of daily movements

The use of the directional pitfall traps gave information on the direction of the beetle's movements during its period of activity. Orientation indexes obtained from the experiments conducted at the beginning of May 1993 (2-5/5/93) (Fig. 3a) showed that in the first part of the night (21:00 h, 23:00 h, 01:00 h) the beetles moved significantly towards sea. At 03:00 h there was a landward tendency but this was not significant. Orienta-

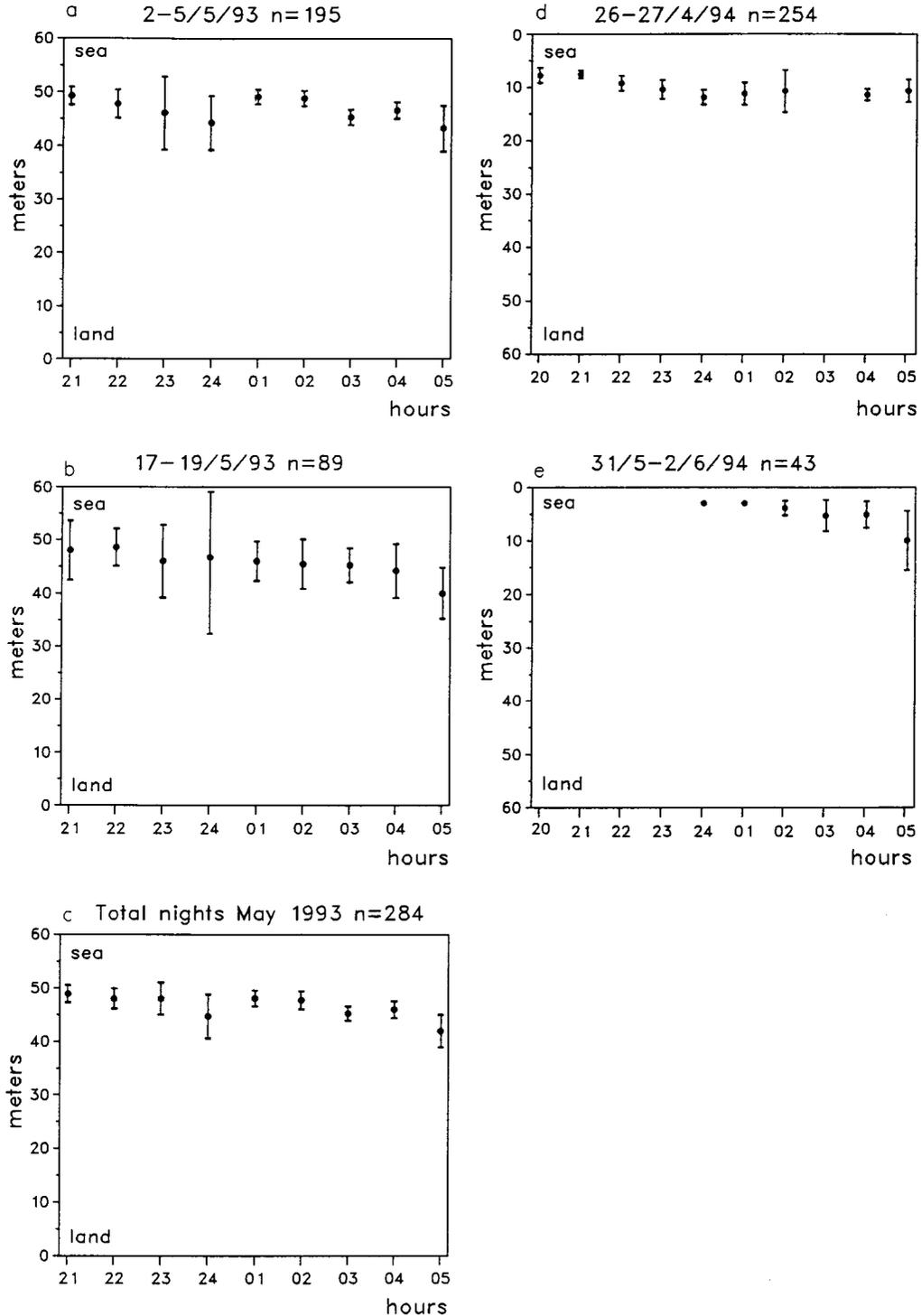


Fig. 2: Hourly mean zonation of the Italian population of *E. complanata* during the nocturnal hours of surface activity. Confidence limits (95%) are shown. In a-c the meters are indicated starting from the base of the dune. In d and e the meters are measured from the shoreline limits.

Zonación horaria media de la población italiana de *E. complanata* durante las horas nocturnas de actividad sobre la superficie. Se muestran los límites de confianza al 95%. En a-c los metros se indican desde la base de la duna. En d y e los metros fueron medidos desde los límites de la línea de marea baja.

TABLE 1

Mean hours of captures, calculated for each set of traps through circular statistic analysis, are shown for the Italian population of *E. complanata*

Horas promedio de captura para cada set de trampas de la población italiana de *E. complanata*; cálculos mediante estadística circular

Trap	Sea	Center	Land
Total nights of May 1993			
mean hour	01: 44	02: 40	03: 26
lower conf. lim.	01: 23	02: 17	02: 00
upper conf. lim.	02: 04	03: 02	04: 52
r	0.823	0.848	0.902
n	187	84	13
26-27/4/94			
mean hour	22: 38	23: 45	01: 43
lower conf. lim.	22: 06	23: 13	01: 03
upper conf. lim.	23: 10	00: 17	02: 23
r	0.826	0.867	0.803
n	132	58	5

tion indexes calculated for movements parallel to the shoreline were never significant.

Analysing the orientation indexes obtained from the experiments conducted the 17-19/5/93 (Fig. 3b) significant landward movements were registered at 23:00 h, 01:00 h, 03:00 h. These were due principally to the capture frequencies obtained in the seaward traps. Significant orientation indexes calculated for movements parallel to the shoreline were recorded only at 22:00 and these were towards NW.

The experiments of April 1994 again showed that *E. complanata* tends to move towards sea in the first part of the night. In fact orientation indexes were significant at 20:00 h and 22:00 h (Fig. 3c). Movements parallel to the shoreline were registered at 22:00 h and 02:00 h and in both cases the animals were moving towards NW.

In May-June 1994 no significant movements were registered perpendicular to the shoreline. Only at 02:00 h and 03:00 h a tendency to move towards NW was recorded and orientation indexes were significant ($p < 0.05$ and $p < 0.005$ respectively).

Environmental factors influencing the daily activity and zonation

During the field experiments of 1989 and 1993 air temperature and relative humidity

were registered together with the beetle's capture frequency. Prey presence was recorded during the experiments of May 1989 and during the experiments of 17-19/5/93.

In the first, third and fourth night of May 1989 the mean temperatures during the period of the beetle's activity ranged from 14.6° C to 12.5° C. The mean relative humidity was always over 88%. In the first part of the second night, instead, the temperature ranged from 18.5° C to 16.5° C and the relative humidity from 55% to 67%. In the second part of the night the temperatures registered were from 16° C to 13° C and the relative humidity from 75% to 91%.

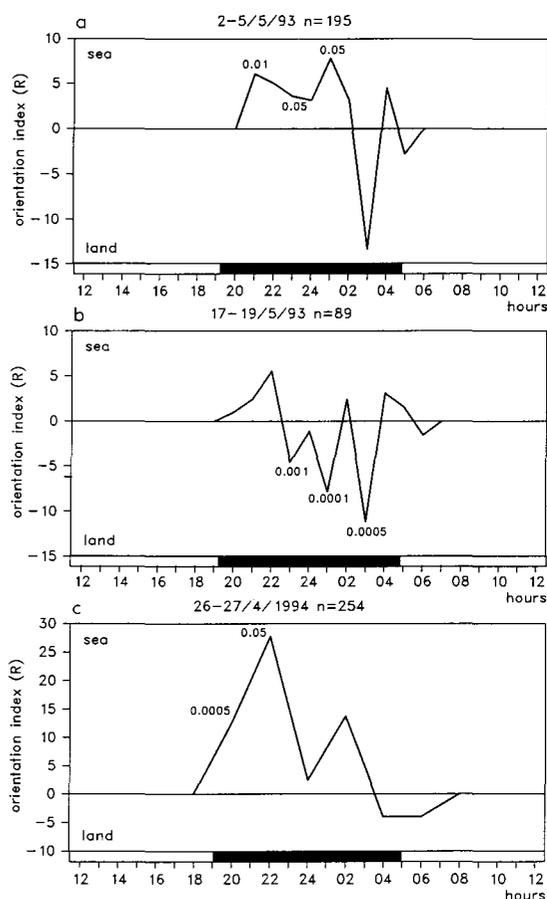


Fig. 3: Orientation indexes (R) of the Italian population of *E. complanata* in two different years. Only significant levels ($p < 0.05$) of seaward and landward movements are shown.

Indices de orientación (R) de las poblaciones italianas de *E. complanata* en dos años diferentes. Sólo se indican los movimientos significativos ($p < 0.05$) hacia el mar y hacia el continente.

During the first field experiments in 1993 (2-5/5/93) the mean temperature in the first part of the night ranged from 16° C to 13.3° C and from 12.33° C to 10° C in the second part. The mean relative humidity varied from 73.3% to 81.3%. During the second field experiments (17-19/5/93) mean temperature ranged from 16.7° C to 15.5° C in the first part of the night and from 14.17° C to 12.5° C in the second part. The mean relative humidity ranged from 79.5% to 83.5% during the entire period of the beetle's activity.

Through multiple regression analysis a significant negative correlation was found

only with the temperature when the beetle's activity was tested against temperature, relative humidity and prey presence (Table 2). This was so for each night tested individually or for the total of the nights of the experiments conducted in May 1989 and May 1993. Only during the third night of the 2-5/5/93 experiments a significant negative correlation was found also with the relative humidity. No significant correlation was ever found with the preys.

In the experiments of 1994 other environmental parameters were registered together with *E. complanata*'s surface activity

TABLE 2

Multiple regression analysis of surface activity for the Italian population of *E. complanata* with environmental parameters (air temperature, relative humidity, prey presence). For each field experiment (1989, 1993) 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.

Slanted lines indicate missing data

Análisis de regresión múltiple de la actividad sobre la superficie de la población italiana de *E. complanata* con parámetros ambientales (temperatura del aire, humedad relativa, presencia de presa). Para cada experimento de terreno (1989, 1993) se muestran los coeficientes de regresión significativos y sus niveles de probabilidad. También se muestran la constante de la ecuación de regresión múltiple y el coeficiente de determinación múltiple (R^2).

