

## Distribution of three intertidal cirolanid isopods (Flabellifera : Cirolanidae) on a South African sandy beach.

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**Abstract :** The vertical zonation pattern of *Eurydice longicornis*, *Pontogeloides latipes* and *Excirologana natalensis*, cirolanid isopods co-existing on Sundays River Beach, was studied, and differed from Dahl's, Salvat's and Trevallion *et al.*'s schemes. In view of the apparent differences in zonation both in the present study and the literature, the use of cirolanid isopods as indicators of zones is questionable.

Environmental factors are suspected to be more important than biological interactions as cause for the observed zonation patterns of the three species. This study suggests longshore distributional differences in the cirolanid isopod populations both on a large scale along a log-spiral bay and on a small scale along a mega-cusp system. Seasonal changes in distribution seem to occur in all three species as well as semilunar zonation changes in *E. natalensis*.

The flexible zonation patterns exhibited by the cirolanid isopods at Sundays River Beach may be an adaptation for survival in the dynamic, unstable conditions of a high energy, microtidal beach.

**Résumé :** L'arrangement de la zonation verticale des isopodes cirolanides coexistants sur la plage de Sundays River a été étudiée ; il s'agit des *Eurydice longicornis* (Stüder, 1883), des *Pontogeloides latipes* (Barnard, 1914 b) et des *Excirologana natalensis* (Vanhöffen, 1914). Ainsi que l'on peut s'y attendre sur les plages qui ont plus d'une seule espèce de cirolanide, il y a sur la plage de Sundays River des différences par rapport aux agencements de Dahl, Salvat, Trevallion et autres. Étant donné les différences apparentes de zonation, à la fois dans la présente étude et dans la littérature, on peut mettre en doute l'utilisation des isopodes cirolanides comme indicateurs de zones.

En ce qui concerne les raisons des arrangements de zonation que l'on observe, on croit que les effets du milieu sont plus importants que les interactions biologiques ; de plus amples travaux sont nécessaires. Bien qu'elle ne soit pas probante, la présente étude suggère des différences dans la distribution, le long du rivage, des populations d'isopodes cirolanides, à la fois à grande échelle selon une baie de forme spirale logarithmique et à petite échelle suivant un réseau mégacuspide. Des changements saisonniers de distribution semblent avoir lieu chez chacune des trois espèces. De plus, l'*Excirologana natalensis* présente des changements de zonation semi-lunaires.

Les arrangements variables de la zonation des isopodes cirolanides sur la plage de Sundays River peuvent être une adaptation à la survie dans les conditions dynamiques et instables d'une plage à micromarées de forte énergie.

### INTRODUCTION

Vertical zonation patterns occur in most animals which inhabit the intertidal zone during all or part of their life cycles in response to the range of physical conditions across the intertidal zone imposed by varying degrees of daily emersion and immersion (Dahl, 1952 ; Newell, 1976, 1979 ; Salvat, 1964, 1966 ; McLachlan, 1977 b, 1978, 1980 b ; Bally, 1983 b, Chelazzi *et al.*, 1983). Zonation of sandy shore animals is dictated by lunar and daily tidal cycles in a manner similar to that of rocky shore species (Newell, 1976, 1979).

However, because of the burrowing habits, high motility and tidal migrations of sandy beach organisms, their zonation patterns are not as apparent as those on rocky shores, therefore causing opinions on sandy beach zonation to vary widely.

Dahl (1952), the first to propose a universal zonation scheme for exposed sandy beaches, defined three intertidal zones in terms of the fauna living in each zone. His supralittoral zone is characterized by the presence of air-breathing crustaceans, dominated by either talitrid amphipods or ocypodid crabs. The midlittoral zone is characterized by cirolanid isopods (*Cirolana*, *Eurydice*) although haustoriid amphipods are also found. The lowest zone is the sublittoral fringe, characterized by the hippid crab *Emerita* in the tropics, several species of amphipods in temperate regions and the Arctic and molluscs and polychaetes on all beaches (Dahl, 1952).

Dahl's classification scheme for sandy beaches has been widely accepted. Though cirolanids are characteristic of the midlittoral zone on high-energy beaches, this scheme does not always hold for more sheltered beaches. Epelde-Aguirre and Lopez (1975) found cirolanids confined to the sublittoral, occurring together with *Emerita* and some polychaetes in Coronel Bay, Chile. Even on some exposed beaches in Chile, Jaramillo (1987 b) found cirolanids in the sublittoral and subterrestrial fringes. Further differences with Dahl's scheme were the absence of cirolanids from the middle zones of some beaches in northern Chile (Jaramillo, 1987 b) and Mozambique (MacNae & Kalk, 1962), whereas Pichon (1967) reported cirolanids in the subterrestrial zone on a sandy beach in Madagascar. Jones (1969, 1971, 1974, 1979) and Eleftheriou and Jones (1976) found that Kenyan, Saudi Arabian and Indian cirolanids (genus *Eurydice*) varied in their zonation patterns both according to species and to locality within a single species. Dexter (1972) found *Cirolana mayana* (*Exciorolana braziliensis* - Glynn *et al.*, 1985) from the high water spring mark almost down to the low-water mark on Panamanian beaches. Several studies on South African beaches (Bally, 1983 b, McLachlan *et al.*, 1981 ; Wendt & McLachlan, 1985) and Namibian beaches (Donn and Cockroft, 1989) also recorded cirolanids in the subterrestrial and sublittoral fringes. On sheltered, fine-grained beaches of the Cape Peninsula, Brown (1973) found that a sphaeromatid isopod replaced a cirolanid. Thus, cirolanids tend to be found not only in the midlittoral zone, but also in the subterrestrial and sublittoral zones.

