Revista Chilena de Historia Natural
66: 439-454, 1993

Down-shore zonation of two cirolanid isopods during two spring - neap tidal cycles in a sandy beach of south central Chile

Zonación vertical de dos especies de isópodos cirolánidos durante dos ciclos mareales sicigia - cuadratura en una playa arenosa del centro sur de Chile

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ABSTRACT

Transect samples were obtained during the low tides of the summers of 1990 and 1991 at a dissipative sandy beach in south central Chile, to investigate spring-neap tide variability in the down-shore zonation of the cirolanid isopods *Excirolana braziliensis* Richardson and *Excirolana hirsuticauda* Menzies. Short periods of sediment accretion alternated with periods of erosion during both summers, primarily at the mid and low intertidal levels. Highest temperatures (25-30°C) were recorded in the driest sediments (0-10% water content). During both summers, *Excirolana braziliensis* had its highest abundances (2-11 ind. 0.03 m^{-2}) 136-318 cm below a bench mark in the supralittoral. This species occupied the sediments with the highest temperatures (17-24°C), the lowest water contents (5-15%), the finest (2.1-2.2 phi) and best sorted particles (0.28-0.29 phi). The highest abundances of *Excirolana hirsuticauda* (8-25 ind. 0.03 m^{-2}) occurred at lower beach levels (202-356 cm below the bench mark) where the physical characteristics (lower temperatures, higher water contents, coarser particles) differed significantly from those measured at the levels occupied by *Excirolana braziliensis* during the summer of 1990. During the summer of 1991, no significant differences were found between the physical characteristics of the sediments occupied by either isopod species. During both summer periods the vertical distribution of *Excirolana braziliensis* did not show temporal variability. The same was observed for *Excirolana hirsuticauda* during the summer of 1991; however, during the summer of 1990 the zonation of this isopod shifted throughout the spring-neap tidal cycle, particularly during the last two samples of that summer. High tide samples carried out at the sediment water interface during the summer of 1990 revealed the presence of just *Excirolana hirsuticauda*. The abundances of *Excirolana hirsuticauda* did not differ significantly between day or night or among tidal levels. Finally, laboratory experiments showed that swimming activity of both isopods lacked tidal rhythmicity.

Key words: Sandy beaches, isopods, spring-neap.

RESUMEN

Con el objetivo de investigar la variabilidad en la zonación vertical de *Excirolana braziliensis* y *Excirolana hirsuticauda* durante ciclos mareales sicigia-cuadratura se muestreó durante los períodos de marea baja en los veranos de 1990 y 1991 en una playa arenosa disipativa en el centro-sur de Chile. Se observó alternancia de cortos períodos de acreción y erosión de arena durante ambos períodos, primariamente en niveles intermareales medios e inferiores. Las temperaturas más altas (25-30°C) se registraron en los sedimentos más secos (contenido de agua: 0-10%). Durante ambos veranos, *Excirolana braziliensis* mostró abundancias más altas (2-11 ind. 0,03 m^{-2}) 136-318 cm bajo un nivel de referencia ubicado en el supralitoral. Esta especie ocurrió en sedimentos con las temperaturas más altas (17-24°C), los contenidos de agua más bajos (5-15%), y las partículas más finas (2,1-2,2 phi) y mejor sorteadas (0,28-0,29 phi). Las mayores abundancias de *Excirolana hirsuticauda* (8-25 ind. 0,03 m^{-2}) ocurrieron en niveles mareales más bajos de la playa (202-356 cm bajo el nivel de referencia) donde las características físicas (temperaturas más bajas, contenidos de agua más altos, partículas más gruesas) fueron significativamente diferentes a aquellas medidas en los niveles ocupados por *Excirolana braziliensis* durante el verano de 1990. Durante el verano de 1991 no se detectaron diferencias significativas entre las características físicas de los sedimentos ocupados por ambos isópodos. Durante ambos veranos la distribución vertical de *Excirolana braziliensis* no mostró variabilidad temporal, situación similar observada para *Excirolana hirsuticauda* durante el verano de 1991. Sin embargo, durante el verano de 1990 la zonación de este isópodo varió durante el ciclo mareal sicigia-cuadratura, particularmente durante los dos últimos muestreos de ese verano. Muestreos realizados durante el verano de 1990 en la interfase agua-sedimento ydurante períodos de marea alta, evidenciaron la presencia de sólo *Excirolana hirsuticauda*. Las abundancias de esta especie no variaron significativamente entre muestreos ciurnos y nocturnos; tampoco entre niveles mareales. Finalmente, experimentos de laboratorio mostraron que la actividad natatoria de ambos isópodos no tuvo ritmicidad mareal.

Palabras claves: Playas arenosas, isópodos, sicigia-cuadratura.

INTRODUCTION

The distribution of amphipods and isopods in relation to different tidal levels is one of the most distinctive characteristic of exposed sandy beaches and several zonation schemes have been proposed for beaches located in different geographic areas (Dahl 1952,

(Recibido el 1 de diciembre de 1992; aceptado el 27 de abril de 1993.)

Trevallion *et al.* 1970, McLachlan *et al.* 1980). In such schemes, talitrid amphipods are typical macroinfaunal organisms of the upper shore levels, whereas cirolanid isopods are mainly distributed in the mid shore (Dahl 1952, Castilla & Mena 1977, Scofer *et al.* 1979, Jaramillo 1987). However, the location of these zones changes temporally, either seasonally (Jaramillo 1987) or during the neap-spring tidal cycles (Fish 1970, Jones & Naylor 1970, Klapow 1972).

Seasonal changes in the zonation patterns have been discussed in relation to temporal variability in temperature and water content of the sediments. Salvat (1966) and Fish (1970) found that in the sandy beaches of France and Wales, respectively, the abundance of the isopod *Excirolana pulchra* Leach decreased at the upper reaches of its distribution during summer. Jaramillo (1987) observed that during the warmer months, the talitrid amphipods and cirolanid isopods of exposed sandy beaches of south central Chile moved toward lower intertidal levels than those previously occupied during the colder months. On the other hand, Jones (1970) observed that in sandy beaches of the south of Wales, the cirolanid isopods *Eurydice pulchra* and *Eurydice affinis* H.J. Hansen, escaped from extreme winter temperatures by moving from intertidal to subtidal levels.

The intertidal distribution of peracarids also changes through the neap-spring tidal cycles (Fish 1970, Fish & Fish 1972, Alheit & Naylor 1976). For example, Fish (1970) observed that from a neap to a full spring tide the population abundance of *Eurydice pulchra* above the level of mean high water neap tide increased and the distribution of the animals shifted upwards. Thus, during neap tides about 3% of the total number of animals collected were above the level of mean high water neap tide, while onspring tides this percentage increased to about 70%. This semi-lunar type of intertidal variability has also been mentioned for other sandy beach isopods; *Excirolana chiltoni* Richardson in sandy beches of California (Klapov 1972) and Japan (Jones & Hobbins 1985) and *Excirolana nipponica* Bruce & Jones in Japan (Jones & Hobbins 1985).

The observed variability in the intertidal distribution of these isopods has been analyzed in relation to the swimming rythm which allows them to stay in the water column for some time (Enright 1965, Jones & Naylor 1970, Fish & Fish 1972, Brown 1973, Alheit & Naylor 1976, Hasting & Naylor 1980, Jones & Hobbins 1985, Reid & Naylor 1985). For example, Fish & Fish (1972), Jones & Naylor (1970) and Alheit & Naylor (1976) have shown that under laboratory conditions, *Eurydice pulchra* showed peaks of swimming activity during expected high tides and expected springs high tides. Neap-spring differences in behavioour would allow the isopods to stay long enough in the water column to be transported downshore to tidal levels where they would be covered by subsequent neap tides. Thus, even during periods of minimum tidal range, these isopods would be covered by high tides.

The intertidal zones of exposed sandy beaches of south central Chile are characterizaed by the cirolanid isopods *Excirolana braziliensis* and *Excirolana hirsuticauda*. A third species, *Excirolana monodi* Carvacho, is also found but in lower abundances than the other two species (Jaramillo 1982, 1987). *Excirolana braziliensis* shows its maximum abundances at the upper levels of the isopod zone (i.e. high intertidal), whereas *Excirolana hirsuticauda* and *Excirolana hirsuticauda* have their highest abundances at the mid levels of that zone (i.e., mid intertidal). However, this general zonation pattern shows seasonal variations; during the warmer months the highest abundances of these species occur at lower levels than during the remainder of the year (Jaramillo 1987).