Datos que faltan se indican con líneas oblicuas

Date	Constant	air temp.	R.H. °C	Talitrids %	R^2
15-16/5/89	26.6826 P = 0.0016	-1.4704 P = 0.0056	N.S.	N.S.	0.2679
16-16/5/89	31.7995 P = 0.0031	-1.5848 P = 0.0074	N.S.	N.S.	0.2509
17-18/5/89	7.9612 P = 0.0006	-3.3614 P = 0.0033	N.S.	N.S.	0.3003
18-19/5/89	5.5856 P = 0.0003	-0.2576 P = 0.0015	N.S.	N.S.	0.3440
15-19/5/89	15.3103 P < 0.0001	-0.7461 P < 0.0001	N.S.	N.S.	0.1693
2-3/5/93	8.6774 P = 0.0003	-0.3965 P = 0.0028	N.S.	/	0.3107
3-4/5/93	12.9369 P = 0.0001	-0.5574 P = 0.0013	N.S.	/	0.3550
4-5/5/93	62.9256 P = 0.0118	-1.7919 P = 0.0054	-0.4064 P = 0.0383	/	0.4628
2-5/5/93	11.4715 P < 0.0001	-0.5096 P < 0.0001	N.S.	/	0.3198
17-18/5/93	9.1397 P = 0.0001	-0.3589 P = 0.0009	N.S.	N.S.	0.3745
18-19/5/93	9.0629 P < 0.0001	-0.3828 P = 0.0002	N.S.	N.S.	0.4422
17-19/5/93	8.9808 P < 0.0001	-0.3644 P < 0.0001	N.S.	N.S.	0.4064

(Table 3). During the night of April 1994 the beetle's activity had a negative correlation with the constant, relative humidity and light intensity and a positive correlation with atmospheric pressure. Multiple regression analysis employed for the experiments of May-June 1994 gave different results. For the total nights (31/5-2/6/94) the beetle's activity was negatively correlated with the atmospheric pressure and positively with the constant, whereas during the first night it was negatively correlated with the temperature and wind intensity and positively with the atmospheric pressure. During the second night *E. complanata*'s activity had a negative correlation with the atmospheric pressure and a positive one with the surface sand temperature near the sea and the constant. Again no correlation was found with the prey presence.

Only for the night of April 1994 the hourly mean zonation of *E. complanata* was correlated with some of the environmental factors measured (Table 4). Negative correlations were found with the air temperature, atmospheric pressure, light intensity and sand moisture. Here the coefficient of determination was quite high ($R^2 = 0.9876$).

THE FRENCH POPULATION

The French population of *E. complanata* was studied in two different seasons of the year

(spring and autumn). Since the beach studied presented large tidal excursions the beetle's activity was analysed in the two different periods of the synodic cycle (spring and neap). Field experiments were conducted for two nights around spring tide and two around neap tide.

Daily surface activity

Spring season

Analysing the surface activity of *E. complanata* during the two nights around spring tide (23-24/6/94 25-26/6/94) (Fig.4a-c) it can be noted that the beetle is nocturnal and its activity starts immediately after sunset and ends at dawn. The distributions of the capture frequencies were unimodal and significantly different from uniform (see Rayleigh test). The mean hours of activity of the first and second night were at 00:10 h and 23:33 h respectively. Pooled data showed a mean hour of activity at 23:59 h. The beetle's activity was significantly concentrated and did not differ from the expected hour of activity (24:00 h, see V test).

Surface activity of *E. complanata* registered during the two nights around neap tide (30/6-2/7/94) (Fig.4d-f) was again exclusively nocturnal and presented only one peak of activity in the first night and two peaks in the second one. During the first night studied a total of 1355 beetles were intercepted

TABLE 3

Multiple regression analysis of surface activity for the Italian population of *E. complanata* with environmental parameters (air temperature, relative humidity, sand temperatures near sea and land, sand moistures near sea and land, atmospheric pressure, light intensity, wind intensity, prey presence). For further explanations see Table 2

Análisis de regresión múltiple de la actividad sobre la superficie de la población italiana de *E. complanata* con parámetros ambientales (temperatura del aire, humedad relativa, temperaturas de la arena cerca del mar y la tierra, humedad de la arena cerca del mar y la tierra, presión atmosférica, intensidad de la luz, intensidad del viento, presencia de presa). Para mayores explicaciones ver Tabla 2

Date	Constant	air temp. °C	air R.H. %	sand temp. sea °C	sand temp. land °C	sand moist. sea %	sand moist. land %	pressure mm Hg	light int. W/m ²	wind int. km/h	talitrids	R ²
26-27/4/94	-0.0002 P = 0.0391	N.S.	-3.5566 P = 0.0151	/	/	N.S.	N.S.	26.6591 P = 0.0382	-5.3912 P = 0.0019	/	N.S.	0.5940
31/5-1/6/94	N.S. P < 0.0001	-3.3366	N.S.	N.S.	N.S.	N.S.	N.S. P < 0.0001	0.0129	/ P = 0.0057	-0.1838	N.S.	0.6667
1-2/6/94	1415.5999 P < 0.0001	N.S.	N.S.	0.0589 P = 0.0355	N.S.	N.S.	N.S.	-1.8589 P < 0.0001	/	N.S.	N.S.	0.6281
31/5-2/6/94	893.5346 P < 0.0001	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	-1.1720 P < 0.0001	/	N.S.	N.S.	0.3868

TABLE 4

Multiple regression analysis of the hourly mean zonation for the Italian and French population of *E. complanata* with environmental parameters (air temperature, relative humidity, surface sand temperature near sea and land, sand moistures near sea, land and intermediate zone, atmospheric pressure, light intensity and tidal levels). For further explanations see Table 2

Análisis de regresión múltiple de la zonación horaria promedio de la población italiana y francesa de *E. complanata* con parámetros ambientales (temperatura del aire, humedad relativa, temperatura superficial de la arena cerca del mar y la tierra, humedad de la arena cerca del mar, la tierra y zona intermedia, presión atmosférica, intensidad de la luz y niveles mareales). Para mayores explicaciones ver Tabla 2

Date	Constant	air temp. °C	air R.H. %	temp. surf. sand sea °C	temp. surf. sand land °C	sand moist. sea %	sand moist. center %	sand moist. land	pressure mm Hg	light int. W/m ²	tidal level m	R ²
Italian population												
2-5/5/93	45.8685 P < 0.0001	N.S.	N.S.	/	/	/	/	/	/	/	/	0.0000
17-19/5/93	44.4300 P < 0.0001	N.S.	N.S.	/	/	/	/	/	/	/	/	0.0000
26-27/4/94	16732.9720 P = 0.0011	-0.7744 P = 0.0003	N.S.	/	/	-1.3589 P = 0.0047	-1.6047 P = 0.0069	N.S.	-21.8927 P = 0.0011	-2.1022 P = 0.0010	/	0.9876
French population												
Spring season 1994												
Spring tide	N.S.	-1.6892 P = 0.0071	-1.0875 P = 0.0020	N.S.	N.S.	N.S.	N.S.	N.S.	0.1885 P = 0.0003	/	N.S.	0.9926
Neap tide	67.7613 P < 0.0001	N.S.	N.S.	-1.3677 P = 0.0002	N.S.	-7.5379 P = 0.0066	-4.5566 P = 0.0334	3.1660 P = 0.426	N.S.	/	N.S.	0.6237
Autumn season 1992												
Neap tide	33.4509 P < 0.0001	N.S.	N.S.	/	/	/	/	/	/	6	N.S.	0.0000
Spring tide	N.S. P = 0.0002	5.8063 P = 0.0389	0.3292	/	/	/	/	/	/	6	N.S.	0.9328

against 560 in the second night. The mean hour of activity were at 22:30 h and at 00:22 h during the first and second night respectively. In both cases the distributions were significantly different from uniform (see Rayleigh test) and did not differ from the expected hour (24:00 h, see V test). Cumulating the two nights of neap tide the distribution is similar to the first night with a mean hour of activity at 23:01 h. Comparing the daily mean hour of activity of the two nights of spring tide with that of neap tide the differences are significant (spring tide mean hour 23:59, lower confidence limit 23:43; neap tide mean hour 23:01, upper confidence limit 23:16).

Autumn season

In 1992 experiments were conducted during two nights around neap tide (5-7/10/92) and two around spring tide (11-13/10/92) (Fig.

5). Surface activity of *E. complanata* was delayed as regards to sunset and dawn of about two hours. During the first night of neap tide (Fig. 5b) the beetle's activity was evenly distributed throughout the entire night with a mean hour of activity at 00:56 h. During the second night (Fig. 5c) the activity was concentrated in its second part with a mean hour of activity at 03:26 h. Pooling the data of the two nights (Fig. 5a) the activity was mainly distributed at the beginning and at the end of the activity period. The mean hour of activity was at 01:50 h.

During spring tide (Fig. 5d-f) the beetle's activity was mainly concentrated in the first part of the night. The mean hours of activity were 22:32 h and 21:42 h for the first and second night respectively and 22:28 h for the total of the two nights. All distributions were significantly different from random and didn't differ from the expected hour of activity (see Rayleigh test and V test).