Salvat (1964, 1966) suggested a zonation system based on physical parameters rather than the presence of characteristic taxonomic groups. However, Salvat's zones may still be recognizable by the species found in them, thus allowing Dahl's zonation to be superimposed on Salvat's scheme. Salvat (1964, 1966) divided the beach into four levels based on the degree of moisture in the sediment. Bally's (1983 a) interpretation of Salvat's zones are : the uppermost zone, consisting of dry sand, is reached only by large waves at high-water springs ; the zone of retention, reached by all tides, retains capillary water during low tide and consists of well drained and oxygenated sand with considerable temperature fluctuations during low tide. Below that is the zone of resurgence (extending shorewards as far as the low tide water table lies within 20 cm of the surface), which experiences considerable water movement both on the falling and rising tides since gravitational water, lost from the zone of retention, flows through the sand of this zone and appears at the surface as a glassy layer. Lowest down, the zone of saturation is permanently saturated with water and interstitial water circulation is considerably reduced, resulting in poor oxygenation and possibly the formation of a black sulphide layer.

Trevallion *et al.* (1970) divided the beach into an upper zone characterized by talitrids and ocypodids, a middle zone characterized by cirolanid isopods, polychaetes and sometimes bivalves and a lower zone which showed the greatest species diversity, but lack cirolanids. A wide variety of zonation patterns thus exist, which increases the problem of establishing a universal system of classification for zonation on sandy beaches.

While vertical distribution is marked by zonation, longshore distribution of beach fauna is characterised by patchiness (Efford, 1965 ; Cubit, 1969 ; Dillery & Knapp, 1970 ; Brown, 1973 ; Dexter, 1972 ; Perry, 1980 ; Bally, 1983 a). Aggregations of sand crabs, *Emerita* spp., have been found on beach cusps (Dillery & Knapp, 1970) while Grant (1981) found a significant preference of haustoriid amphipods for ripple crests. McLachlan and Hesp (1984) looked at faunal response to morphology and water circulation on a sandy beach with cusps and found that two donacid bivalves and meiofauna avoided the cusp horn and concentrated on the sides of the rip current running down the cusp bay. Longshore distribution of beach fauna along log-spiral bays in the eastern Cape has been investigated in the bivalve *Donax serra* (Donn, 1987) and in the sand burrowing mysid *Gastrosaccus psammodytes* (McMurray, 1985).

Many macrofaunal species on open sandy beaches exhibit a characteristic tidal or semi-lunar migratory pattern, moving up and down the shore with the waves and swash (Ansell & Trevallion, 1969 ; McLachlan *et al.*, 1979). This movement is best known in *Donax* (Ansell, 1983), the gastropod *Bullia* (Brown, 1971) mysids (McLachlan *et al.*, 1979) and isopods (Fish, 1970 ; Alheit & Naylor, 1976). Seasonal migrations of cirolanid isopods on temperate beaches in Europe have been noted by Elmhirst (1932), Salvat (1966), Jones (1970 a, b) and Fish (1970). These workers reported offshore migration during winter in *Eurydice pulchra* in Britain and France and ascribed this to low temperatures and stormy conditions during this period, while Jaramillo (1987 a) reported offshore migration in cirolanids in summer in Chile. Similar seasonal movements have also been recorded in amphipods (Crocker and Hatfield, 1980 ; Donn and Crocker, 1986).

*Eurydice longicornis* (Stüder), *Pontogeloides latipes* (Barnard) and *Excirolana natalensis* (Vanhöffen) are intertidal cirolanid isopods that co-exist on most of the sandy beaches in southern Africa (McLachlan *et al.*, 1981, McLachlan & Wendt, 1985 ; Bally, 1983 a, b ; Donn, 1986, 1988 a, b). They remain buried in the intertidal sand and emerge to swim and scavenge when the rising tide covers their zone, the adults exhibiting peak activity during nocturnal spring high tides (De Ruyck *et al.*, 1991 a). *E. longicornis* exhibits an annual, multivoltine life history with a more extended breeding period than the other two species. *P. latipes* and *E. natalensis* both have biennial, univoltine life histories with lower fecundities than *E. longicornis* (De Ruyck *et al.*, 1991 b).

The co-occurrence of three cirolanids on a high energy, microtidal beach provided a neat opportunity to test the above ideas with regards to zonation, longshore distribution (on meso- and macro scales) and tidal and seasonal migration.

## METHODS

### Study area

Sundays River Beach lies east of the Sundays River estuary in Algoa Bay (Fig. 1), a log-spiral bay (Bremner, 1983) on the south-eastern corner of Africa ( $33^{\circ} 43'S$ ,  $25^{\circ} 53'E$ ). On McLachlan's (1980 a) 20 point exposure rating system the beach rates 15.0, which classifies it as exposed to very exposed, with wave height ranging from 1 m to more than 6 m (Donn *et al.*, 1986). Talbot and Bate (1987) found an increase in rip frequency and intensity from west to east across Algoa Bay under south-westerly conditions, an indication of increasing wave height from west to east. Although the beach is occasionally dissipative, its modal morphodynamic state is high energy intermediate (Short & Wright, 1983). Intertidal slopes vary from 1/28 to 1/40 and the sand consists of well sorted medium quartz particles with diameters of 225 - 335  $\mu\text{m}$ , with a  $\text{CaCO}_3$  content of 29 - 47 % (Wendt & McLachlan, 1985). McLachlan (1977 a) gives a detailed description of the physico-chemical properties of Sundays River Beach. The mean spring tidal range in Algoa Bay is 1.6 m (Wagenfeld, 1989).

During prolonged periods of calm weather the beach exhibits a cusp circulation pattern. Large mega-cusps are formed with horns at 100 - 300 meter intervals. In contrast to the cusp system described by McLachlan and Hesp (1984) on a reflective beach, the horns of mega-cusps on intermediate beaches are characterized by a flatter slope than at the cusp bay (Donn *et al.*, 1986 ; McLachlan, A., pers. comm.).