Whether further variability in the zonation of these isopods also occurs over neap-spring tidal cycles is inknown. However, since differences in tidal amplitude should result in matching sand moisture profiles on the beach, one would expect that such variability occurs, and specially during the summer months when the intertidal zone experiences the highest variability in temperature and water content of the sediment (Jaramillo 1987). We hypothesize that the common cirolanid isopods of exposed sandy beaches of south central Chile show changes in their zonation during neap-spring tidal cycles. To test this hypothesis we sampled the populations of *Excirolana braziliensis* and *Excirolana hirsuticauda* on the dissipative beach of Mehuín (ca. 40°S) at different times of the tidal cycle, and during periods of low tides summers of 1990 and 1991. Further, we studied the day-night activity patterns of these isopods under field and laboratory conditions to decipher their role in the maintenance and eventual modification of zonation.

MATERIAL AND METHODS

Study Area

The suty area was in the middle of the dissipative beach of Mehuin (39°26'S, 73°13'W), south central Chile (Fig. 1), about 2,000 m long, and ranging from 24 to 140 m wide. Most of the beach is limited landward by dunes that rise up to 2-3 m height above beach level.

Sampling and processing

The variability in abundance and intertidal distribution of *Excirolana braziliensis* and *Excirolana hirsuticauda* was studied during the day low tides of the periods 12-29 January 1990 and 17 January-28 February 1991. The 1990 samplig period covered three moon phases, namely full moon, third quarter and new moon and sampling took place every 2-3 days. The 1991 sampling period extended from new moon, for one and a half lunar cycle until the second full moon, with sampling every 7-8 days.

During the 1990 sampling period, two 0.03 m^{-2} replicates of sediment, 20 cm deep, were collected at 2 m intervals on a transect perpendicular to the coast line. During the summer of 1991 two 0.03 m^{-2} replicates of sediment, 20 cm deep, were collected at 15 m intervals, a distance judged to be adequate to cover the amplitude and location of the cirolanid zone. During both summer periods, the replicates were 1 m apart and the transects were approximately located at the same place. These extended over the same location and the whole intertidal and part of the supralittoral to a bench

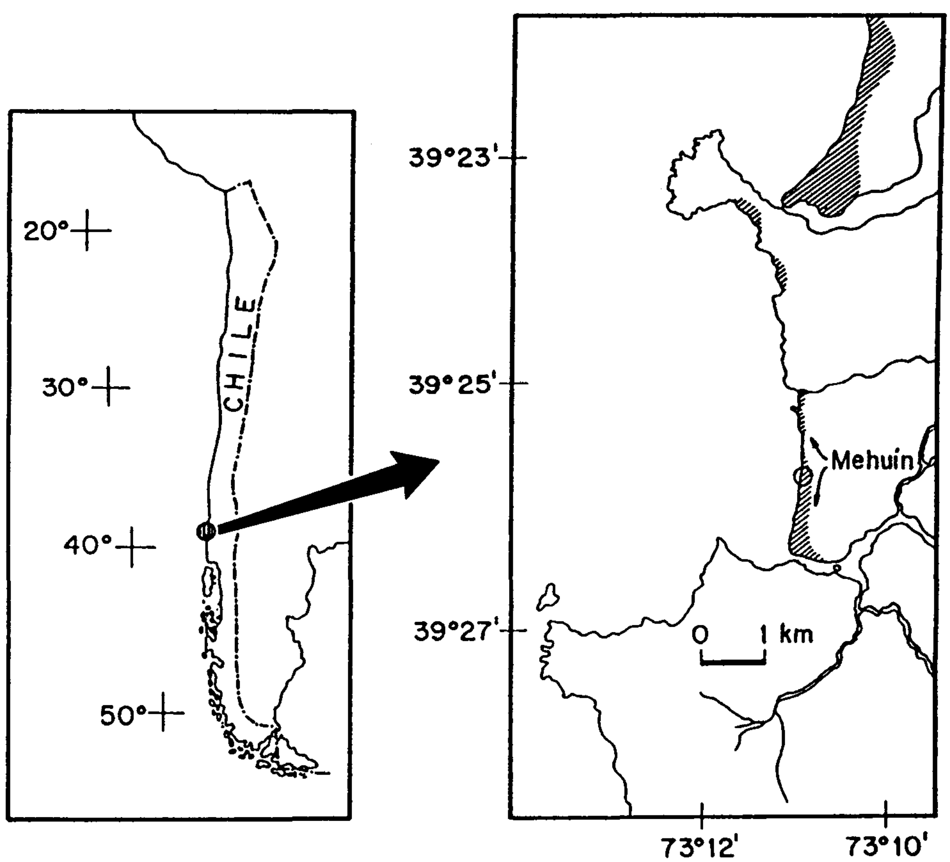

Fig. 1: Location of the study area at Playa Grande de Mehuín, south central Chile.
Localización del área de estudio en la Playa Grande de Mehuín, centro sur de Chile.

mark 30-40 m above the maximum high tide level, using Emery (1961) profiling technique. This was done in order to have a fixed point to calculate the temporal variability of each tidal level sampled. The sediment samples were sieved on a 1 mm mesh sieve and the residue preserved in 5% formalin. Later the animals were sorted, identified, counted, and sexed to explore if different life cycle stages convey differences in zonation. Mean density values per 0.03 m^2 were calculated and used to draw kite diagrams to describe zonation patterns.

Two replicate samples of sediment were collected (day low tides) at each macroinfaunal station for water content and grain-size analyses. Samples were collected with a plastic tube (1.7 cm diameter) to a depth of 10 cm and wrapped in aluminum fil. Water content of sand samples was estimated as the loss in weight of wet sediments after drying (70°C for 96 h). Afterwards, sediment samples were de-salted (tap water washing) and analyzed for grain-size characteristics through a settling tube (Emery 1938). Mean grain-size and sorting were calculated with a moments computational method (Seward-Thompson & Hails 1973) using a program written in Turbo-Basic. Sediment temperatures were monitored at each station with a mercury thermometer accurate to 0.1°C. Temperatures were read near the sand surface (approximately 5 mm depth) and at a depth of 20 cm; the values reported here are the averages of these two readings. Multiple regression with forwards stepwise inclusion was used t test the relationships between the abundances of the isopods and the physical characteristics of the sediment.

Laboratory observations of swimming activity were carried out visually during the summer of 1990. The se observations were made on 10 animals of each species kept in plastic containers (10 x 7 x 15 cm), three of them filled only with sea water and three filled with sea water and a shallow layer of sand (ca. 3 cm) in which the isopods could burrow. During three weeks the isopods were collected and kept in laboratory conditions for 48 h before initiation of the experiments, which lasted two days. Swimming activity was recorded throughout the day and night by counting the number of isopods crossing a mid-water line (11 cm) during a 60 seconds period. During counts carried out in darkness (night time) visual observations were made using a dim red light. The counts were made at the same times of high and low tides as obtained from the Tide Tables of the Chilean Navy (Anonymous 1990). Comparisons between the swimming activity of *Excirolana braziliensis* and that of *Excirolana hirsuticauda* for each counting period were made with one-way analyses of variance.

To determine whether the isopods leave the substrate while their burrowing areas are flooded, samples were taken during the summer of 1990 from the sediment-water interface. These samples were collected during both day and night flood tides using a net (500 m sieve) attached to a semi-circular metallic frame (40 cm wide, 10 cm high). On each sampling date, the frame was maintained against the receding swash for 5 minutes at the upper, middle and lower reaches of the swash (n = two replicates et each level). Abundance comparisons between day and night samplings and among swash levels were done by one-way analyses of variance. If the analyses of variance indicated significant differences among means in the multiple comparisons (i.e., variability among swash levels), all means were compared with the *a posteriori* Tukey-Kramer multiple comparison test (in Stoline 1981).

RESULTS

The sediment

During both summers, stations located at the highest beach levels had lower topographic variability (accretion and erosion of sands) than those located at the mid and low beach levels (Fig. 2). During the intervals 12-18 and 20-23 January 1990, the mid and low beach levels gained sand; from 18 till 20 and from 23 till 29 January, the same levels lost sand. During the intervals 17 January-1 February and 9-16 February 1991, the mid and low beach levels showed erosion of sand, while during most of the remainder of that summer these levels had sand accretion. During the summer of 1990, the top of the transects were located in higher positions than during the summer of 1991; thus, during the accretion