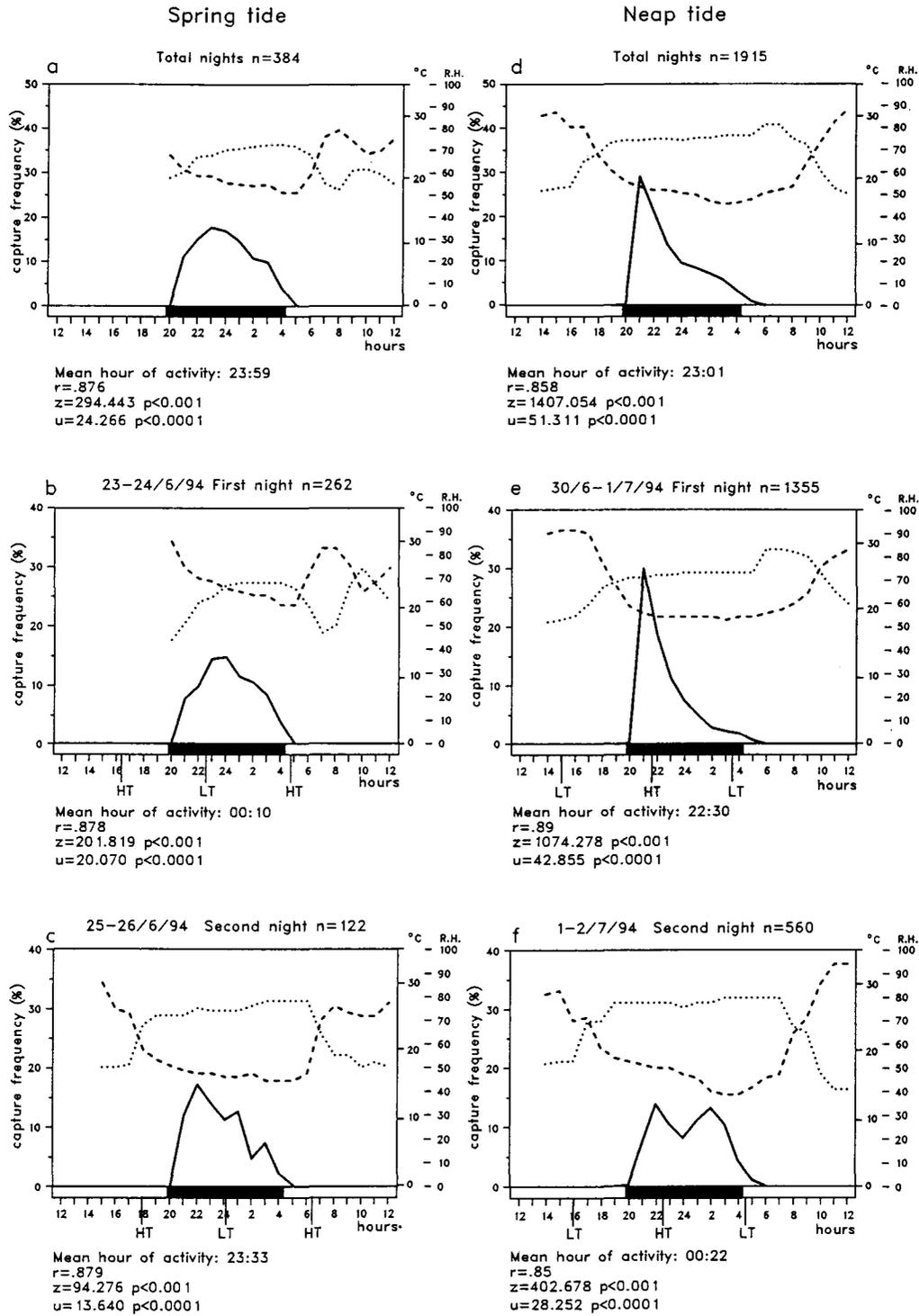


Fig. 4: Surface activity of the French population of *E. complanata* during spring tide (a-c) and neap tide (d-f) of spring season 1994. The high (HT) and low tides (LT) are indicated. For further explanations see Fig. 1.

Actividad sobre la superficie de las poblaciones francesas de *E. complanata* durante mareas de sicigia (a-c) y cuadratura (d-f) de la primavera de 1994. Se indica la posición de la marea alta ("HT") y marea baja ("LT"). Para mayores explicaciones ver Fig. 1.

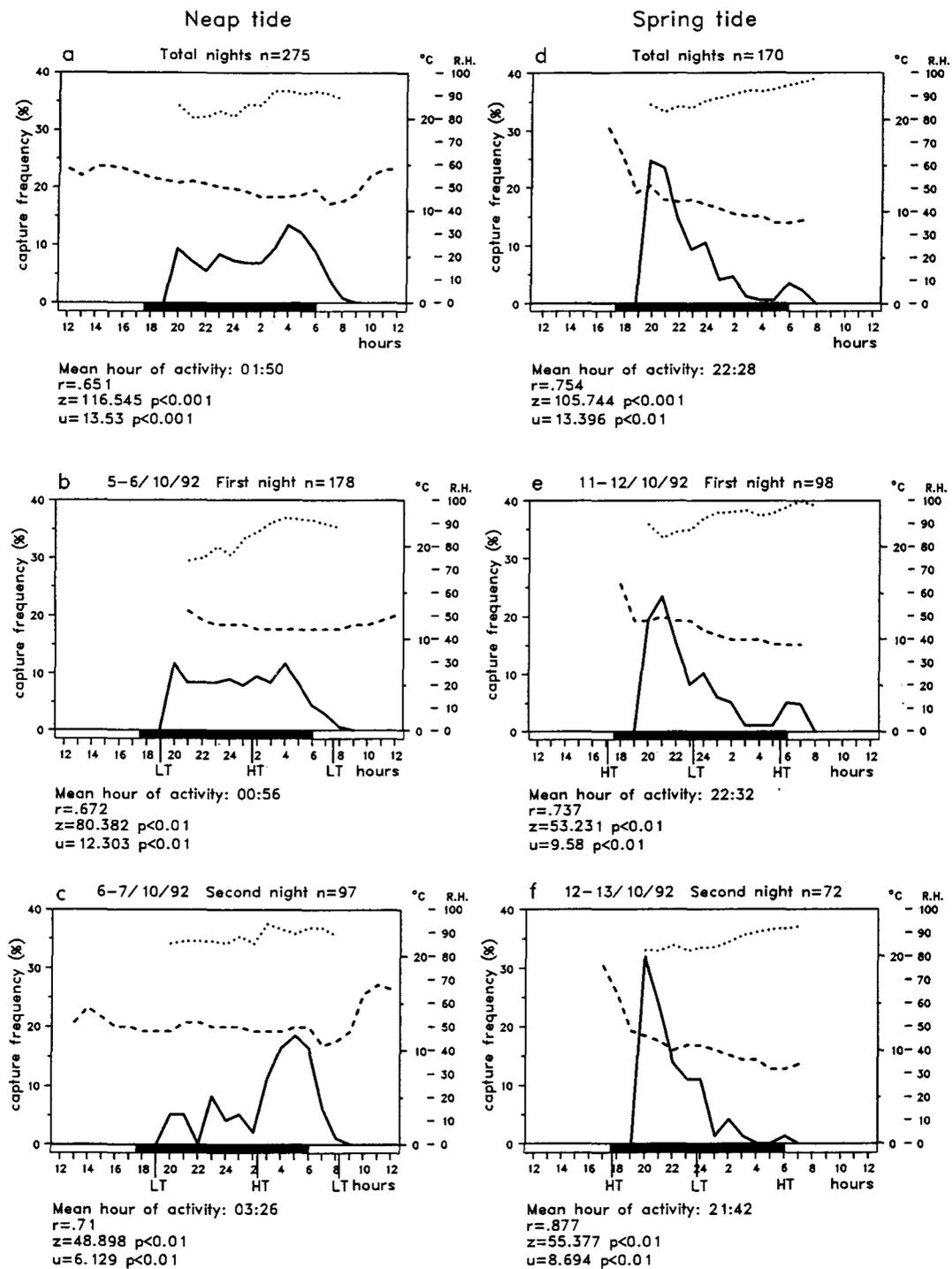


Fig. 5: Surface activity of the French population of *E. complanata* during neap tide (a-c) and spring tide (d-f) of autumn season 1994. For further explanations see Fig. 1 and 4.

Actividad sobre la superficie de las poblaciones francesas de *E. complanata* durante mareas de cuadratura (a-c) y sicigia (d-f) del otoño de 1994. Para mayores explicaciones ver Fig. 1 y 4.

Zonation of the surface activity

Spring season

Considering the capture frequencies for each pitfall trap at the different distances from the dune's base and at the different hours of the night a total mean zonation and an hourly mean zonation was calculated (Fig. 6).

The total mean zonation of *E. complanata* during its activity period was significantly more landwards in spring tide than in neap tide (spring tide mean zonation 33.78 ± 3.31 m; neap tide mean zonation 44.28 ± 2.21 m).

During the two nights of spring tide analysed either separately or together (Fig. 6a-c), *E. complanata* had a significant seaward zonation at the beginning of its surface activity compared to the other hours of the night (first night: 21:00 h mean zon. 43.40 ± 5.43 m compared with 23:00 h mean zon. 34.14 ± 2.93 m, 24:00 h mean zon. 32.29 ± 2.98 m, 02:00 h mean zon. 29.11 ± 1.95 m, 03:00 h mean zon. 31.66 ± 2.69 m and 04:00 h mean zon. 29.16 ± 3.27 m; second night: 21:00 h mean zon. 40.55 ± 4.58 m compared with 03:00 h mean zon. 29.54 ± 4.62 m; total nights: 21:00 h mean zon. 41.04 ± 3.55 m compared with 24:00 h mean zon. 32.84 ± 2.57 m, 02:00 h mean zon. 29.14 ± 1.87 m, 03:00 h mean zon. 31.05 ± 2.23 m and 04:00 h mean zon. 29.66 ± 2.87 m).

During the first night of neap tide (Fig. 6d) the differences observed in the hourly mean zonation were never significant. Instead, during the second night (Fig. 6e), the hourly mean zonation in the first part of the night (21:00-24:00 h) was significantly more landwards than in the second part (01:00-03:00 h) (21:00 h mean zon. 39.50 ± 2.41 m, 22:00 h mean zon. 40.97 ± 2.45 m, 23:00 h mean zon. 40.47 ± 2.94 m, 24:00 h mean zon. 40.26 ± 3.44 m compared with 01:00 h mean zon. 47.17 ± 4.05 m, 02:00 h mean zon. 47.71 ± 3.55 m, 03:00 h mean zon. 48.97 ± 5.14 m). Cumulating the hourly mean zonations of the two nights of neap tide no significant differences were found in the different hours of the night (Fig. 6f).

During spring tide the mean hour of activity of *E. complanata* was calculated for each of the eight traps (Fig. 7). Trap 1 (the closest to the dune's base) presented a mean

hour of activity that occurred later on in the night with regards to all the other traps and trap 2 with regards to traps 4 and 5. All these delays were significant (trap 1 mean hour of capture, abbreviated m. h., $00:36 \pm 12$ min., trap 2 m. h. $23:54 \pm 16$ min., trap 3 m. h. $23:12 \pm 30$ min., trap 4 m. h. $22:32 \pm 42$ min., trap 5 m. h. $22:00 \pm 51$ min.). Note that traps 6, 7, 8 never captured surface active animals. During neap tide (Fig. 7) the mean hour of activity calculated for traps 2 and 3 was anticipated significantly compared to traps 1, 4, 5. Trap 7 and 8 were active later on in the night because of the tidal phase and resulted with a delayed mean hour of activity. (trap 1 mean hour of capture $23:25 \pm 16$ min., trap 2 m. h. $22:41 \pm 12$ min., trap 3 m. h. $22:41 \pm 12$ min., trap 4 m. h. $23:21 \pm 17$ min., trap 5 m. h. $23:07 \pm 13$ min., trap 7 m. h. $02:06 \pm 46$ min., trap 8 m. h. $02:30 \pm 40$ min.).

Autumn season

In October 1992 the total mean zonations of *E. complanata* were calculated during the nights of spring and neap tides. At spring tide this was 31.41 ± 7.23 m from the base of the dune and at neap tide 34.43 ± 2.65 m. In this case the differences were not significant.