### Zonation

To investigate zonation patterns, tidal and seasonal changes in distribution of *Eurydice longicornis*, *Excirrolana natalensis* and *Pontogeloides latipes*, the intertidal zone was sampled at 3-weekly intervals over 14 months at both 5 km and 25 km from the Sundays River mouth, thus alternating between spring and neap tides. Transects were done around diurnal low tides and extended upshore and downshore from the drift line, for as far as isopods were obtained. Along each transect, five replicate 0.1 m<sup>2</sup> quadrats were taken to 20 cm depth, at 3 m intervals across the beach in a modified stratified random design (Pielou, 1974, p. 107). All isopods retained by sieving sand through a 1 mm mesh were preserved in 10 % formalin in seawater. In the laboratory, isopods were identified, sexed, counted and measured to 0.1 mm with a stereomicroscope fitted with an ocular micrometer.

Beach profiles were taken from the observed low water mark to above the drift line with a dumpy level. The last drift line was taken as the division between the zones of drying and retention (Salvat, 1964). The low water mark was defined as a third of the distance from the lower to the upper limit of the swash at low tide and the upper edge of the glassy layer (water table outcrop) was taken to separate the zones of resurgence and saturation. The division between the zones of resurgence and retention was defined as the level at which the sand became thixotropic.

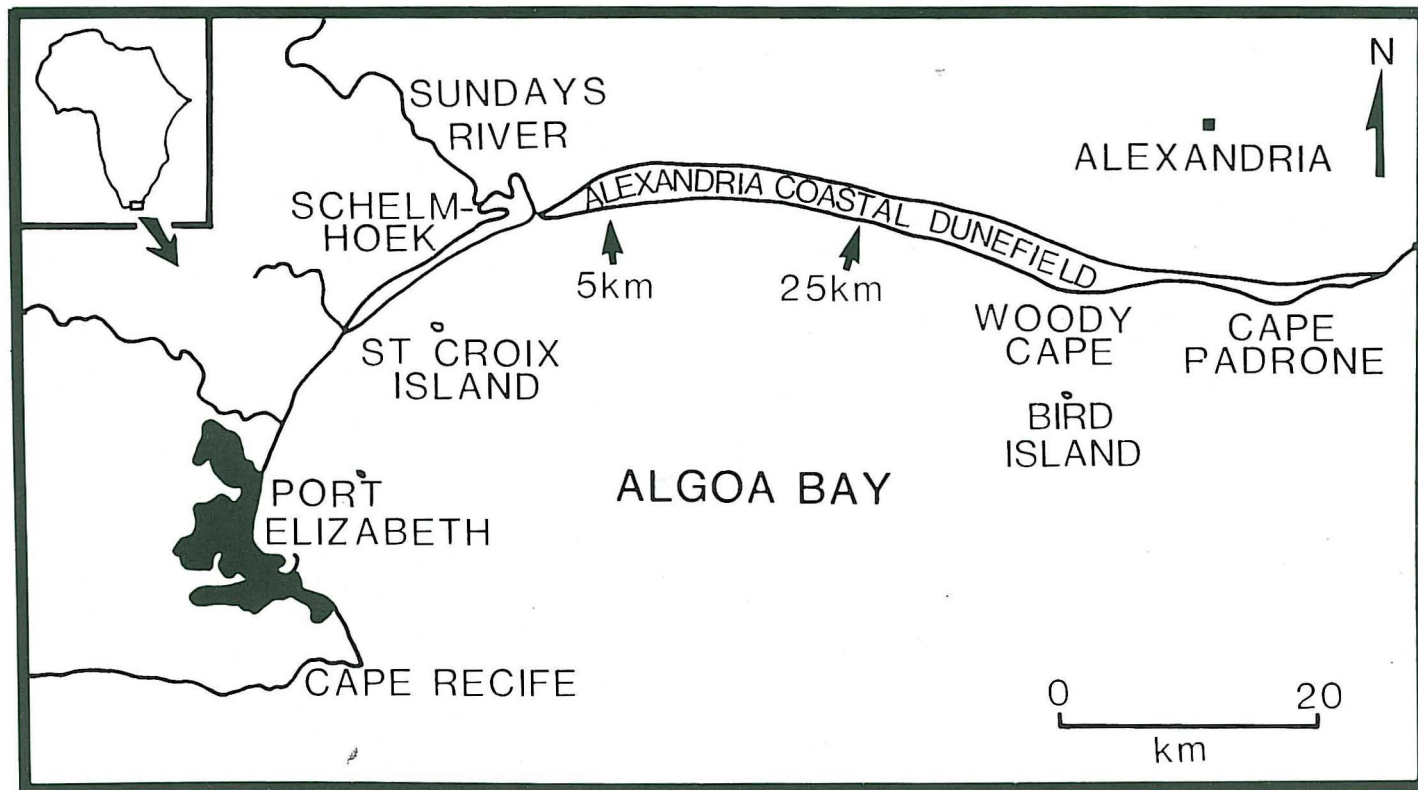


Fig. 1 : Map of Algoa Bay, showing the 5 km and 25 km sites.

Samples of the top 5 cm of sand were collected at 6 m intervals along each transect once during low tide. Moisture content was determined in the laboratory by drying the sediment at 70 °C for 48 hours and obtaining the percentage weight loss.

Abundance was calculated per running meter, i.e. the number of isopods occurring in a meter wide strip of beach perpendicular to the shore, from above the drift line down to the low water mark for as far as isopods were found in both directions. This makes allowance for uneven distribution of fauna exhibiting vertical zonation across the beach and for the dynamic morphology of sandy beaches with changing profiles (McLachlan, 1983). Because of patchy isopod distribution,  $\log_{10}(x + 1)$  transformation was done prior to analysis in order to normalize the abundance data.