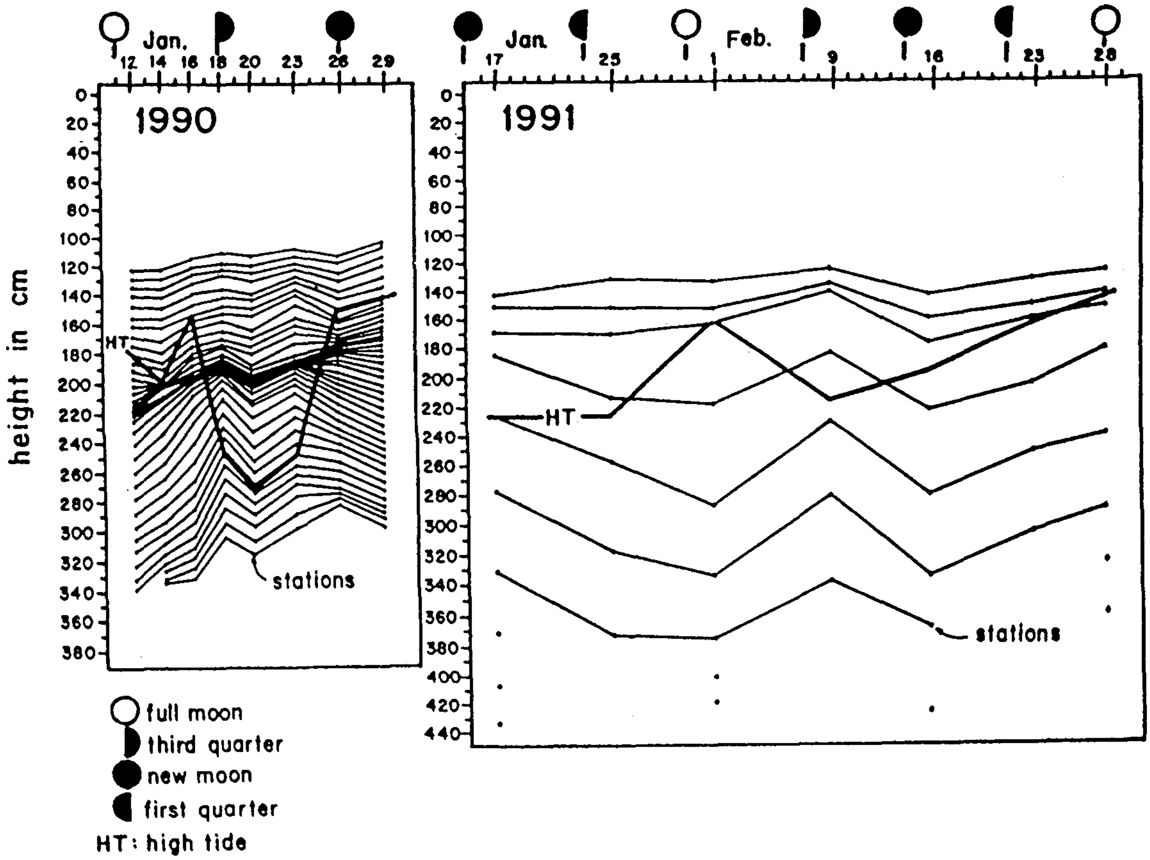

Fig. 2: Temporal variability in the topography of the study area during the summers of 1990 and 1991. Black dots represent sampling stations; position in relation to Y axis represents the height difference between the stations and a fixed bench mark (0 cm) located at the beginning of the sampling transect.

Variabilidad temporal de la topografía del área de estudio durante los veranos de 1990 y 1991. Los puntos negros representan estaciones de muestreo; la posición en relación al eje Y representa la diferencia de altura entre las estaciones y una marca fija de referencia (0 cm) localizada al inicio del transecto de muestreo.

periods of 1990 the beach gained more sand than during that of 1991.

The sediments of the study area were represented by gains whose sizes correspond to medium (1-2 phi) and fine sands (2-3 phi) (Folk 1980). A down-shore gradient of grain size was observed during both summers; i.e., mean grain sizes increased towards the lower beach. During most of the summers of 1990 and 1991 the sands were very well sorted (< 0.35 phi) (Folk 1980). The lowest values (good sorting) were primarily found at stations with the finest particles, while the highest values (poor sorting) were calculated for the coarsest sediments, and sorting decreasing towards the lower beach.

Figure 3 shows the temporal variability of sediment temperatures during the summers of 1990 and 1991. The highest temperatures (25-30°C) were detected at the highest stations. The beach zone affected by high temperatures (> 20°C) hd a wider amplitude during neap tides (20-23 January 1990, 25 January and 23 February 1991) than during spring tides. The spatial variability of water content of the sediments was related to temperature; thus, the driest sediments experienced the highest temperatures (cf. Fig. 3 and 4). Water content and temperature were significantly and negatively correlated (R^2 for 1990: 0.52; n = 317; R^2 for 1991: 0.50, n = 55, $p < 0.05$). Figure 4 shows a gradual increase in water content of sediments from high to low beach levels; it also shows that during the summer of 1990 the beach zone with the driest sediments (0-10% water content) was wider during neap

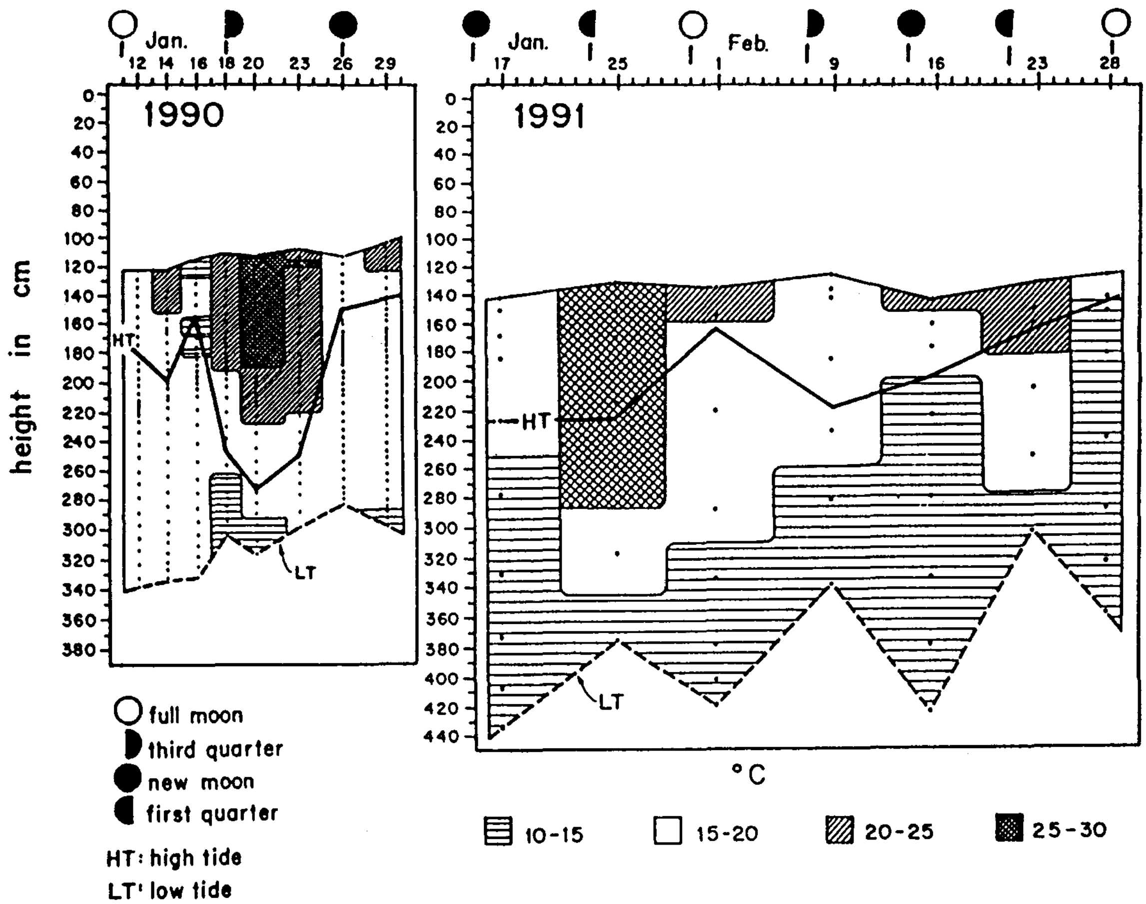

Fig. 3: Temporal variability in the emperature of sands during the summers of 1990 and 1991.

Variabilidad temporal en la temperatura de la arena durante los veranos de 1990 y 1991.

tides (20-23 Janury) than during spring tides. A similar trend was not readily observed during the summer of 1991, because the driest zone was moving, getting smaller, and was located higher on the beach by late February.

Down-shore zonation of Excirolana braziliensis *and* Excirolana hirsuticauda *throughout spring-neap tidal cycles*

Figure 5 shows the temporal/variability in the down-shore zonation of isopods during the summer of 1990. The highest levels at which *Excirolana braziliensis* and *Excirolana hirsuticauda* were collected were located at 122 cm and 171 cm below the bench mark respectively; the lowest ones were located at 301 and 335 cm, respectively. *Excirolana braziliensis* showed a similar pattern of zonation throughout the sampling period, but *Excirolana hirsuticauda* occupied higher levels during spring tides and particularly during the last two sampling days. Thus, the ranges occupied by both species were similar and high on the shore during the 26th and 29th of January. During neap tides (18-23 January) most of the population of *Excirolana braziliensis* occurred above the high water line, whereas the entire population of *Excirolana hirsuticauda* always occurred below that line (Fig. 5).