Analysing the hourly mean zonation during spring tide (Fig. 8) here again during the first two hours of activity (20:00 h and 21:00 h) *E. complanata* had a more seawards mean zonation with regards to 01:00 h and 02:00 h (20:00 h mean zon. 46.90 ± 6.18 m, 21:00 h mean zon. 42 ± 6.16 m compared to 01:00 h mean zon. 21.42 ± 11.24 m and 02:00 h mean zon. 20 ± 7.74 m). No significant variations in the hourly mean zonation were found during the two nights of neap tide (Fig. 8).

When the mean hour of activity of *E. complanata* was calculated for each trap at spring tide traps 5 and 6 (closer to the sea) were temporally anticipated with regards to trap 1 (trap 1 mean hour of capture $23:29 \pm 79$ min., trap 5 m. r. $21:17 \pm 49$ min., trap 6 m. h. $21:17 \pm 30$ min.).

Directional variation of daily movements

Spring season

Orientation indexes calculate through circular statistic analysis during the first night of

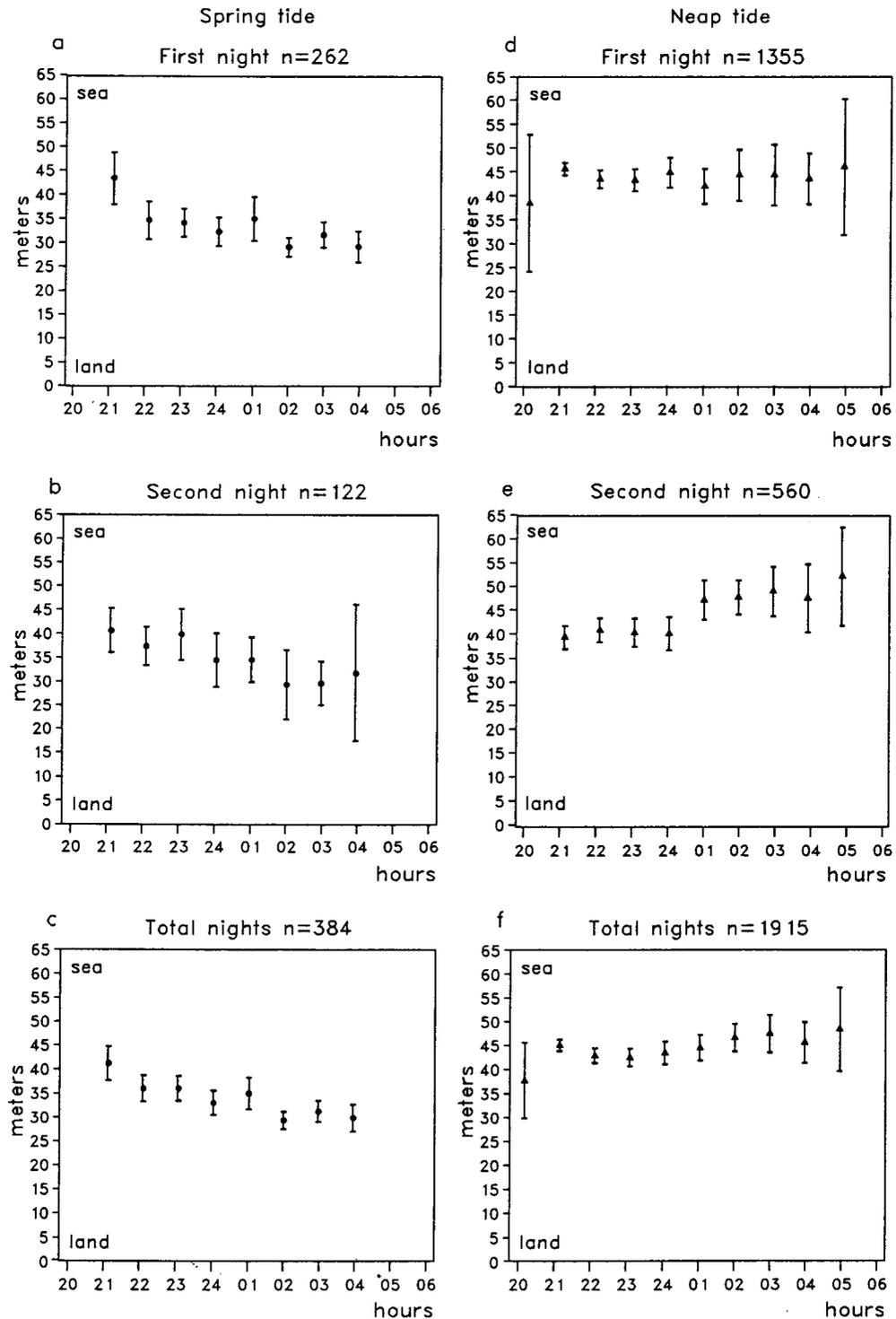


Fig. 6: Hourly mean zonation of the French population of *E. complanata* during spring season 1994. The zonation of the surface activity during the nocturnal hours is shown at spring (a-c) and neap (d-f) tides. Confidence limits (95%) are indicated. In all cases the meters are calculated from the dune's base.

Zonación horaria media de la población francesa de *E. complanata* en la primavera de 1994. Se muestra la zonación de la actividad sobre la superficie durante las horas nocturnas de mareas de sicigia (a-c) y cuadratura (d-f). Se muestran los límites de confianza al 95%. En a-c los metros se indican desde la base de la duna. En todos los casos los metros fueron medidos desde la base de la duna.

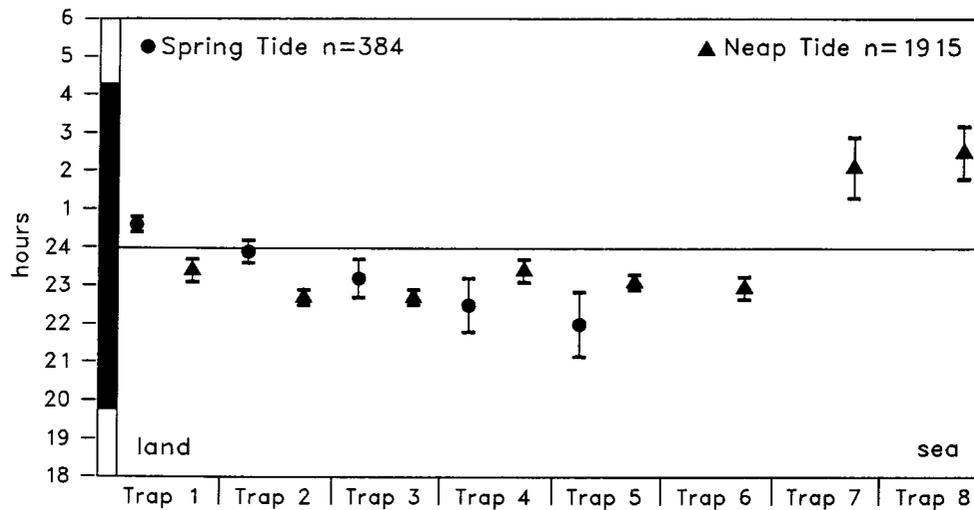


Fig. 7: Mean hour of capture frequency calculated for each trap for the French population of *E. complanata* during spring season 1994. Confidence limits (95%) are shown.

Hora promedio de captura calculada para cada trampa usada para la población francesa de *E. complanata* durante la primavera de 1994. Se muestran los límites de confianza al 95%.

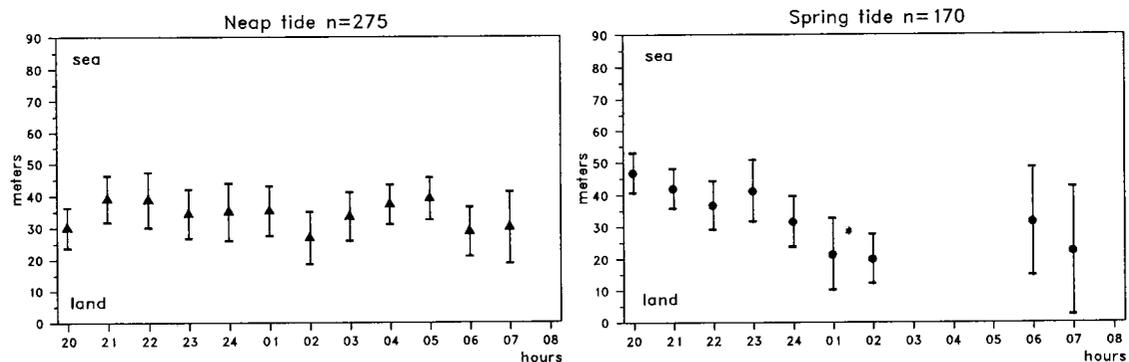


Fig. 8: Hourly mean zonation of the French population of *E. complanata* during autumn season 1994. For further explanations see Fig. 6.

Zonación media horaria de la población francesa de *E. complanata* durante el otoño de 1994. Para mayores explicaciones ver Fig. 6.

spring tide (Fig. 9a) showed significant seaward movements only at 21:00 h ($p < 0.05$). Instead from 22:00 h to 01:00 h significant oriented movements were obtained towards N (Fig. 9b) (i.e. parallel to the shoreline). During the second night (Fig. 9c) a significant seaward tendency was registered at 21:00 h and at 22:00 h. No significant directional movements were obtained at 23:00 h, whereas at 24:00 h and 01:00 h significant movements were found towards N (Fig. 9d). In the latter case these were more significant ($p < 0.0025$) than those found towards sea ($p < 0.05$). At 03:00 h significant

seaward movements were again detected. Similar movements were registered even when the two night of spring tide were cumulated (Fig. 9e, f).