Students t-test was used to test for significant differences in abundance between 5 km and 25 km sites. For tidal and seasonal changes in distribution the median elevation of the three species relative to the drift line was compared during 8 neap and 8 spring tides, using the t-test. The median elevation was calculated from the profile, as the elevation half way between the highest and lowest levels where individuals of a species were found for each of the 16 sampling dates. Intraspecific distribution differences were investigated by comparing, with ANOVA, the mean elevation of the different sexes (males, females, ovigerous females and immatures) and size classes relative to the drift line on 5 sampling dates.

Association between pairs of species in the areas of overlap was tested on 6 sampling dates (3 neaps and 3 spring tides) with the Chi-square test for independence in a 2 x 2 table (Pielou, 1974, p. 258), based on the presence or absence of a species in each quadrat.

#### Distribution along a rhythmic shoreline

Distribution of the three isopod species along a cusp system was examined on 2 June 1988 and 7 June 1990. Three equally spaced transects were taken along a cusp system, one each running down the cusp horn and cusp bay and one intermediate between the two. Transects were sampled as before, but three quadrats per level were taken rather than five.

Analysis was done separately for the two sampling dates. Numbers of each species found in all quadrats were added to obtain totals for each transect (position). The Chi-square test was used to test for differences in abundance between the three positions. The independence of species abundance and position was tested for each species separately, with the 2 x 3 contingency table. No statistical analysis of differences in vertical zonation between different size or sex classes within the cusp system could be done due to low numbers of isopods obtained on both occasions.

## RESULTS

#### Abundance at 5 km and 25 km

The t-test indicated a significant difference in the mean abundance between the 5 km and 25 km sites for both *E. longicornis* and *P. latipes* but not for *E. natalensis* (Table I), numbers being higher at 5 km (Fig. 2).

TABLE I

The mean annual abundance  $\pm$  95 % confidence intervals for *E. longicornis*, *P. latipes* and *E. natalensis* at the 5 km and 25 km sites with Chi-square values. (\*\* denotes significant difference at  $p < 0.01$ ).

Species	Abundance (numbers per running meter).		
	5 km	25 km	t-statistic
<i>E. longicornis</i>	493 $\pm$ 152	115 $\pm$ 39	5,08 **
<i>P. latipes</i>	288 $\pm$ 79	126 $\pm$ 66	3,31 **
<i>E. natalensis</i>	88 $\pm$ 23	105 $\pm$ 39	- 0,79 ns

### Zonation

The three species were found predominantly in the mid to upper intertidal. *E. natalensis* occurred highest up on the beach, around the drift line, and was recorded in sand with 2.8 - 17.5 % moisture content, maximum abundance occurring at 4 - 5 % moisture. *P. latipes* was found from the drift line to below mean tidal level in sand with moisture contents of 3.8 - 20 % maximum abundance occurring at 8 - 10 % sand moisture. *E. longicornis* concentrated around mean tidal level in sand with 5 - 20 % moisture, often extending down to and below the glassy layer where the sand was saturated ( $> 22$  % moisture content), especially during neap tides. Highest abundance of *E. longicornis* occurred in sand containing 16 - 18 % moisture.

Compared to Dahl's scheme, *E. natalensis* was found in the subterrestrial and midlittoral zones, *E. longicornis* in the midlittoral and sublittoral zones, whereas *P. latipes* occurred in all three zones. According to Salvat's scheme, *E. natalensis* occurred both in the zones of drying and retention, *E. longicornis* in the zones of retention, resurgence and saturation, while *P. latipes* was found from the zone of drying down to the zone of saturation, although most abundantly in the zone of retention.

There was no significant difference between the median distances or elevations (relative to the drift line) of the different sexes or size classes within any of the species. However, the largest *E. longicornis* individuals (8 - 10 mm) tended to occur lowest down and ovigerous females highest up on the beach within the zone. No negative or positive association could be demonstrated between the species in the areas of overlap.





### Changes in zonation

Kite diagrams of the three species' distribution and the glassy layer relative to the drift line at the 5 km and 25 km sites (Fig. 3-5) suggest that both the position of the drift line and the glassy layer had an effect on the species' vertical distribution. This was especially evident during Spring (early August to October), when the glassy layer occurred high up on the beach, due to strong south-westerly winds blowing onshore during this season. The *E. longicornis* zone stopped well above the glassy layer during spring tides (Fig. 3), but extended below the glassy layer during neap tides. The occasions when *E. longicornis* and *P. latipes* occurred below the glassy layer during spring tide were in September and late October, when Spring storms prevented the low water mark and glassy layer from dropping to "normal" levels during low tide.

Both *P. latipes* and *E. natalensis* were occasionally found above the drift line (Figs. 4 & 5), mostly during neap tides, or when the position of the glassy layer was relatively high up on the beach due to strong onshore winds. These conditions resulted in a narrow intertidal zone with greater overlap of the different isopod zones to conform to a narrow intertidal range. The median position of the *P. latipes* population at the 5 km site was situated above the drift line on only one occasion : at neap tide in August, compared to four occasions for *E. natalensis*.

There was a slight but significant difference in median elevation relative to the drift line between spring and neap tides for both *E. longicornis* and *P. latipes* (Table II). The median position of both populations occurred closer to the drift line during neap, possibly because these two species maintain a constant position on the beach, unaffected by semilunar cycles and the fluctuating drift line, or secondly, because their zones may be compressed within the narrower intertidal during neap as compared to spring tides. The difference is not significant in *E. natalensis*, indicating that this species, moves up and down with the fluctuating drift line.

TABLE II

The mean median elevation (m) of three intertidal isopods relative to the drift line (DL) compared during 8 neap and 8 spring tides t-test statistics are shown and\* denotes a significant difference at  $p < 0.05$ .