During the summer of 1991 *Excirolana braziliensis* occupied a beach zone located 149-334 cm below the bench mark (Fig. 6). On the other hand, the zone occupied by *Excirolana hirsuticauda* was 232-377 cm below the bench mark. No major differences were detected in the temporal variability of the zonation of the two spcies. During two spring tides (17 January and 16 February) and

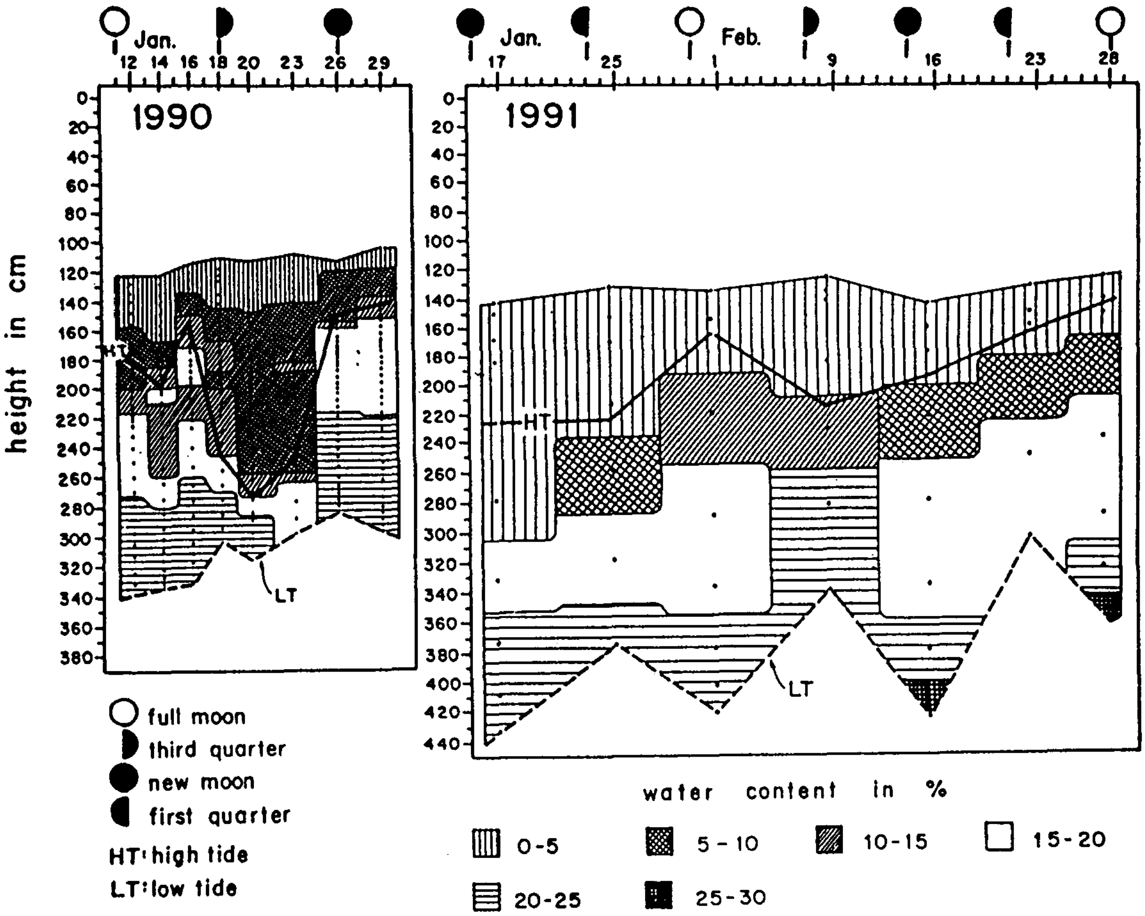

Fig. 4: Temporal variability in the water conent of sands during the summers of 1990 and 1991.
Variabilidad temporal en el contenido de agua de la arena durante los veranos de 1990. y 1991.

two neap tides (25 January and 9 February), part of the population of *Excirolana braziliensis* occurred above the high water line, whereas the whole *Excirolana hirsuticauda* populations was always found below that level (Fig. 6).

The abundance of *Excirolana hirsuticauda* was significantly higher than that of *Excirolana braziliensis* during the summer of 1990 (Fig. 7). The mean abundance of the former ranged 9-32 ind. 0.03 m^{-2}, while the latter ranged 2-5 ind. 0.03 m^{-2}. During the period 12-23 January *Excirolana braziliensis* occupied sediments with physical and textural characteristics which differed significantly from those of the sands occupied by *Excirolana hirsuticauda* (Fig. 7). *Excirolana braziliensis* occupied the warmest (17-24°C), driest (5-15% water content), finest (2.1-2.2 phi) and best sorted sediments (0.28-0.29 phi). During the last two sampling trips of 1990 (26 and 29 January) both species occurred at stations with similar abiotic characteristics. No significant differences were found between the population abundances of either isopod during the summer of 1991 (Fig. 7); the ranges in mean abundance were 2-16 ind. 0.03 m^{-2} for *Excirolana braziliensis* and 7-17 ind. 0.03 m^{-2} for *Excirolana hirsuticauda.* During this summer, *Excirolana brzziliensis* also occupied stations with the warmest, driest, finest and best sorted sediments. However, for most samples, no significant differences were found between the abiotic characteristics of the stations where each species was collected (Fig. 7).

Figure 8 shows the temporal variability in the zonation and mean abundances of males, females and juveniles of both isopods during

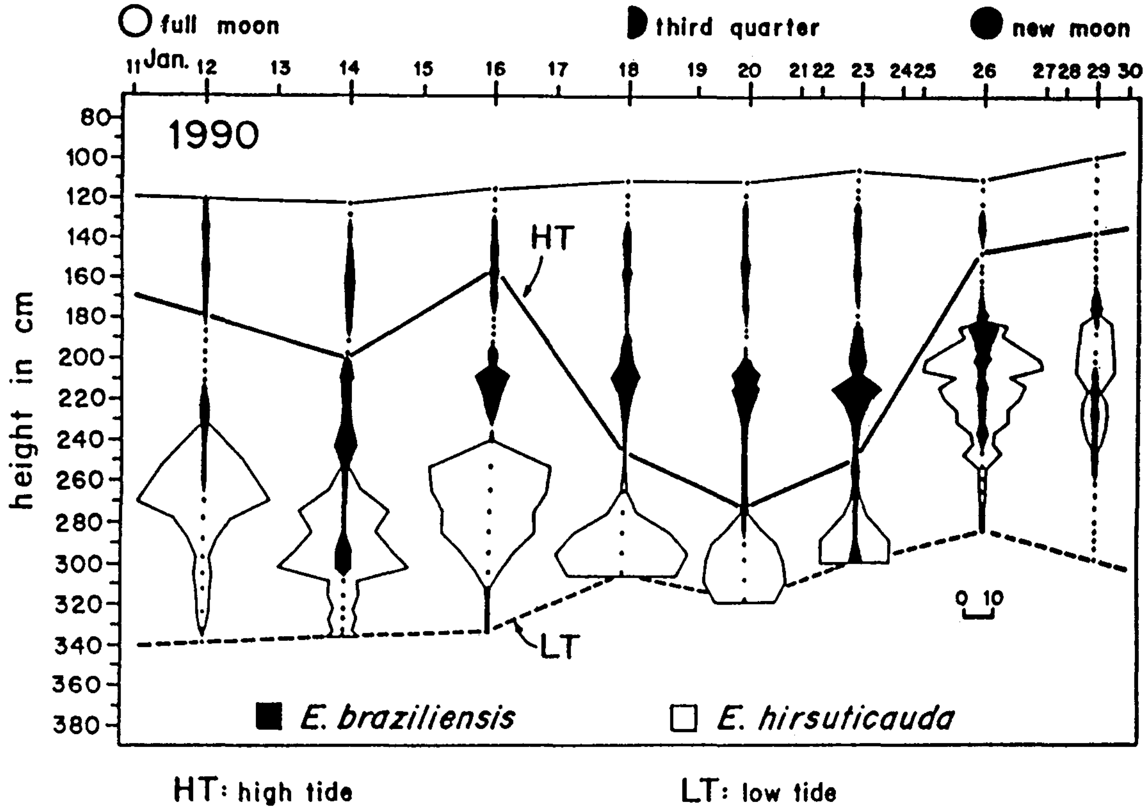

Fig. 5: Temporal variability in the mean abundances and down-shore zonation of *Excirolana braziliensis* and *Excirolana hirsuticauda* during the summer of 1990. The scale represents 10 ind. 0.03 m².