During the first night of neap tide (Fig. 10a) significant seaward movements were recorded at 21:00 h, while significant landward movements were registered at 22:00 h and 24:00 h. Significant movements parallel to the shoreline were obtained from 22:00 h to 24:00 h and at 4:00 h (Fig. 10b). At 05:00 h (Fig. 10a) there were again significant movements towards sea. During the second night of neap tide (Fig. 10c) orientation

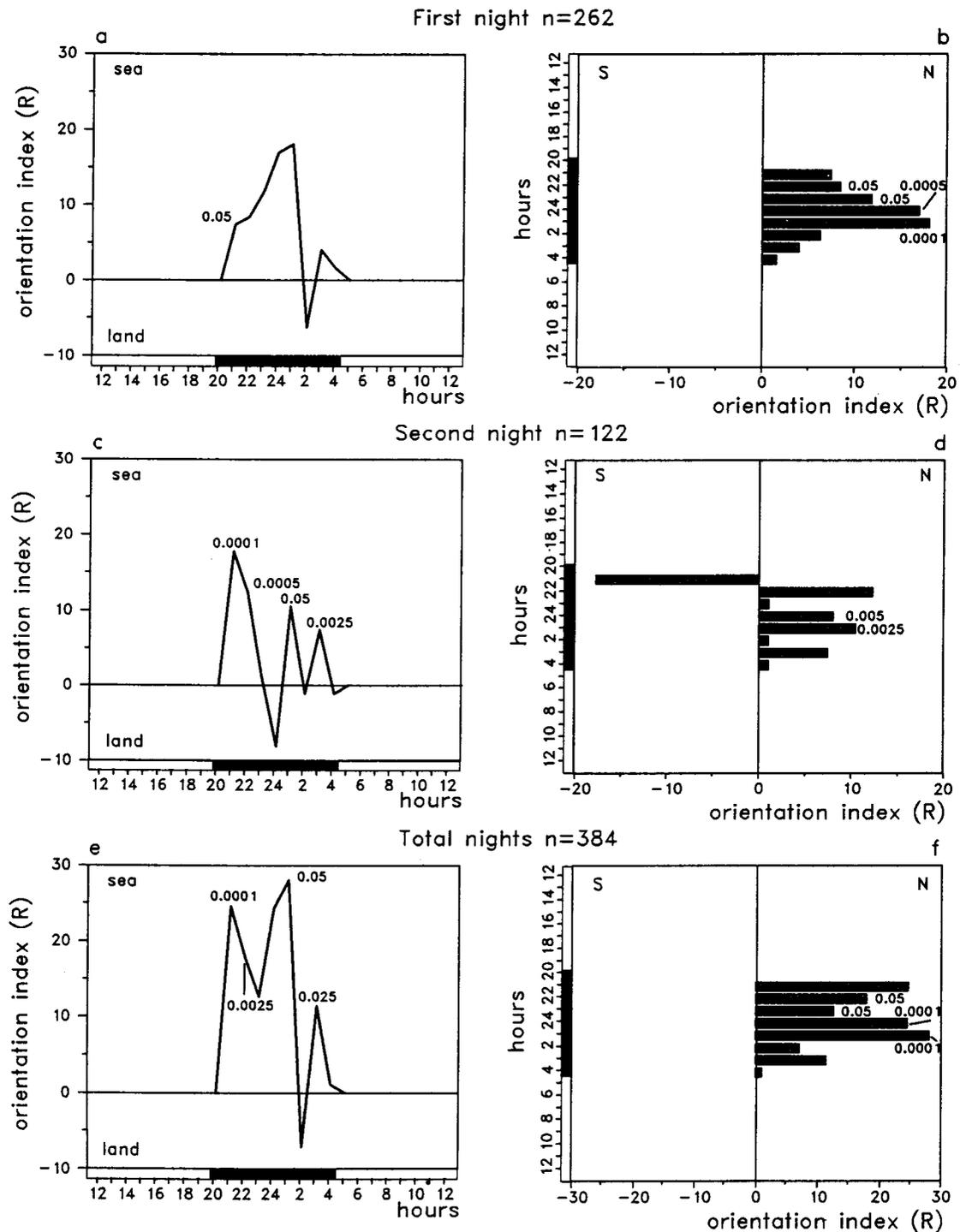


Fig. 9: Orientation indexes (R) of the French population of *E. complanata* during the spring tide of the spring season 1994. In a, c and e the seaward and landward movements are shown. In b, d and f the orientation indexes are calculated along the N-S axis. Only significant levels of $p < 0.05$ are indicated.

Indices de orientación (R) de la población francesa de *E. complanata* durante la marea de sicigia de la primavera de 1994. En a, c y e se muestran los movimientos hacia el mar y hacia tierra. En b, d y f los índices de orientación se calcularon a lo largo del eje N-S. Sólo se indican los valores significativos a $p < 0.05$.

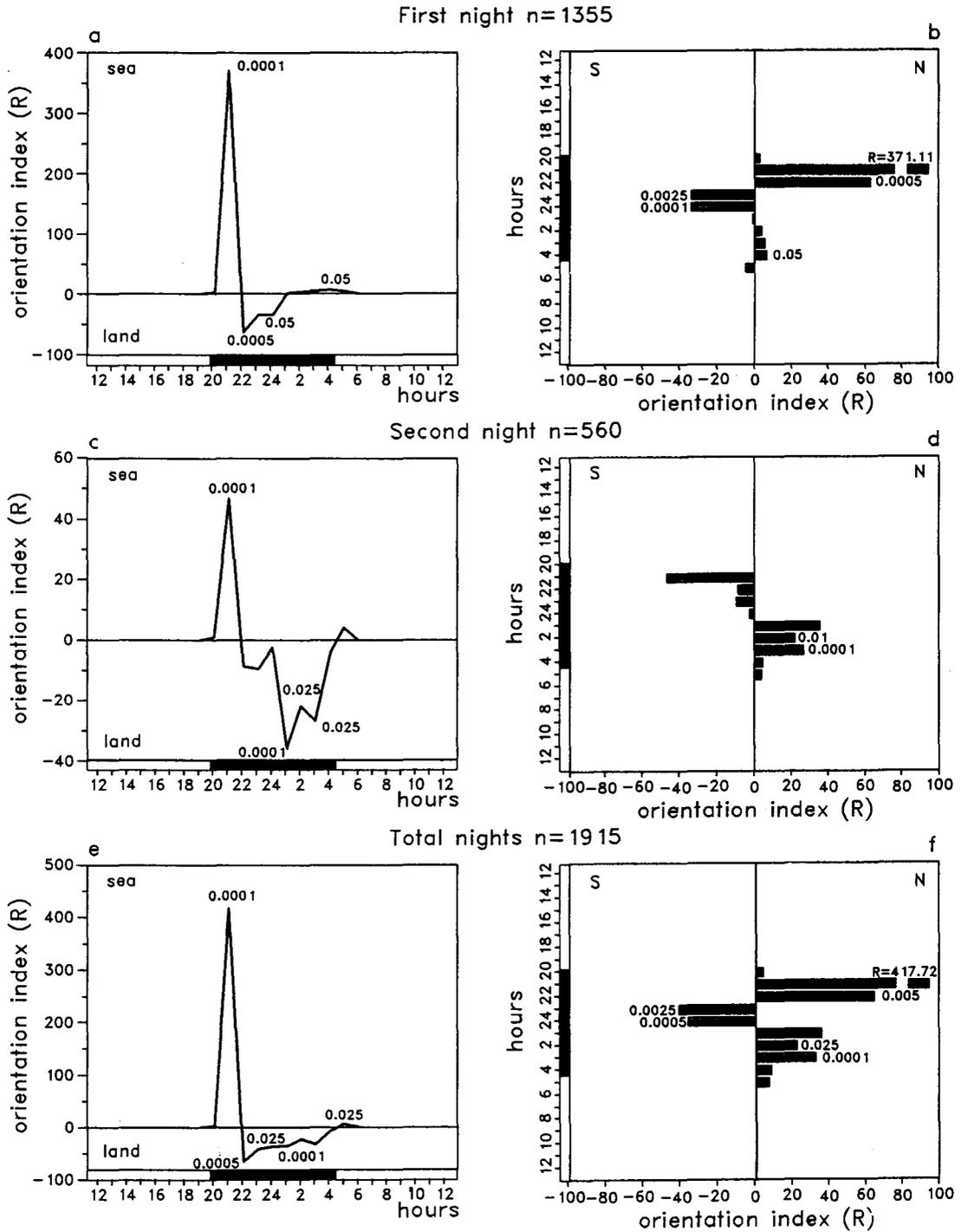


Fig. 10: Orientation indexes (R) of the French population of *E. complanata* during neap tide of spring season 1994. For further explanations see Fig. 9.

Indices de orientación (R) de la población francesa de *E. complanata* durante la marea de cuadratura de la primavera de 1994. Para mayores explicaciones ver Fig. 9.

indexes were significant towards sea at 21:00 h and towards land at 01:00 h, 02:00 h, 03:00 h. In the latter two hours significant movements towards N were also registered (Fig. 10d). Pooling the data from the two nights of neap tide (Fig. 10e, f) similar movements (first seawards then landwards and again towards sea) were obtained.

Autumn season

In October 1992 the data of the two nights around spring tide were pooled and the orientation indexes were calculated (Fig. 11). Significant seaward movements were registered at 20:00 h and these were followed by significant landward ones at 21:00 h, 22:00 h, 24:00 h and 01:00 h. Movements parallel to the shoreline were registered at 20:00 h, 22:00 h, 01:00 h, 02:00 h but these had probability levels inferior to those of the perpendicular movements, except at 02:00 h when the opposite occurred. The pooled data obtained in the two nights of neap tide never showed significant orientation indexes (Fig. 11) along the sea-land axis. Instead, significant parallel movements were registered at 02:00 h and 04:00 h (orientation indexes $p < 0.0025$ and $p < 0.025$).

Analysis of the data in tidal hours

During the experiments of spring 1994 the nocturnal low tide (LT) was at 22:38 h and at 00:06 h in the first and second night re-

spectively. The frequency distribution of captures for the two nights pooled (Fig. 12a) was significantly different from random and did not differ from the expected time of activity (LT during spring tide see Rayleigh test and V test). The mean hour of activity was in fact 6 h 34 min. after high tide (HT). Significant orientation indexes were obtained towards sea at Hour 3 and Hour 4 (Fig. 12b). Significant movements towards N, parallel to the sea were registered around LT i.e. from Hour 5 to Hour 8 (Fig. 12c). This was especially true for the traps higher up on the eulittoral. The hourly mean zonation (Fig. 12d) of the beetle's activity calculated in tidal hours was significantly more towards sea at ebbing tide than both LT and during the rising tide (Hour 3 mean zon. 40.55 ± 4.58 m, Hour 4 mean zon. 40.29 ± 3.35 m compared at LT mean zon. 34.21 ± 2.53 m, Hour 7 mean zon. 32.91 ± 2.46 m, Hour 9 mean zon. 29.22 ± 1.75 m, Hour 10 mean zon. 31.66 ± 2.47 m, Hour 11 mean zon. 29.16 ± 3.27 m).