Species	Vertical distance below DL (m)		t statistic
	Neap	Spring	
<i>E. longicornis</i>	- 0.86	- 1.15	- 2.21*
<i>P. latipes</i>	- 0.38	- 0.79	- 2.26*
<i>E. natalensis</i>	- 0.07	- 0.33	- 1.21 ns

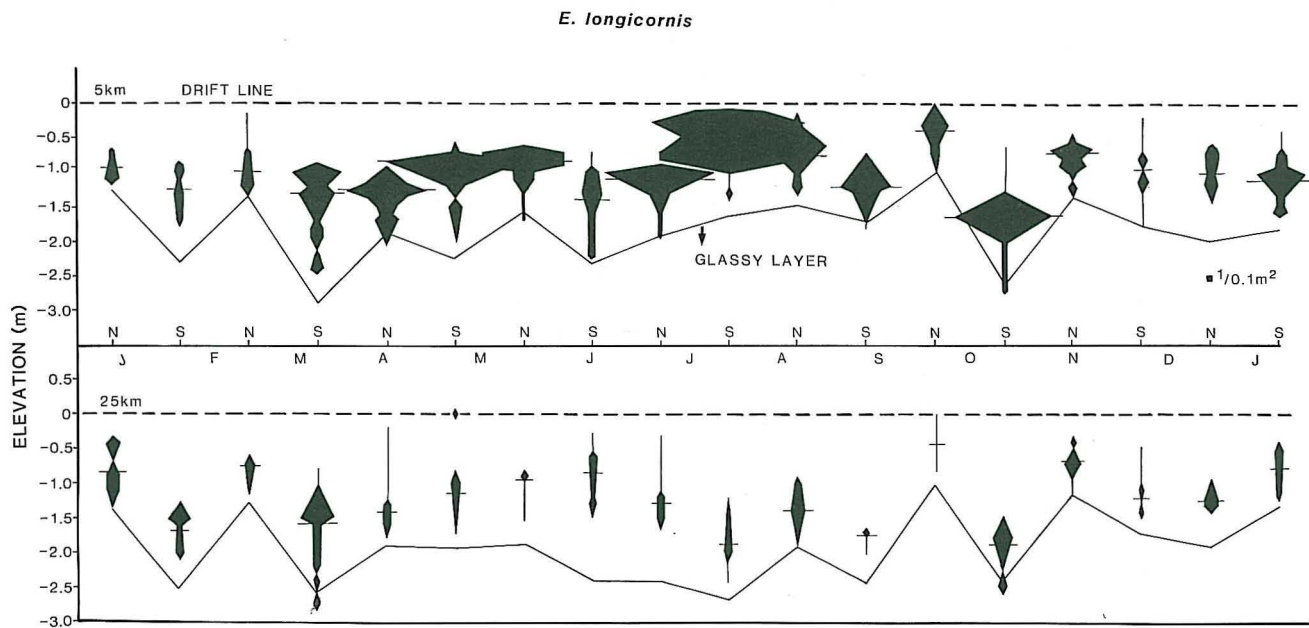


Fig. 3 : The position of *E. longicornis* and the glassy layer relative to the drift line at the 5 km and 25 km sites. Horizontal bars indicate the median elevation of the population.

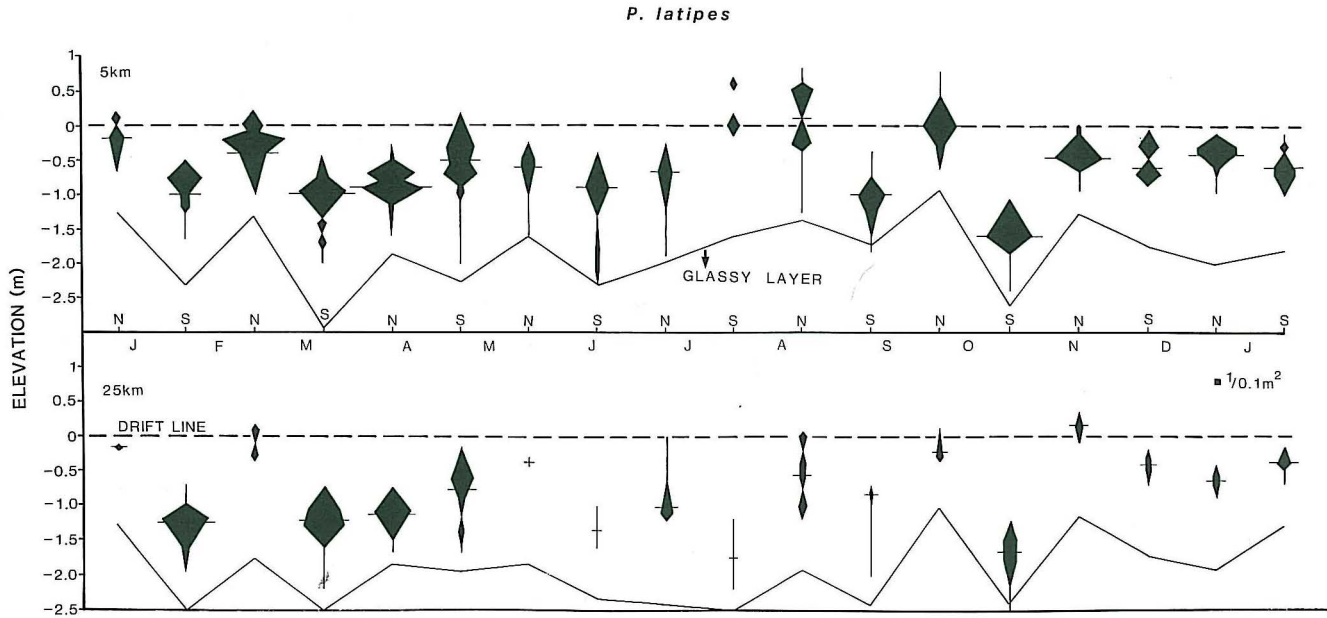


Fig. 4 : The position of *P. latipes* and the glassy layer relative to the drift line at the 5 km and the 25 km sites. Horizontal bars indicate median position of the population.