Variabilidad temporal en las abundancias promedio y zonación vertical de *Excirolana braziliensis* y *Excirolana hirsuticauda* durante el verano de 1990. La escala representa 10 ind 0,03 m⁻².

the summer of 1990. The juveniles of *Excirolana braziliensis* occupied lower beach levels than adult males and females; they generally occurred in sediments with lower temperatures, higher water content, coarser and less well sorted grains than those occupied by the adults. Males, females and juveniles of *Excirolana hirsuticauda* occurred at similar beach levels (Fig. 8) where the physical and textural characteristics of the sediments did not differ much. During the summer of 1991, no significant differences were detected in the characteristics of the sediments occupied by males, females or juveniles of either species.

The spatio-temporal variability of temperature, water content and mean grain size of the sediments had a limited influence (multiple regression, R^2: 0.05-0.08) on the spatio-temporal variability of the abundance of *Excirolana braziliensis* during the summers of 1990 and 1991 (Table 1). During both summers, the spatio-temporal variability of these abiotic factors had greater influence on the spatio-temporal variability of the abundance of *Excirolana hirsuticauda*; during both summers, the water content of sediments was the variable with higher accounting for most variability in this species (Table 1).

Abundance of isopods in the sediment-water interface

During the diurnal and nocturnal flood tides of 12, 13 and 24 March, 1990 we observed numerous specimens of *Excirolana hirsuticauda* moving at the sediment-water interface. This movement was not detected in *Excirolana braziliensis*. Comparisons of the mean abundances of the whole populations and those of females, males and juveniles of *Excirolana hirsuticauda* at the high, mid and low levels of the swash zone did show no significant differences, neither during the diurnal or nocturnal samples (Fig. 9). During

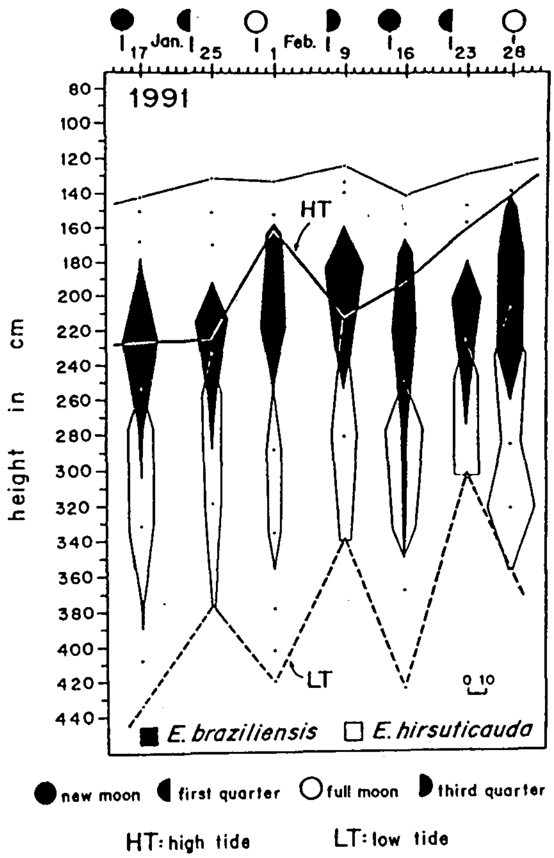

Fig. 6: Temporal variability in the mean abundances and down-shore zonation of *Excirolana braziliensis* and *Excirolana hirsuticauda* during the summer of 1991. The scale represents 10 ind. 0.03 m^{-2}.

Variabilidad temporal en las bundancias promedio y zonación vertical de *Excirolana braziliensis* y *Excirolana hirsuticauda* durante el verano de 1991. La escala representa 10 ind. 0,03 m^{-2}.

the sampling period of the 12th of March, total abundance and abundance of females and males of *Excirolana hirsuticauda*, were significantly higher during the diurnal sampling period (all levels combined). Mean abundance of juveniles was also higher during the diurnal sampling of the 13th of March.

Laboratory experiments

Excirolana braziliensis and *Excirolana hirsuticauda* did not show swimming activity in the aquaria with sediment; they remained continuously buried for observation periods of up to 48 hours. Both species showed swimming activity in the aquaria without sediment, the levels of activity tending to decrease steadily during the final hours of each experiment (Fig. 10). In general, the swimming activity of *Excirolana braziliensis* was greater than that shown by *Excirolana hirsuticauda*, though usually not significantly (Fig. 10). The temporal variability in the number of isopods swimming showed no relationship with the day-night cycle, nor with the expected tidal cycle.

DISCUSSION

We hypothesized that differences in sand desiccation during the spring-neap tidal cycle, should result in variable zonation of cirulanid isopods living in a dissipative sandy beach of

TABLE 1

Summary of multiple regression analyses with samples collected during the summers of 1990 and 1991. The values given in this table (other than intercept and multiple coefficient of determination) are the partial regression coefficients or values of each variable in the multiple regression equation. Values in parentheses correspond to the coefficient of determinations at each step of the model.

Resumen de los análisis de regresión realizados con muestras colectadas durante los veranos de 1990 y 1991. Los valores dados en esta tabla (además de interceptos y coeficientes múltiples de determinación) son coeficientes parciales de regresión o valores de cada variable en la ecuación de regresión múltiple. Los valores en paréntesis corresponden a los coeficientes de determinación en cada paso del modelo.

	Excirolana braziliensis				*Excirolana hirsuticauda*			
	1990, n = 215*		1991, n = 55		1990, n = 100		1991, n= 55	
Temperature	--		--		--		--	
Water content	–0.01	(0.04)	--		0.05	(0.38)	0.05	(0.28)
Mean grain size	–0.50	(0.05)	1.58	(0.08)	–1.11	(0.41)	2.24	(0.34)
Intercept	1.60		–2.92		2.13		–4.73	
R^2	0.05		0.08		0.41		0.34	

-- : Variable not entered in the model
* : Number of samples in which the species was cllected

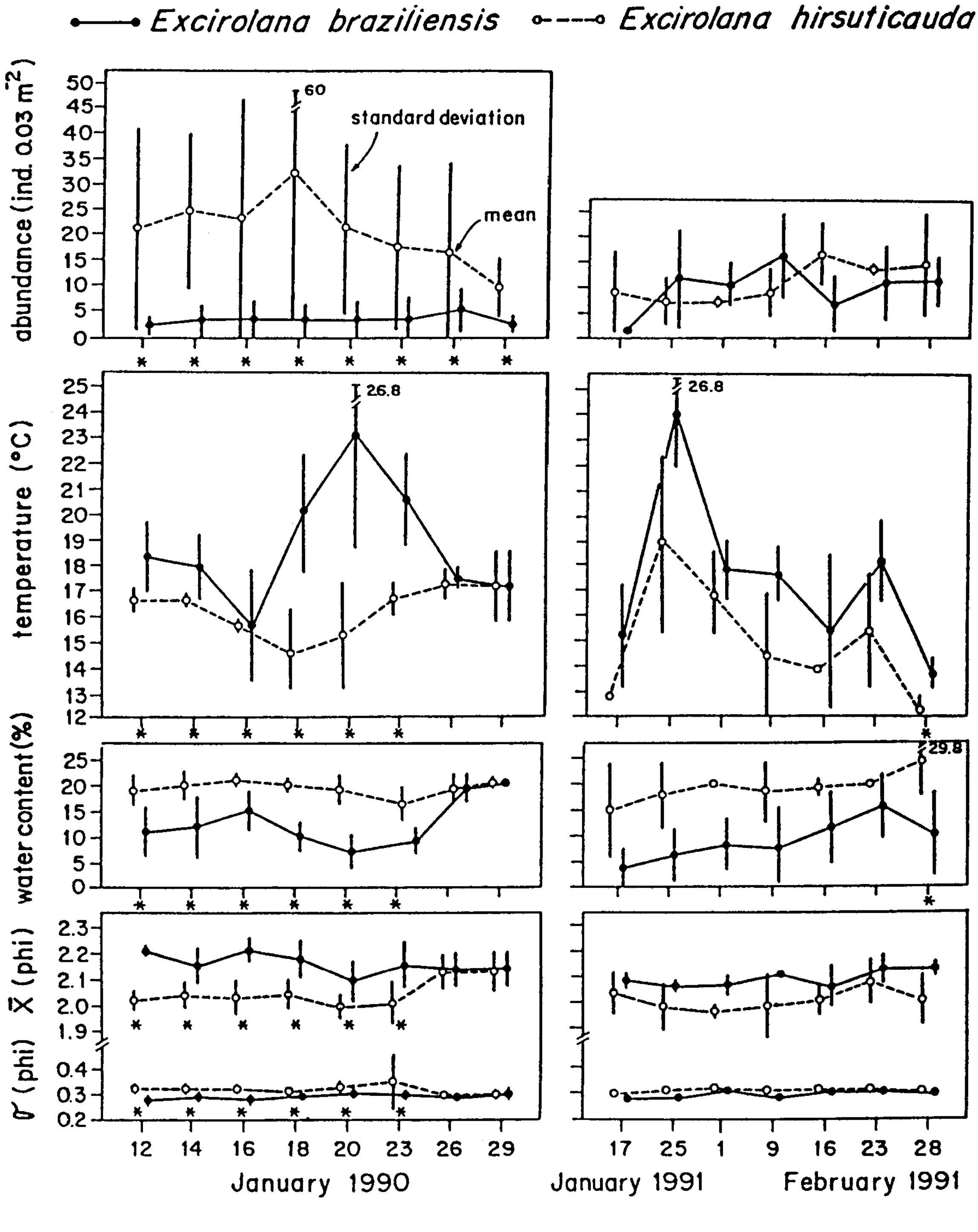

Fig. 7: Temporal variability in the mean abundances of *Excirolana braziliensis* and *Excirolana hirsuticauda* and in the physical and textural characteristics of the sands occupied by both species during the summers of 1990 and 1991.