During the two nights of neap tide the nocturnal HT was at 21:34 h and 22:35 h in the first and second night respectively. Circular statistic analysis showed that the frequency distribution of captures was significantly different from uniform and that the mean hour of tidal activity was 27 min. after HT (Fig. 13a). Orientation indexes calculated in tidal hours showed significant landward movements at HT and at Hour 2 and seaward movements at Hour 7, Hour 10 and Hour 11

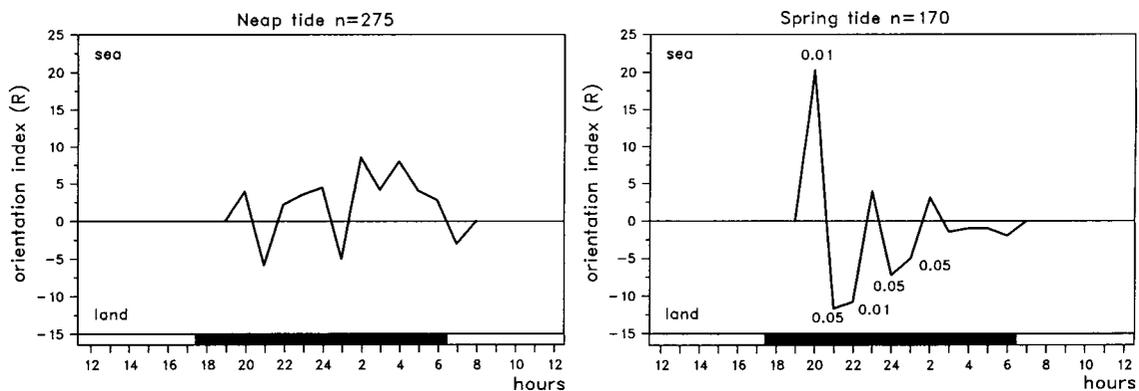


Fig. 11: Orientation indexes (R) along the sea-land axis of the French population of *E. complanata* during neap and spring tide of autumn season 1992. For further explanations see Fig. 9.

Indice de orientación (R) a lo largo del eje mar-tierra de la población francesa de *E. complanata* durante la marea de cuadratura del otoño de 1992. Para mayores explicaciones ver Fig. 9.

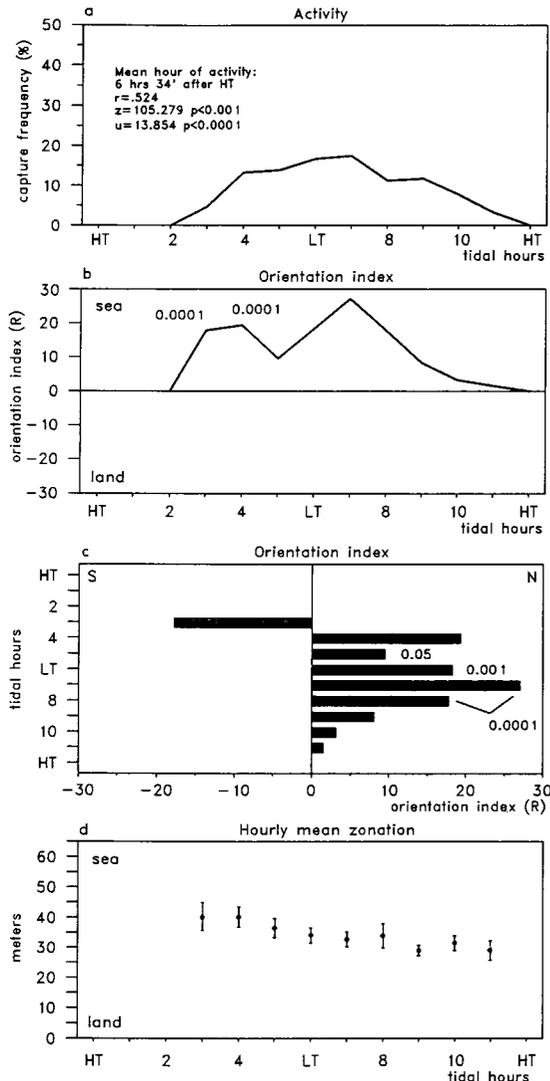


Fig. 12: Surface activity (a), orientation indexes (R) along the sea-land (b) and N-S axis (c) and hourly mean zonation (d) calculated in tidal hours of the French population of *E. complanata* during spring tide of spring season 1994. Significant probability levels and confidence limits (95%) are indicated. Mean hour of activity calculated through circular statistic analysis (Rayleigh test and V test) are also shown.

Actividad sobre la superficie (a), índices de orientación (R) a lo largo del eje mar-tierra (b) y eje N-S axis (c) y zonación horaria promedio (d) calculada en horas mareales de la población francesa de *E. complanata* durante la marea de sicigia de la primavera de 1994. Se indican niveles significativos de probabilidad y límites de confianza (95%). Hora promedio de actividad calculada mediante estadística circular (test de Rayleigh y test V).

i.e. during the rising tide (Fig. 13b). Furthermore around HT and at ebbing tide significant movements along the N-S axis were registered (Fig. 13c). The hourly mean zonation of *E. complanata* in the different tidal hours was never significantly different (Fig. 13d).

The comparison made between the mean hours of activity calculated in daily and in tidal hours (Fig. 14) indicates that the daily mean vector is always greater than the tidal one both during spring and neap tides.

Also in the experiments of Autumn 1992 the beetle's activity was calculated in tidal hours. During the two nights of spring tide the frequency distribution of captures was significantly different from random and did not differ from the expected time of activity (LT) (see Rayleigh test and V test) (Fig. 15d). The mean hour of activity was 3 h 58 min. after HT. Orientation indexes were significant towards sea at Hour 2 and towards land at Hour 1, Hour 4 and LT (Fig. 15e). Significant orientation indexes for the N-S direction were obtained only in one case: Hour 9 ($p < 0.05$).

During the two nights of neap tide the frequency distribution of captures differed from uniform (see Rayleigh test) and was not significantly concentrated around the expected time (HT) (see V test) (Fig. 15a). The mean hour of activity was 2 h 19 min. after HT. During neap tide significant movements along the sea-land axis were found towards land at HT and Hour 5 and towards sea at LT (Fig. 15b). Only at HT and Hour 1 significant movement towards N were registered (orientation index HT $p < 0.05$, Hour 1 $p < 0.01$).

The hourly mean zonations in tidal hours during neap tide were never significantly different from each one another (Fig. 15c) whereas at spring tide (Fig. 15f) the mean zonations at Hour 3, Hour 4 and Hour 5 were significantly towards sea in comparison to the mean zonations registered during the rising tide at Hour 8 and Hour 9 (Hour 3 mean zon. 44.44 ± 6.89 m; Hour 4 mean zon. 43.03 ± 6.73 m and Hour 5 mean zon. 41.73 ± 8.31 m compared with Hour 8 mean zon. 21.11 ± 8.1 m and Hour 9 mean zon. 16.66 ± 10.84 m).

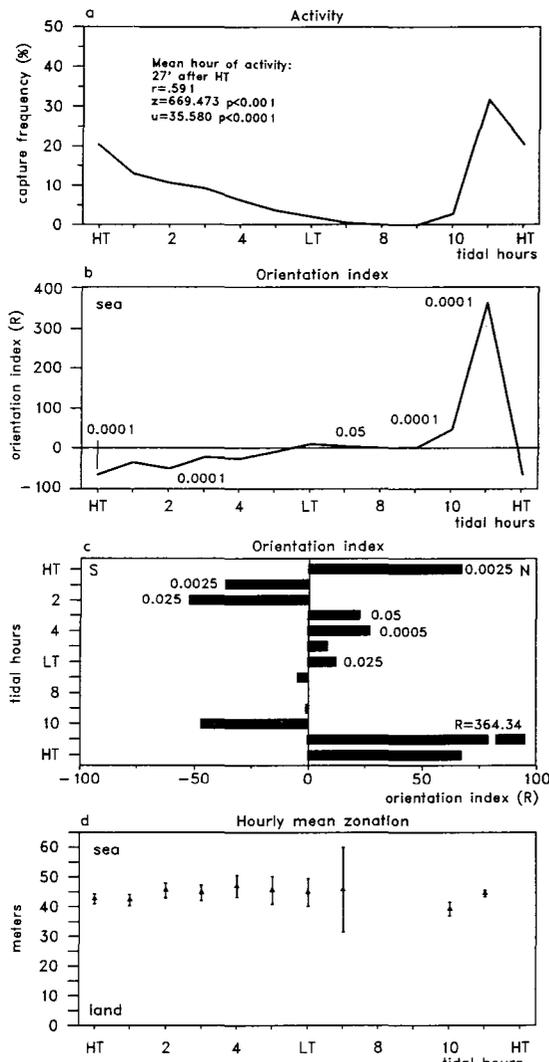


Fig. 13: Surface activity (a), orientation indexes (R) along the sea-land (b) and N-S axis (c) and hourly mean zonation (d) calculated in tidal hours for the French population of *E. complanata* during neap tide of spring season 1994. For further explanations see Fig. 12.

Actividad sobre la superficie (a), índices de orientación (R) a lo largo del eje mar-tierra (b) y eje N-S axis (c) y zonación horaria promedio (d) calculada en horas mareales de la población francesa de *E. complanata* durante la marea de cuadratura de la primavera de 1994. Para mayores explicaciones ver Fig. 12.

Environmental factors influencing the daily activity and zonation

Spring season 1994

During the first night of spring tide a mean temperature of 23.3° C (maximum 26° C and minimum 20.5° C) and a mean relative

humidity of 64% (maximum 68%, minimum 51%) were registered. During the second night the mean temperature was 16.2° C (maximum 17° C, minimum 15.5° C) whereas the mean relative humidity was 74.9% (maximum 78%, minimum 73%). The atmospheric pressure during the first night regularly decreased varying from 758 mm Hg at the beginning to 755 mm Hg at the end of the night. During the second night the atmospheric pressure had an increasing tendency from 759 mm to 762 mm Hg.

Through multiple regression analysis the activity of *E. complanata* was correlated to different environmental parameters. This was done using the data obtained in the first and second day of spring (24 h) and considering the two night periods (10 h) (Table 5). The results of the multiple regression showed a lower coefficient of determination when a smaller number of hours were considered. During the first 24 hours of spring tide the activity of *E. complanata* was positively correlated with the constant, the sand temperature measured at the resting site and with the prey presence. A negative correlation was found with sand temperature under the surface towards sea, tidal level and with the atmospheric pressure. Instead during the second night a positive correlation was found only with the presence of prey. Considering only the night period (10 h) during the first night a negative correlation was found with the surface sand temperature towards sea, the tidal level and with the atmospheric pressure, whereas a positive one was obtained with the constant and the prey presence. During the second night there was a positive correlation with the constant. A negative correlation was instead found with tidal level and atmospheric pressure.

During the first night of neap tide a mean air temperature of 19.1° C (20° C maximum, 18.5 minimum) and a mean R.H. of 74.55% (maximum 83%, minimum 71%) was registered. Atmospheric pressure ranged from 757 mm Hg to 758 mm Hg. During the second night the mean air temperature and mean relative humidity were 15.8° C (maximum 18° C, minimum 13.5° C) and 78.8% (maximum 80%, minimum 78%) respectively. Atmospheric pressure decrease from 758 mm Hg to 757 mm Hg.