### Distribution along a rhythmic shoreline

There was a significant difference between the total number of isopods at the three positions in the megacusp systems on both occasions ( $X^2 = 37.3$ , 2 df,  $p < 0.001$  for June 1988 ;  $X^2 = 74.74$ ,  $p < 0.001$  for June 1989), the highest number occurring at the intermediate position. The 3 x 3 contingency table analysis showed a significant preference by the three species for certain positions along the cusp systems ( $X^2 = 9.74$ , 4 df,  $p < 0.001$  for June 1989 ;  $X^2 = 57.34$ ,  $p < 0.001$  for June 1990).

*E. natalensis* was most abundant at the intermediate position in June 1988 and equally abundant at the bay and intermediate positions in June 1990 (Table 2.4). The highest number of *P. latipes* occurred in the cusp bay June 1988, while no significant difference could be found between the three positions in June 1990. No significant difference was found for *E. longicornis* in June 1988, but in June 1990 the highest number occurred along the intermediate position.

The intertidal distance was widest at the intermediate position in June 1988 and narrowest at the bay on both occasions, whereas the horn and intermediate positions were of equal length in June 1990. The zones of the three species overlapped to a greater degree at the cusp bay. Both *P. latipes* and *E. natalensis* extended down to the glassy layer on the cusp bay ; lower than on the intermediate and cusp horn positions.

The 2 x 3 contingency table analysis revealed a significant differences in abundance of adults between the 3 different positions in June 1990 ( $X^2 = 8.13$ , 2 df,  $p < 0.05$ ). Adults showed a significant preference for the intermediate position, while immatures were uniformly distributed.

That highest abundance at the intermediate position is purely a function of intertidal width is unlikely, since more isopods occurred at the intermediate position than at the horn in June 1990, despite the equal width of the intertidal at both positions. This suggests active selection of the intermediate site along mega-cusp systems by adults. Possibly due to their weaker swimming ability, juveniles did not show this selective distribution.

## DISCUSSION

### Abundance at 5 km and 25 km

The lower abundance of *E. longicornis* and *P. latipes* at the 25 km as compared to the 5 km site could be due to increased surf energy (Bremner, 1983 ; Talbot & Bate, 1987), if wave energy is an unfavourable factor for these two species at the former site. McMurray (1985) recorded a steady decrease in biomass of the sandy beach mysid, *Gastrosaccus psammodytes*, east of 10 km to a minimum at 35 km along this beach, and ascribed this to increased surf energy conditions from west to east. Donn (1988 a) also found *E. natalensis* replacing *E. longicornis* as the dominant isopod on a more exposed, coarse grained beach at the eastern side of Plettenberg Bay, a similar log-spiral bay in the eastern Cape, whereas

*E. longicornis* dominated the more protected beaches on the western side. *E. natalensis* was also the most abundant of the three species on relatively coarse-grained beaches in Maputoland and Namibia (Donn, 1986, 1988 b) as well as on the west coast of South Africa (Bally, 1983 b). Although particle size is not sufficient to characterize beaches, coarse-grained beaches often reflect higher surf energy (Eleftheriou & Nicholson, 1975).

Brown (1973) reported that the sphaeromatid isopod, *Exosphaeroma truncatitelson* replaced *E. longicornis* on more sheltered beaches, whereas Bally (1983 b) showed that *E. natalensis* replaced *E. longicornis* as the dominant cirrolanid isopod on coarse-grained beaches, and suggested possible competitive interactions between these species. According to Brown (1973) and Bally (1983 b), *P. latipes* occurs in small numbers on all beaches, but this study shows higher numbers at the less exposed site as compared to more exposed sites on Sundays River Beach (Fig. 2), suggesting that *P. latipes*, like *E. longicornis*, is also affected by surf zone energy. Jones (1971) also considered the genus *Pontogeloides* to prefer less exposed beaches.

*E. natalensis* occurs highest on the beach and is only reached by the surf at high tide when swash turbulence is reduced near the drift line compared to the mid and lower intertidal, where the other two species occur. This may explain why *E. natalensis* is not adversely affected by high surf energy as the other two species appear to be. Alternatively, the larger size of *E. natalensis* compared to the other two species could be an advantage for burrowing into coarse sediment.

Dexter (1977) found that the abundance of *Excirrolana braziliensis* on sandy beaches of the Pacific and Atlantic coasts of Panama was not directly related to wave action, beach slope or median grain size, although the isopods tended to comprise a larger percentage of the total fauna on less protected beaches. Jones (1970) also found a difference in abundance of *Eurydice affinis* between two beaches with different degrees of exposure in Britain, but a difference in sand particle size was considered the main reason. Sand grain size is not thought to be a factor on Sundays River Beach, since there is no significant difference in sand particle size between the two sites (Donn, 1987).