Variabilidad temporal en las abundancias promedio de *Excirolana braziliensis* y *Excirolana hirsuticauda* y en las características físicas y texturales de las arenas ocupadas por ambas especies durante los veranos de 1990 y 1991.

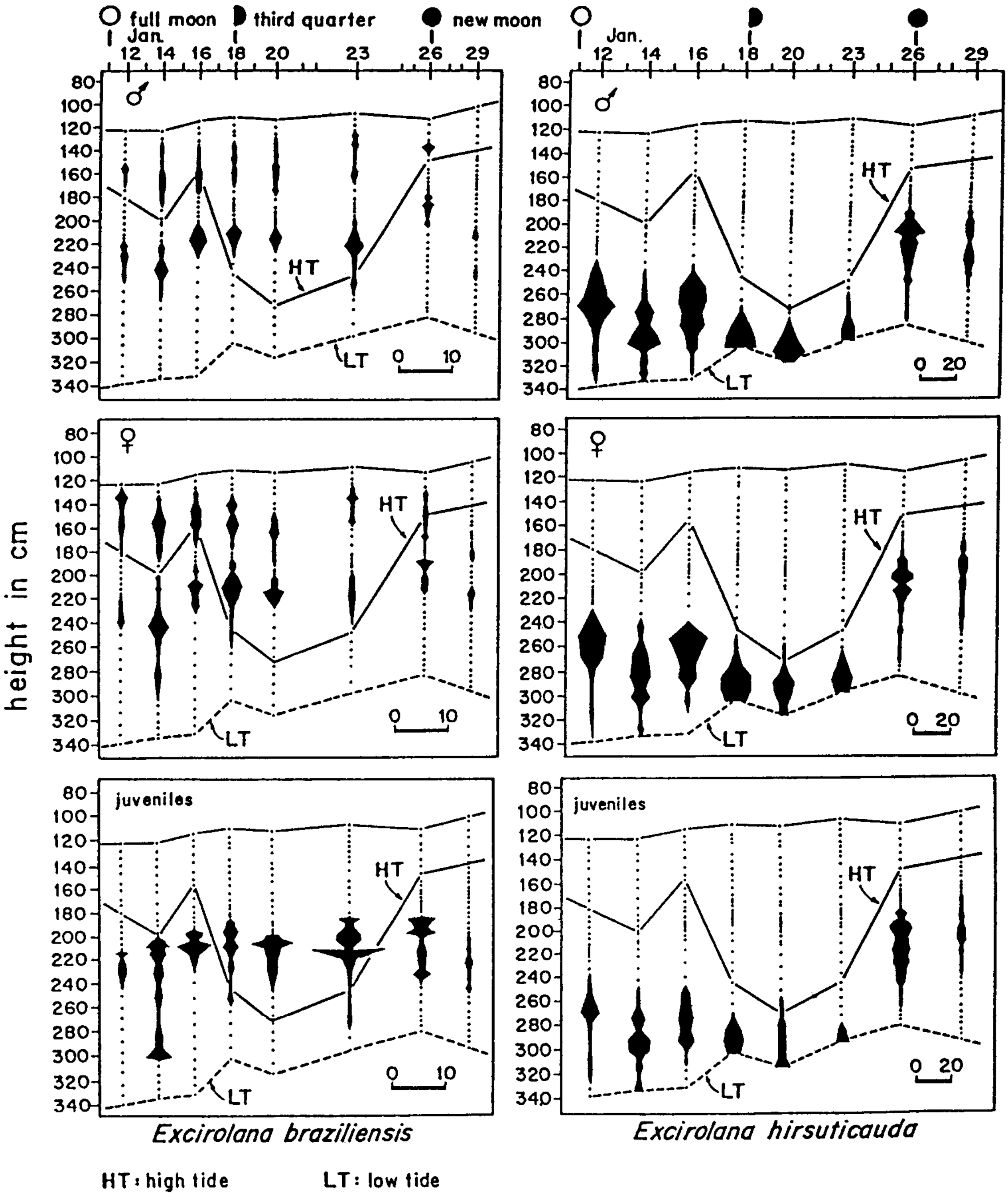

Fig. 8: Temporal variability in the mean abundances and down-shore zonation of males, females and juveniles of *Excirolana braziliensis* and *Excirolana hirsuticauda* during the summers of 1990 and 1991. The scale represents 10 and 20 ind. 0.03 m^{-2}, respectively.

Variabilidad temporal en las abundancias promedio y zonación vertical de machos, hembras y juveniles de *Excirolana braziliensis* y *Excirolana hirsuticauda* durante los veranos de 1990 y 1991. La escala representa 10 y 20 ind. 0,03 m^{-2}, respectivamente.

south central Chile, particularly during summer, when sand dessication would be greatest. The results of this study showed that only *Excirolana hirsuticauda* had temporal variability in its zonation, and that only during the summer of 1990. Thus, the marked gradients of sand desiccation observed during the neap tide samples did not adversely affect

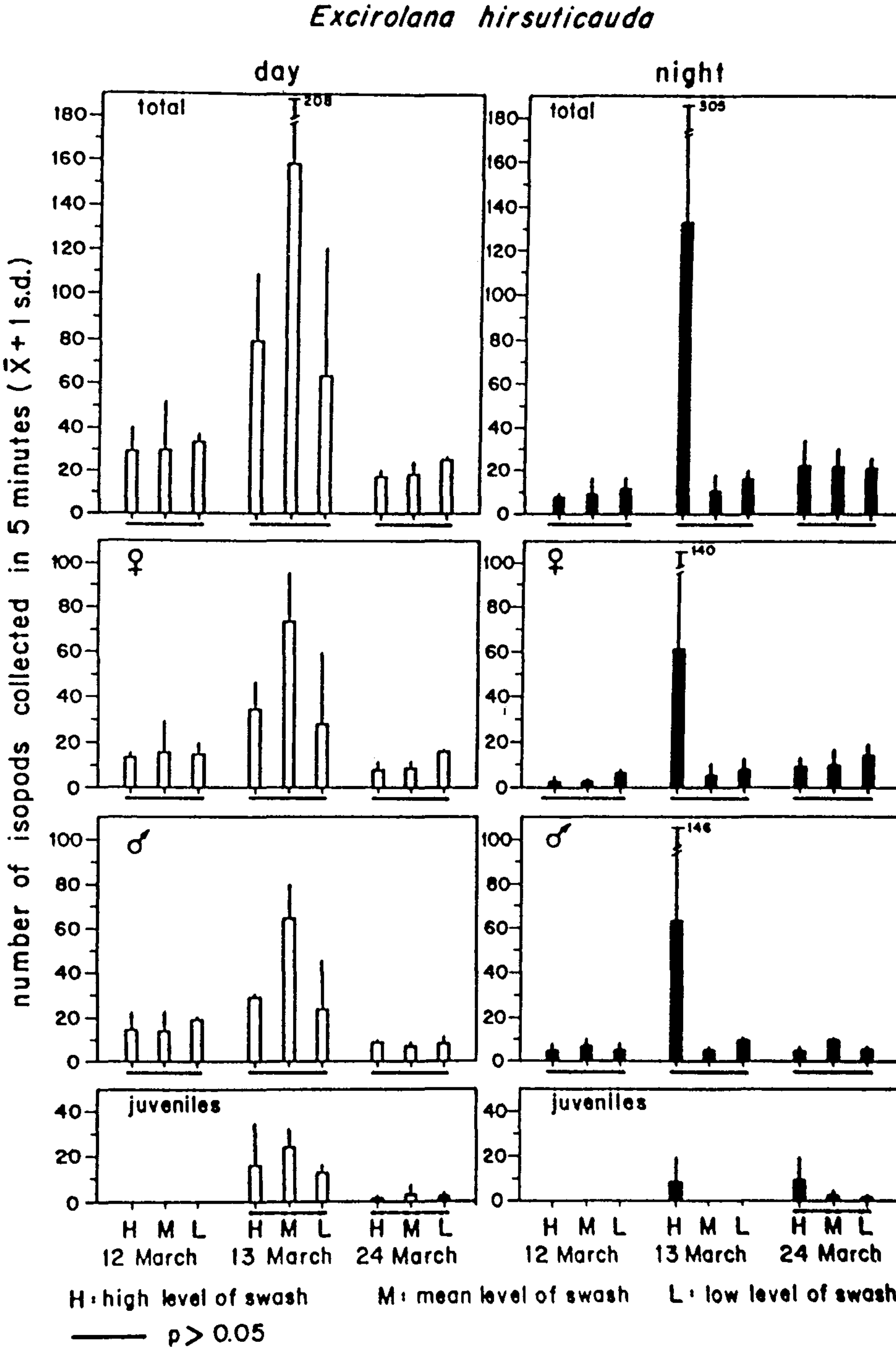

Fig. 9: Temporal and spatial variability in the abundance of *Excirolana hirsuticauda* collected in the sediment-water interface (swash zone) of the study area during the diurnal and nocturnal flood tides of the 12th, 13th and 24th of March, 1990. The columns represent the means of two replicates.