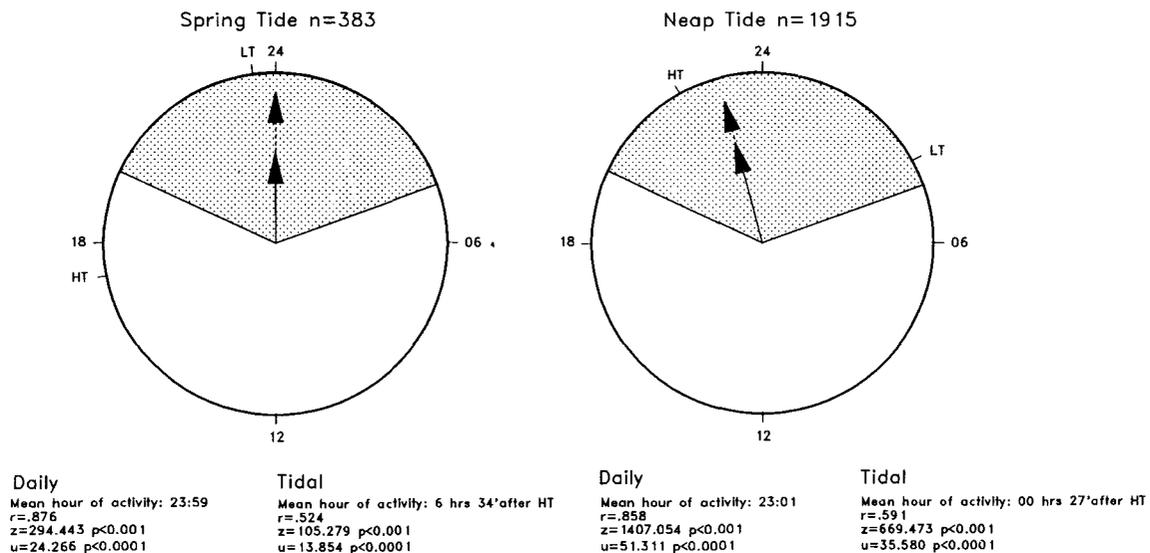


Fig. 14: Mean hour of activity of the French population of *E. complanata* during spring and neap tide of spring season 1994. The mean hours of activity are calculated both in daily and tidal hours through circular statistic analysis (Rayleigh test, V test). The dotted area indicates the period of dark. HT and LT are also shown as means of the two days of field experiments. The dotted arrows indicate the vector length of the daily mean hour of activity whereas the full arrows that of the mean hour of activity in tidal hours.

Hora promedio de actividad de la población francesa de *E. complanata* durante la marea de sicigia y cuadratura de la primavera de 1994. Las horas medias de actividad se calcularon en base a horas diarias y mareales mediante estadística circular (test de Rayleigh y test V). El área punteada indica el período de oscuridad. HT y LT se muestran como promedios de dos días de experimentos de terreno. Las flechas punteadas indican la longitud del vector de la hora promedio de actividad diaria mientras que las flechas enteras muestran la hora promedio de actividad en horas mareales.

Multiple regression analysis carried out during neap tide, both in a 24 h and 10 h, again showed that the coefficient of determination decreased when a lower number of hours was considered (Table 5). During the first 24 hours of neap tide the activity of the beetles was positively correlated with the constant and with the tidal level. A negative correlation was instead found with air temperature and relative humidity. During the second 24 h period of neap tide the beetle's activity was positively correlated with tidal level, atmospheric pressure and prey presence. A negative correlation was found with the constant and with air temperature. Analysing the 10 h periods in the first and second night when sand humidity was recorded, the atmospheric pressure was significantly correlated positively in both cases. In the first case a negative correlation was also found with the air temperature. Furthermore during the second night the activity of the beetle was correlated negatively with the constant and positively with the prey presence. During spring tide the hourly mean

zonation of the beetle's activity was correlated with different environmental parameters through multiple regression analysis (Table 4). The results suggest that at spring tide the zonation pattern of *E. complanata* is regulated by air temperature and R.H., with which there is a negative correlation and with atmospheric pressure with which it is positively correlated. In this case, a high coefficient of determination ($R^2 = 0.9926$) was found. At neap tide the beetle's hourly mean zonation was correlated negatively with the surface sand temperature near sea, the sand moisture of the areas closer to the sea (sea, center) and positively with the constant and the sand moisture near land. Here the coefficient of the determination was 0.6237.

Autumn season 1992

In this period only the air temperature and R.H. were registered. The beetle's activity during the two nights of field experiments of spring tide was correlated positively with air

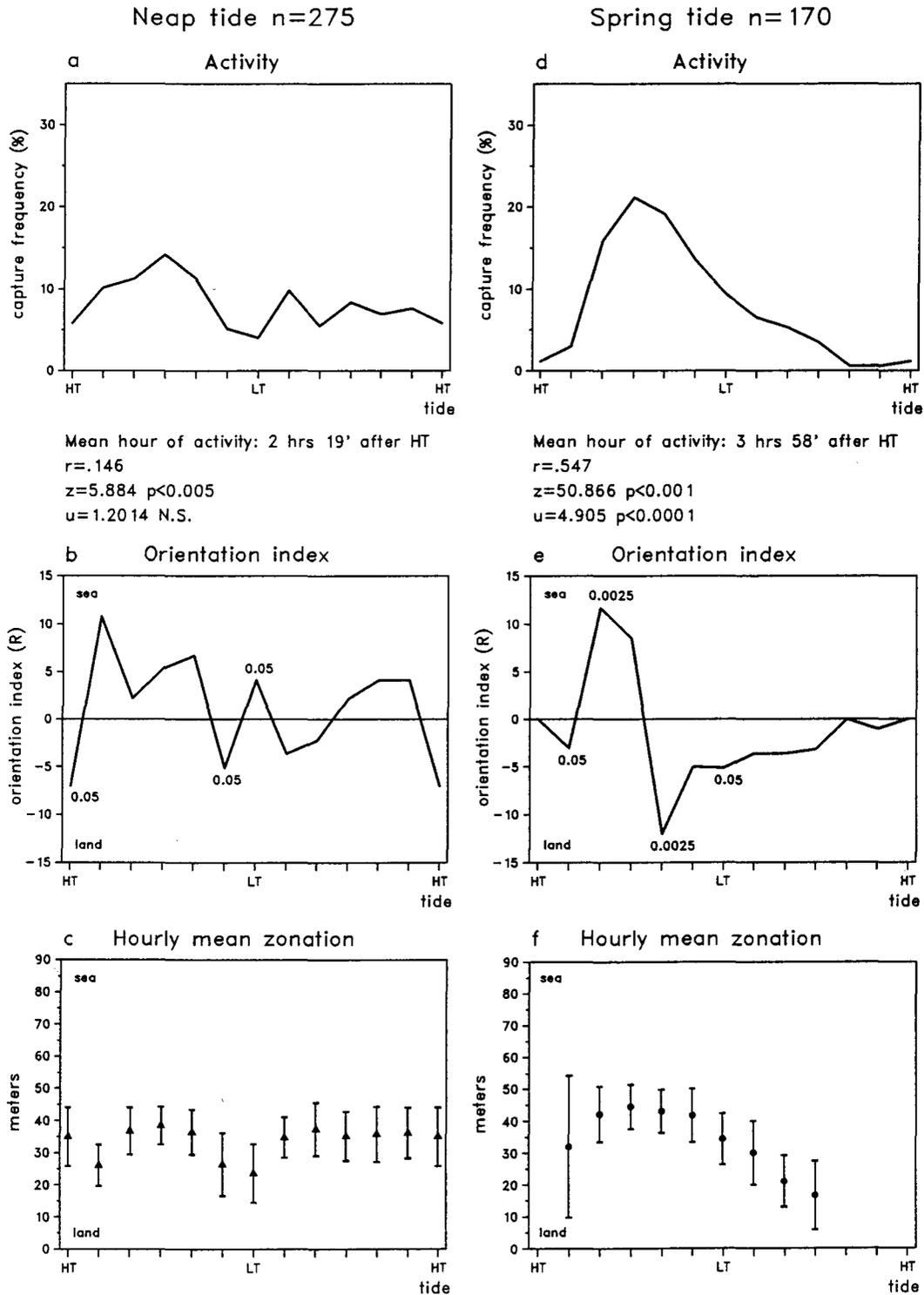


Fig. 15: Surface activity (a, d), orientation indexes (R) along the sea-land axis (b, e) and hourly mean zonation (c, f) calculated in tidal hours for the French population of *E. complanata* during spring (a-c) and neap (d-f) tide of autumn season 1992. For further explanations see Fig. 12.

Actividad sobre la superficie (a,d), índices de orientación (R) a lo largo del eje mar-tierra (b,e) y zonación horaria promedio (c,f) calculada en horas mareales para la población francesa de *E. complanata* durante la marea de sicigia (a-c) y de cuadratura (d-f) del otoño de 1992. Para mayores explicaciones ver Fig. 12.

temperature and with tidal level and negatively with relative humidity (Table 5). The temperatures in the first part of the first night ranged from 12° C to 11° C, whereas in the second part temperatures were below 10° C. Relative humidity had a minimum of 83.9% but during most of the night they were above 90%. Also during the second night temperatures below 10° C were registered in the second part of the night. Relative humidity were above 82.4%.

During neap tide the activity of *E. complanata* was correlated positively only with the tidal level (Table 5). During the two nights of neap night temperature were never below 11° C. Relative humidity, except for the first part of the first night, were always above 83.3%.

When the hourly mean zonation of *E. complanata*'s activity at spring tide was correlated with air temperatures and R.H. a positive and negative correlation was found respectively for each parameter ($R^2 = 0.9328$) (Table 4). During neap tide the mean hour zonation of the beetle's activity was never significantly correlated with the three environmental parameters tested.