### Zonation

The typical distribution of the three cirrolanid species on Sundays River Beach is presented in Fig. 6. *E. longicornis* occurs lowest on the beach, is the most abundant and prefers sand with a relatively high moisture content. *E. natalensis* occurs highest on the beach, is least abundant and prefers sand with a relatively low moisture content. *P. latipes* occurs between the above species and overlaps with both of them most of the time. The vertical zonation of the three species across the beach corresponded to that described by Bally (1983 b), McLachlan *et al.* (1981) and Wendt and McLachlan (1985). At neap tide, *E. longicornis* was also occasionally found in the 20 - 26 % moisture zone in the present study, which is lower down than the 7 - 20 % moisture zone in which Wendt and McLachlan (1985) recorded *E. longicornis* during spring tide. Bally (1983 b) found *E. longicornis*, *P. latipes* and *E. natalensis* to occur higher up on fine-grained beaches than on coarse-grained beaches on



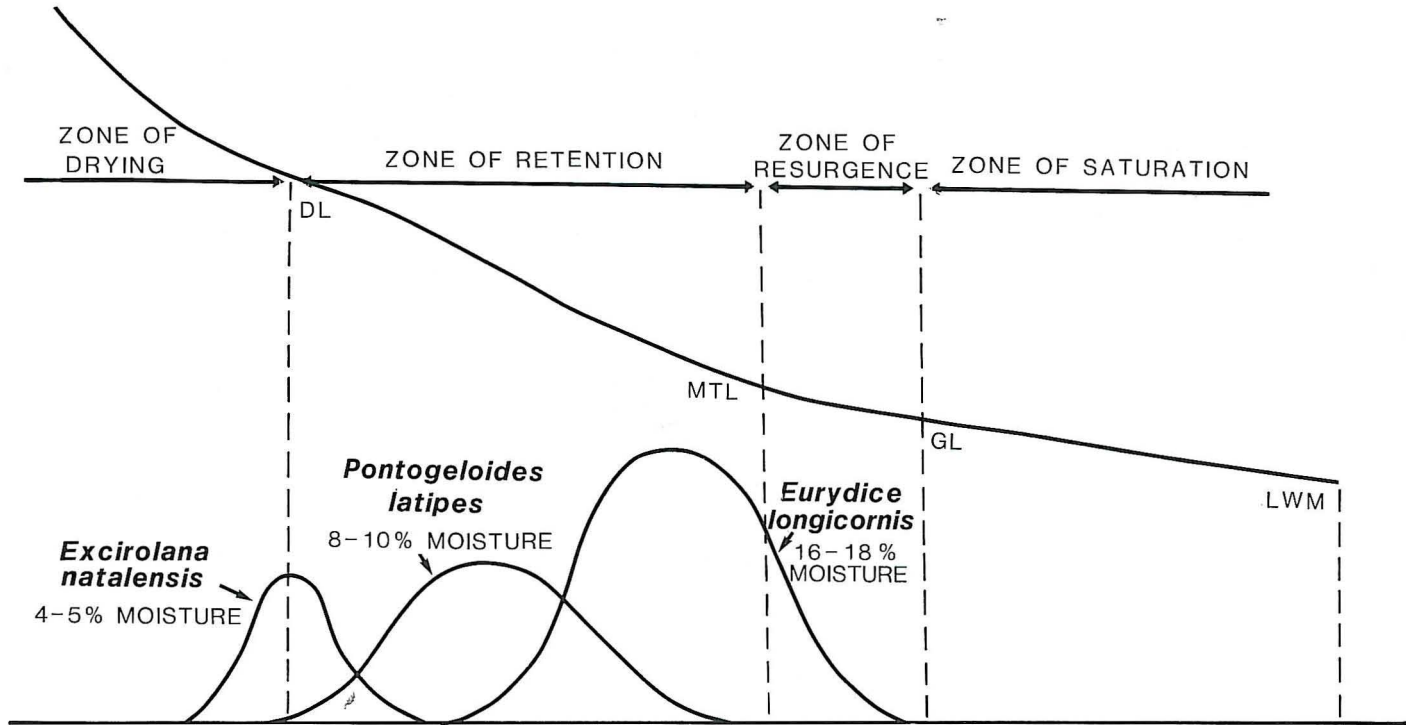


Fig. 6 : Typical distribution of *E. longicornis*, *P. latipes* and *E. natalensis* on Sundays River Beach, showing their distribution in relation to Salvat's scheme. Percentage sand moisture in the areas of highest abundance is given for each species. DL - drift line ; MTL - mean tidal level ; GL - glassy layer ; LWM - low water mark.

the west coast of South Africa. This could be due to poorer drainage and higher sand moisture content on the upper intertidal of fine-grained beaches (Bally, 1983 b).

The interspecific zonation shown by the three cirrolanid species on Sundays River Beach and other exposed sandy beaches in South Africa (McLachlan, 1977 b ; Bally, 1983 b ; McLachlan *et al.*, 1981 ; Wendt & McLachlan, 1985) is of interest since the zone of retention on many beaches supports only one cirrolanid isopod species (Dahl, 1952 ; Trevallion *et al.*, 1970 ; Dexter, 1972 ; Jones, 1974 ; Glynn *et al.*, 1975). Where geographical distributions overlap there may be a replacement of one species by another as in *Eurydice indicis* and *Eurydice peraticis* on the west coast of India (Eleftheriou & Jones, 1976). In Britain, *Eurydice pulchra* and *Eurydice affinis* occur together in mixed populations occupying the same zone (Jones & Naylor, 1967), but in France they occur in different zones (Salvat, 1966). Jones (1971) found up to 5 eurydicid isopod species co-existing on beaches in Kenya.

Attempts by Dahl (1952), Salvat (1964) and Trevallion *et al.*, (1970) to establish a universal classification system for zonation on sandy beaches have met with limited success, especially where more than one species of cirrolanid inhabits the same beach. Many authors have reported zonation patterns that differed from the above schemes (MacNae and Kalk, 1962 ; Pichon, 1967 ; Jones, 1969, 1971, 1974, 1979 ; Dexter, 1972 ; Epelde-Aguirre and Lopes, 1975 ; Eleftheriou & Jones, 1976 ; Bally, 1983 b ; Jaramillo, 1982, 1987 b ; Donn & Cockroft, 1989). Because three cirrolanid species inhabit Sundays River Beach, zonation differences with the schemes proposed by Dahl, Salvat and Trevallion *et al.* are not surprising. Zonation of isopods on Sundays River Beach differed from Dahl's scheme in that *E. natalensis* and *P. latipes* occurred also in the subterrestrial and *E. longicornis* also in the sublittoral zones ; from Salvat's scheme in that *E. natalensis* and *P. latipes* extended above the zone of retention and *E. longicornis* extended below the zone of resurgence and from Trevallion *et al.*'s scheme in that *E. natalensis* occurred also in the upper and *E. longicornis* and *P. latipes* also in the lower zones. In view of the deviations in zonation of cirrolanids from the proposed zonation schemes described by this and other studies, none of the schemes of Dahl, Salvat or Trevallion *et al.* seem to be applicable to Sundays River Beach and the use of cirrolanid isopods as indicators of zones is questionable. This is not surprising, considering the mobility of cirrolanids and the many factors which may influence their zonation, i.e., semilunar migration in (*E. natalensis*) and seasonal migration (in all three species). It is understandable why differences in zonation could be found by different studies, depending on what stage of the seasonal or semilunar cycle sampling is undertaken. A further problem may be the absence of uniformity in defining the boundaries of the different zones on different beaches.