Variabilidad temporal y espacial en la abundancia de *Excirolana hirsuticauda* colectada en la interfase agua-sedimento (zona de lavado de la ola) del área de estudio durante las mareas altas diurnas y nocturnas del 12, 13 y 14 de marzo de 1990. Las columnas representan el promedio de dos réplicas.

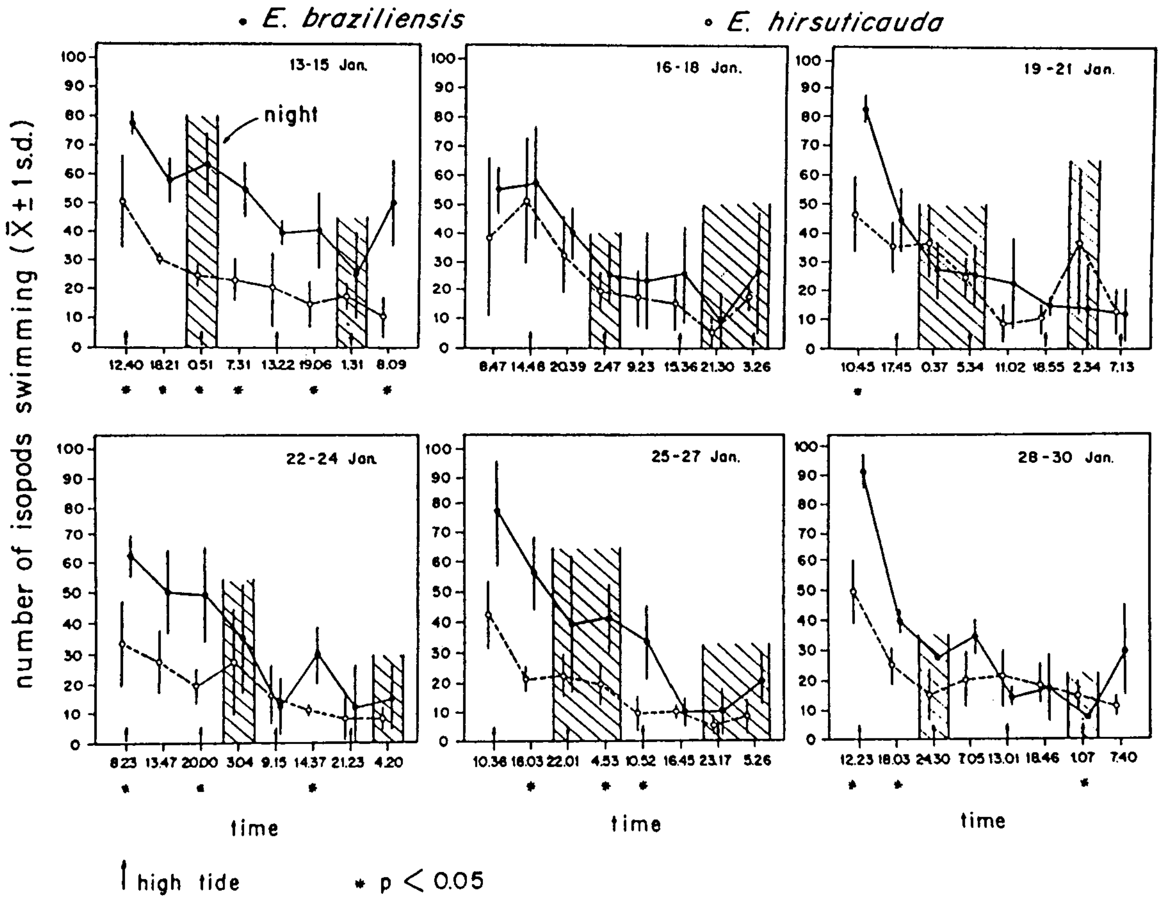

Fig. 10: Temporal variability in the swimming activity (number of isopodos swimming per two minutes of observation) of 10 specimens of *Excirolana braziliensis* and *Excirolana hirsuticauda* in aquaria without sediment. Hatched columns indicate night observation periods, while arrows indicate times of expected high tides. Six experimental runs were carried out during a eriod which covered different moon's phases which occurred during the following days: 11th of January, full moon; 18th of January, last quarter; 26th of January, new moon and 2th of February, first quarter. The means are based upon three replicates.

Variabilidad temporal en la actividad natatoria (número de isópodos nadando durante dos minutos de observación) de 10 especímenes de *Excirolana braziliensis* y *Excirolana hirsuticauda* en acuarios sin sedimentos. Las columnas achuradas indican períodos de observación nocturna, mientras que las flechas indican las horas de mareas altas predichas por tablas. Se realizaron seis corridas experimentales durante un período que cubrió diferentes fases lunares y que ocurrieron los siguientes días: 11 de enero, luna llena, 18 de enero, cuarto menguante; 26 de enero, luna nueva y 2 de febrero, cuarto creciente. Las medias están basadas en tres réplicas.

the distribution of *Excirolana braziliensis* which occurred above the high tide line in approximately 80% of the samples. This is in agreement with the results of Jones & Hobbins (1985) which found that *Eurydice pulchra* and *Excirolana chiltoni* were able to tolerate stranding during neap tides.

The absence of temporal variability in the zonation of *Excirolana braziliensis* differs from that observed in other sandy beach peracarids. For example, Fish (1970), Fish & Fish (1972) and Alheit & Naylor (1976) found in sandy beaches of Wales that during spring tides, *Eurydice pulchra* occupied higher beach levels than during neap tides. In sandy beaches of California, *Excirolana chiltoni* moved to the highest beach levels during the days before new and full moon, while after that it moved down shore (Klapow 1972). In the same area and during spring tides, the amphipod *Orchestoidea corniculata* Stout occurred higher in the beach than during neap tides (Bowers 1964). In sandy beaches of Japan, *Eurydice nipponica* also showed a tidal migration throughout the spring-neap tidal cycle (Jones & Hobbins 1985).

The differences between our results and those of the above mentioned studied, might be related to the tide ranges of each region. For example, Wales has tide ranges as wide as 4 m (Pethick 1984), whereas the widest tide ranges on the coast of south central Chile do not exceed 2 m. Differences in tidal range may result in differences in pressure of the water column overlying over the isopod zones. Authors such as Enright (1965) and Jones & Naylor (1970) have concluded that water pressure is a significant factor involved in the emergence of *Eurydice pulchra* and *Excirolana chiltoni* from the sediment, and consequently in the variability of zonation showed by these species.

The topography, textural and physical characteristics of the study site showed temporal and spatial variability. Jaramillo (1987) has argued that such variability (e.g., sand desiccation) may be the primary cause of the seasonal variability observed in the zonation of isopods at the beach of Mehuín, inducing for example, *Excirolana braziliensis* and *Excirolana hirsuticauda* to occur at lower beach levels in summer than in winter. In this study, the temporal variability in textural and physical characteristics of sediments had some influence in the eventual explanation of the temporal variability in zonation of only *Excirolana hirsuticauda*. Thus, the variability of, e.g., sand desiccation, would be important at an annual scale, when interseasonal differences are higher than during a spring-neap tidal cycle of the same season.

The maintenance of zonation by isopods such as *Eurydice pulchra* and *Excirolana chiltoni* is primarily related to their swimming activity. Thus, Alheit & Naylor (1976) observed that *Eurydice pulchra* emerges from the sand, swims in the surf and moves up and down the beach according to the stage of the spring-neap tidal cycle. A similar behaviour has been described in the Californian *Excirolana chiltoni* by Enright (1972). We collected *Excirolana hirsuticauda* from the shallow layer of water (5-10 cm deep) that covered its burrowing zone during flood tides, but did not record *Excirolana braziliensis* in this layer. These differences might be related to the fact that *Excirolana braziliensis* mostly occurred above the high water line; i.e., above the zone affected by wave turbulence.