DISCUSSION

The data here reported on the surface activity of *E. complanata* give interesting results on the behavioural strategies employed by two different populations subjected to different environmental conditions. Clearly this spe-

TABLE 5

Multiple regression analysis of surface activity for the French population of *E. complanata* with environmental parameters (air temperature, relative humidity, surface sand temperatures near sea and land, temperature under diurnal shelter, tidal levels, sand moistures near sea and land, atmospheric pressure, prey presence). For further explanations see Table 2

Análisis de regresión múltiple de la actividad sobre la superficie de la población francesa de *E. complanata* con parámetros ambientales (temperatura del aire, humedad relativa, temperatura superficial de la arena cerca del mar y la tierra, temperatura diurna a la sombra, niveles mareales, humedad de la arena cerca del mar y la tierra, presión atmosférica, presencia de presa). Para mayores explicaciones ver Tabla 2

Date	Constant	air temp. °C	air R.H. %	temp. surf. sand sea °C	temp. surf. sand land °C	temp. under shelter °C	tidal levels m	sand moist. sea %	sand moist. land %	pressure mm Hg	talitrids	R ²
Spring Season 1994												
Spring tide												
First night (24 h)	3442.527 P=0.0315	N.S.	N.S.	-1.860 P<0.0001	N.S.	3.6522 P=0.0029	-8.0697 P<0.001	/	/	-4.5577 P=0.0301	0.0036 P=0.0413	0.8570
Second night (24 h)	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	/	/	N.S.	0.0057 P<0.0001	0.7653
First night (10 h)	5716.503 P=0.0027	N.S.	N.S.	-1.4530 P=0.0051	N.S.	/	-8.4980 P=0.0003	N.S.	N.S.	-7.4748 P=0.0029	0.0073 P=0.002	0.7750
Second night (10 h)	2877.825 P=0.0002	N.S.	N.S.	N.S.	N.S.	/	-5.0771 P=0.0001	N.S.	N.S.	-3.7576 P=0.0002	N.S.	0.5482
Neap tide												
First night (24 h)	1187.319 P=0.0089	-24.4850 P=0.0019	-11.4271 P=0.0083	N.S.	N.S.	N.S.	78.1321 P=0.0093	/	/	N.S.	N.S.	0.4078
Second night (24 h)	-1.0877 P=0.0059	-2.6498 P=0.0006	N.S.	N.S.	N.S.	N.S.	27.1440 P=0.0001	/	/	14.3333 P=0.0059	0.0371 P=0.0004	0.8095
First night (10 h)	N.S. P=0.0469	-9.7222	N.S.	N.S.	/	/	N.S.	N.S.	N.S.	0.3767 P=0.0176	N.S.	0.2878
Second night (10 h)	-1.5003 P=0.0092	N.S.	N.S.	N.S.	/	/	/	N.S.	N.S.	19.8035 P=0.0092	0.0577 P<0.001	0.5557
Autumn Season 1992												
Spring tide	N.S.	5.0867 P<0.0001	-0.5785 P<0.0001	/	/	/	2.3223 P=0.0189	/	/	/	/	0.8832

cies has adapted to particular ecological constraints such as presence or absence of large tidal excursions due to the synodic and tidal cycles or to different trends in microclimatic factors. Furthermore, the results indicate how the same population is capable of modulating its behaviour in relation to the current microclimatic conditions.

The particular instability of sandy beach environments induces continuous or sudden changes to which the beetle actively responds both during the resting and active period of the day. A previous study (Colombini 1989, Colombini & Chelazzi 1991) showed that with changes in the season the beetle varied its resting site and searched suitable shelters closer or farther away from the sea according to the current microclimatic conditions. Other behavioural strategies employed by *E. complanata* included the capacity of varying the surface activity both in space and in time.

It had been demonstrated that during summer months Atlantic populations never interrupted their nocturnal surface activity (Caussanel 1965, Rudolph 1970, King & Stabins 1971) whereas Mediterranean populations did (Colombini & Chelazzi 1991). Since *E. complanata* during daytime rests under driftwood or other jetsam stranded on the high eulittoral, during its period of activity the beetle leaves its shelters and moves to the trophic zone near the shoreline limits. Through capture-recapture methods of individual animals, field observations indicated that not all animals leave their shelters every night (Colombini 1989). In the Italian population this occurred more frequently when the beetles were close to their period of summer aestivation. The low capture frequency obtained for the experiments of May-June 1994 are due to this fact. The beetle's surface activity is strictly nocturnal as demonstrated by circular statistic analysis (Rayleigh test) except in autumn when the activity ceased after dawn as demonstrated in the French population. In this case the onset of surface activity appeared some hours after dusk. Furthermore, in days with long periods of darkness (autumn-winter) the beetle's activity can decrease around midnight and its distribution can present two peaks. The first is associated to an emergence of beetles from the shelters

of the high eulittoral and to their movements towards the low eulittoral in search of prey. Orientation indexes in fact demonstrated significant seaward movements. The morning peak is again due to predator activity but it is probably also caused by an active search for suitable shelters.

During nights with shorter periods of darkness (for example in France at the end of June) the distribution of the capture frequency is unimodal and concentrated around midnight as demonstrated by V test. The timing and magnitude of the beetle's activity peaks varies according to weather conditions. On some occasions (May 1989-1993) the activity of the Italian population was concentrated in the second part of the night when suitable temperatures and relative humidities were reached. The opposite occurred in the French population (Autumn 1992) when the activity was concentrated in the first part of the night. This indicates that for the Italian population high temperature and low relative humidity are limiting factors that forbid surface activity. The latter in fact took place when temperatures decreased below 16°C and relative humidity increased reaching values above 70%. For the French population temperatures below 10°C registered in the second part of the night of spring tide 1992 totally suppressed the beetles activity. Preliminary laboratory experiments of temperature preferences showed that *E. complanata* definitely prefers mean temperatures of 16.2°C and 12.9°C respectively in the Italian and French population (Colombini 1989). In spring season of 1994 during the first night of neap tide there was a sharp decrease of the activity after the first hours of activity. This was not due to adverse climatic conditions but to a high concentration of animals in the study area caused by the mechanical beach cleaning activities to the north and south of the study site that were in progress in those days. Multiple regression analysis confirmed the strict relationship between the activity of *E. complanata* with air temperatures. In fact a negative correlation was found with this parameter when temperatures were high (experiment May 1989, 1993 in Italy) and a positive one was obtained when temperatures were low (experiment spring tide 1992). This indicates

that *E. complanata* presents certain thresholds limiting surface activity.

The correlation of the beetle's activity with the relative humidity was always negative (experiment spring tide France 1992, April 1994 Italy, experiment neap France 1994). In the first and second case as the relative humidity increased (values already above 80%) a decrease in the temperature was recorded and this was associated with the decrease of the activity of *E. complanata*. In the third case the negative correlation with the relative humidity was due to the great decrease of the capture frequencies in the second part of the night caused by the above explained reasons. In some case (April 1994 Italy, first night May-June 1994 Italy, experiment neap 1994 France) the atmospheric pressure was correlated positively with the activity. In other cases (first night spring tide France 1994, second night May-June Italy 1994) the correlation was negative.

During the first night of spring tide 1994 the correlation was negative due to a decrease of this parameter around midnight that corresponded to an increase of the beetle's activity. In the second case, even if the atmospheric pressure increased throughout the night, a negative correlation was obtained because the capture frequency decrease in relation to the low temperatures registered after midnight. When the capture frequency of the sandhoppers was recorded, this was included in the multiple regression analysis. For the Italian population this parameter was never significantly correlated with the beetle's activity, whereas for the French population in some cases a positive correlation was found. Also the tidal level was found to be correlated with the activity of the French population of *E. complanata*. During spring tide the negative correlation with the tidal level was due to the fact that LT occurred around midnight. Instead during neap tide the correlation was positive because in this case the HT occurred in the first part of the night.

Considering now the variations in zonation of the beetle's activity the Italian population showed a seaward zonation in the first hours of the night followed by a landward zonation in the morning hours. Since the beetle has its diurnal shelters in the high

eulittoral, the variation in the hourly mean zonation corresponded to the feeding period and to a zonal recovery of the resting sites. The absence of variations in the zonation of *E. complanata* found in May-June 1994 are explained by the fact that in this period the suitable diurnal resting sites are closer to the shoreline i.e. to the trophic zone.

In the French population, different results were obtained in the variations of zonation according to the synodic phase and season. During spring season the total mean zonation of the activity was farther down from the dune's base at neap tide when compared to spring tide. This difference was not scored in Autumn due to the fact that in this season microclimatic parameters are less stressing. Other differences were found in the hourly mean zonation. At spring tide of both seasons (spring-autumn) during the first hours of the night the beetle's activity had a more seaward zonation in comparison to the following hours. At neap tide no variations in zonation were found. This is explained considering that the trophic zone in this synodic phase is more restricted and also by the fact that the fascia of the resting sites is more distant from the base of the dune. Multiple regression analysis on the hourly mean zonation confirms that the zonation of *E. complanata* depends on certain climatic factors such as air temperature, relative humidity, atmospheric pressure, sand temperature and moisture with which the correlation differs according to the season.

As shown by the orientation indexes *E. complanata* presents daily movements along the sea-land axis. This was found to be true both for the Italian and French population. Movements towards sea were clear at the beginning of the beetle's activity and corresponded to the departure from the diurnal shelters and to movements towards the lower part of the beach where talitrids are generally found. The seaward movements were followed by landward ones that corresponded to the zonal recovery of the resting sites during the second part of the night. Statistic analysis shows that in some cases these movements can be considered real migrations. These generally appeared clear towards sea at the onset of activity whereas during the following hours not always the landward migrations

were obtained. The latter became evident in particular cases when sudden climatic changes occurred such as in the case of spring tide 1992 when low temperatures were registered. Another case is represented by the experiments of spring 1994 on the French population where only during neap tide both seaward and landward migrations were found. This is explained by the differences in the microclimatic conditions of the beach registered in the different synodic periods.

During neap tide of Autumn season 1992 no significant migrations were recorded probably because of the more uniform microclimatic conditions along the sea-land axis. Furthermore movements parallel to the shoreline were particularly evident in France and became real migrations especially around midnight. The difference in the direction of the migration (N-S) found at spring and neap tide (1994) are explained by the disturbance caused by the massive cleaning of the beach that during spring tide had been done only to the south of the study area, whereas at neap tide this had been accomplished both to the north and south. Analysing the beetle's activity in tidal hours the fact that at spring tide of spring season 1994 the activity is at LT and at neap around HT makes us believe that *E. complanata* does not possess a real tidal rhythm because in the first case LT corresponded to midnight and in the second case this correspondence was found with the HT. The same results were obtained also for autumn season. This is confirmed also by the comparison of the mean hours of activity in tidal and daily hours. In fact the daily component was more significant than the tidal one (see vector length).

But tidal and synodic phases do have an influence on *E. complanata*'s activity and this mainly regards spatial variations (see zonations) more than temporal ones. Real tidal rhythms were instead found in other arthropods (Chelazzi et al. 1983) that have mean zonations closer to the sealine limits. McLachlan (1991) affirms that near the beach and supralittoral tidal rhythms are evident whereas in true dune fauna rhythms are primarily diel.

It is concluded that *E. complanata* is a highly specialized beetle with a great plas-

ticity in behavioral adaptations that enables the species to survive in predictable and unpredictable environmental conditions.

ACKNOWLEDGMENTS

We thank the World Wildlife Fund of Italy for having given us the opportunity to work in the oasis of Burano. We also would like to thank Mr. J. P. Duval of the Office National des Forêts, Maison Forestière du Grand Piquet for his assistance during our stay at Cap Ferret.

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