The swimming activity of sandy beach isopods from other coasts is tidally rhythmic (Jones & Naylor 1970, Fish & Fish 1972, Alheit & Naylor 1976; Hastings & Naylor 1980, De Ruyck *et al.* 1991), even though some results are apparently contradictory. For example, Jones & Naylor (1970) found that specimens of *Eurydice pulchra* kept in aquaria with water and no sand added were more active during hig tide periods but when sand was added to the aquaria, no activity was registered. On the other hand, Fish & Fish (1972), Alheit & Naylor (1976) and Hasting & Naylor (1980) studied the same species and found swimming activity in aquaria with sand. These differences were explained by Alheit & Naylor (1976) who found that the activity peaks of *Eurydice pulchra* occurred when the amplitude of the spring tides was decreasing, while almost no activity was registered during neap tides. Cirolanid isopods from exposed beaches of South Africa also showed swimming activity in aquaria with sediments and evenduring neap tides (De Ruyck *et al.* 1991).

The results of this study indicate that *braziliensis* and *Excirolana hirsuticauda* do not show swimming activity in aquaria with sediment. It has been observed that simulated wave turbulance in laboratory experiments produces swimming activity and rhythmicity in sandy beach peracarids, for example in *Excirolana chiltoni* and in *Euridice pulchra* (Jones & Naylor 1970). No mechanica stimulation was used inthis study; thus, we could not evaluate such effects on producing an eventual rhthmicity in the swimming activity of *Excirolana braziliensis* and *Excirolana hirsuticauda*. Both species were active in the aquaria without sediment; however, the swimming activity deteriorated with time, a situation also observed by Fish & Fish (1972) in *Eurydice pulchra*. The swimming activity of *Excirolana braziliensis* and *Excirolana hirsuticauda* did not show evidence of circadian and circatidal rhythmicity as shown by *Eurydice pulchra* (Jones & Naylor 1970, Fish & Fish 1972, Alheit & Naylor 1976, Jones & Hobbins 1985, Reid & Naylor 1985, De Ruyck *et al.* 1991), *Excirolana chiltoni*

(Enright 1965) and *Pseudaega punctata* Thomson (Fincham 1972). Some of these authors have suggested that the primary role of circatidal rhythmicity in swimming is to allow organisms to return to their optimal zones before tidal ranges change. Swimming activity would allow isopods to move down shore and thus avoid stranding during the neap tides (Alheit & Naylor 1976).

Apparently, temporal variability in tidal ranges does not affect the down-shore distribution of *Excirolana braziliensis* nor the swimming activities of this species and *Excirolana hirsuticauda* at the beach of Mehuín. On the contrary, the results obtained during the summer of 1990 suggested that the down-shore *Excirolana hirsuticauda* was affected to some extent by the tidal variability occurring throughout the spring-neap tidal cycle. It is also possible that sudden environmental disturbances, like unusual high tides occurring primarily during winter time when wave turbulence usually reach higher beach levels than that reached during the summer, may affect the down-shore variability of *Excirolana braziliensis* and *Excirolana hirsuticauda*.

ACKNOWLEDGMENTS

We thank Sandra Silva, Marcia González, Claudia Añazco, Jacqueline Muñoz, Luis Filún, Pedro Quijón, Antonio Low and Victor Poblete for assistance with field and laboratory work. We also acknowledge to Drs. Anton McLachlan (University of Port Elizabeth, South Africa), Ernest Naylor (University of Wales, Bangor, U.K.) and two anonymous reviewers for suggestions and critical reading of an earlier draft of this manuscript. Financial support from CONICYT (Fondecyt) through Project 0904-88 is gratefully acknowledged.

LITERATURE CITED

ALHEIT J & E NAYLOR (1976) Behavioural basis of intertidal zonation in *Eurydice pulchra* Leach. Journal of Experimental Marine Biology and Ecology 23: 135-144.

ANONYMOUS (1990-1991) Tablas de marea de la costa de Chile, Instituto Hidrográfico de la Armada de Chile, Valparaíso.

BOWER DE (1964) Natural history of two beach hoppers of the genus *Orchestoidea* (Crustacea: Amphipoda) with reference totheir complemental distribution. Ecology 45: 677-696.

BROWN AC (1973) The ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 1: observations on two intertidal isopoda *Eurydice longicornis* (Studer) and *Exosphaeroma truncatitelson* (Barnard). Transaction of the Royal Society of South Africa 40: 381-400.

CASTILLA JC & O MENA (1977) Estudios ecológicos en la zona costera afectada por contaminación del "Northern Breeze". I. Introducción general y comunidades de playas de arena. Medio Ambiente 2: 53-64.

DAHLE E (1952) Some aspects of the cology and zonation of the fauna on sandy beaches. Oikos 4: 1-27.

DE RUYCK A, A McLACHLAN & Th DONN (1991) The activity of three intertidal sand beach isopods (Flabellifera: Cirolanidae). Journal of Experimental Marine Biology and Ecology 146: 163-180.

EMERY K (1938) Rapid method of mechanical analysis of sand. J Sedimentary Petrology 8: 105-111.

EMERY K (1961) A simple method of measuring beach profiles. Limnology and Oceanography 6: 90-93.

ENRIGHT JT (1965) Entrainment of a tidal rhythm. Science 147: 864-867.

ENRIGHT JT (1972) A virtuoso isopod. Journal of Comparative Physiology 77: 141-160.

ESCOFET A, N GIANUCCA, S MAYTIA, V SCARABINO (1979) Las playas arenosas del Atlántico Sudoccidental entre los 29° y los 43° Lat. S: características generales y consideraciones bioceanológicas. Seminario sobre Ecología Bentónica y Sedimentación de la Plataforma Continental de la parte Sudoccidental de América Latina, UNESCO: 247-258, Montevideo (1978).

FINCHAM AA (1973) Rhythmic swimming behaviour of the New Zealand sand beach isopod *Pseudaega punctata* Thomson. Journal of Experimental Marine Biology and Ecology 11: 229-237.

FISH S (1970) The biology of *Eurydice pulchra* (Crustacea: Isopoda). Journal of the Marine Biological Association of the United Kingdom 50: 753-768.

FISH JD & S FISH (1972) The swimming rhythm of *Eurydice pulchra* Leach and a possible exlanation of intertidal migration. Journal of Experimental Marine Biology and Ecology 8: 195-200.

FOLK E (1980) Petrology of sedimentary rocks. Hemphill Publ. Co. Austin, Texas, 182 pp.

HASTINGS MH & E NAYLOR (1980) Ontogeny of an endogenous rhythm in *Eurydice pulchra*. Journal of Experimental Marine Biology and Ecology 46: 137-145.

JARAMILLO E (1982) Taxonomy, natural history and zoogeography of sand beach isopods from the coast of southern Chile. Studies on Neotropical Fauna and Environment 17: 175-194.

JARAMILLO E (1987) Community ecology of Chilean sandy beaches. Ph. D. dissertation, University of New Hampshire, Durham, USA: 216 pp.

JONES DA (1970) Factors affecting the distribution of the intertidal isopods *Eurydice pulchra* Leach and *E. affinis* Hansen in Britain. JOurnal of Animal Ecology 39: 455-472.

JONES DA & C HOBBINS (1985) The roles of biological rhythms in some sand beach cirolanid Isopoda. Journal of Experimental Marine Biology and Ecology 93: 47-59.

JONES DA & E NAYLOR (1970) The swimming rhythm of the sand beach isopod *Eurydice pulchra*. Journal of Experimental Marine Biology and Ecology 4: 188-199.

KLAPOW LA (1972) Fortnightly molting and reproductive cycles in the sand beach isopod *Eurydice chiltoni*. Biological Bulletin, Woods Hole 143: 568-591.

McLACHLAN A (1980) Intertidal zonation of macrofauna and stratification of meiofauna on high energy sandy beaches in the Eastern Cape, South Africa. Transactions of the Royal Society of South Africa 44: 213-223.

PETHICK JS (1984) An introduction to coastal geomorphology. Edward Arnold (Publ.) Ltd. London: 260 pp.

REID DG & E NAYLOR (1985) Free-running, endogenous semilunar rhythmicity in a marine isopod crustacean. Journal of the Marine Biological Association of the United Kingdom 65: 85-91.

SALVAT B (1986) *Eurydice pulchra* - Leach, 1815. *Eurydice affinis* Hansen, 1905 (Isopodes Cirolanidae). Taxonomie, ethologie, ecologie, repartition verticale et cycle reproducteur. Actes de la Societé Linneenne de Bordeaux 103: 1-77.

SEWARD-THOMPSON B & J HAILS (1973) An appraisal on the computation of statistical parameters in grain size analysis. Sedimentology 11: 83-98.

STOLINE MR (1981) The status of multiple comparisons: simultaneous estimation of all pairwise comparisons in one way anova designs. The American Statistician 35: 134-141.

TREVALLION A, AD ANSELL, P SIVADAS & B NARAYANAN (1970) A preliminary account of two sandy beach in south West India. Marine Biology 6: 268-279.