The differences in vertical zonation observed in the three isopods under investigation could be due to different swash energy, temperature and desiccation tolerances. Salvat (1966) ascribed the separation of zones in *E. pulchra* and *E. affinis* to different temperature tolerances and Jones (1974) demonstrated that *E. affinis*, which occurred highest on the beach in France, survived high temperatures better than *E. pulchra*. Since *E. natalensis* and



*P. latipes* always occurred higher up on the beach than *E. longicornis*, this suggests a higher temperature tolerance and resistance to desiccation in the former two species. Predator-prey relationships could also be a reason for the observed vertical zonation patterns. In addition to the observation that all three species attack sick and weak individuals of their own and other species (pers. obs.), *E. natalensis* was observed to attack live and healthy *E. longicornis* and *P. latipes* when put in the same container with water, but less so when sand was added to enable burrowing. Perhaps this is not an important factor in the field since the densities there are much lower and sand is always available for protection. In addition, the level at which *E. natalensis* occurs is covered by the swash for a shorter period during the tidal cycle compared to that of the other two species, so that interspecific contact in the surf and the opportunity for interspecific predation is reduced.

The absence of negative or positive association in the areas where their zones overlapped suggest no obvious interactions between the species in the present study and zonation is suspected to be influenced mainly by environmental factors.

#### Changes in zonation

Zonation changes can be caused by dynamic changes in beach slope and conformation, often coupled to seasonal storms, seasonal temperature fluctuations or due to semilunar cycles. Storms and beach erosion will affect the median population positions relative to the drift line, both in terms of distance and elevation and it is difficult to separate these causes from possible semilunar influences. Zonation changes in the present study, although slight, seem to occur due to interaction of semilunar cycles and seasonal storms.

All three species appeared to move onshore during Spring, when strong onshore winds prevailed, thus exhibiting seasonal zonation changes. *P. latipes* and *E. longicornis*, unthreatened by stranding during neap, due to their lower position on the beach, maintained a relatively constant zonation on the beach for the rest of the year, as reflected by the difference in median elevation relative to the drift line between neap and spring tides (Table II). In *E. natalensis*, however, no difference was found between population position relative to the drift line during neap and spring tides. The latter species seems to follow the fluctuating drift line to a greater extent than the other two, its endogenous semilunar rhythm (De Ruyck *et al.*, 1991 a) serving to avoid stranding. *E. natalensis* thus exhibits semilunar migration in addition to seasonal zonation changes.

Fish (1970) found that the total number of *Eurydice pulchra* above the level of mean high water neap tides increased and that the upper limit of distribution occurred higher up on the beach with the increase in tidal height from neap to spring tides. McLachlan *et al.* (1979) also recorded semilunar migration in the adults of *Donax serra* and a compression of zones in the intertidal during neap tides. In this study a similar compression occurred, causing the zones of *P. latipes* and *E. natalensis* to extend above the drift line and the zone of *E. longicornis*, and occasionally *P. latipes*, to extend down to, and even below, the glassy layer during neap tides. Jones and Hobbins (1985) also reported more overlap in the zones of *Excirolana chiltoni* and *Eurydice nipponica* in south west Japan during neap tides. Jones

and Naylor (1970) and Hastings and Naylor (1980) described offshore migration in *E. pulchra* during winter storms, whereas Jaramillo (1987 a) reported offshore migration in cirrolanids during warm summer months in Chile.

TABLE III

Numbers of *E. longicornis*, *E. natalensis* and *P. latipes* collected on transects along mega-cusp systems in June 1988 and June 1990 (\* and \*\* denote significance at  $p < 0.05$  and  $p < 0.01$  respectively).  
June 1988 :

Species	Bay	Intermediate	Horn	X <sup>2</sup>
<i>E. longicornis</i>	4	10	4	4.0 ns
<i>E. natalensis</i>	3	10	6	6.46*
<i>P. latipes</i>	16	11	3	8.60*
Total	23	30	13	37.3**

June 1990 :

Species	Bay	Intermediate	Horn	X <sup>2</sup>
<i>E. longicornis</i>	10	118	53	98.1*
<i>E. natalensis</i>	21	21	4	12.6*
<i>P. latipes</i>	11	15	18	1.68 ns*
Total	41	154	75	74.7**

#### Distribution along a rhythmic shoreline

A significant preference for the intermediate position between cusp horns and bays was exhibited and, despite some variability between bay and horn abundances for the two cusp studies, the concentration of all three species was intermediate overall. No similar studies have been done on isopods. Cubitt (1969) and Perry (1980) found aggregations of *Emerita* spp. between bay centres and horns and the bivalves *Donax faba* and *Donacilla angusta* spp. were found in greater concentrations in similar positions (McLachlan & Hesp, 1984).

On sub-tropical beaches in Natal, South Africa, the filter feeding mole crab, *Emerita austroafricana* is concentrated near the centres of large mega-cusp bays, whereas the scavenging mole crab, *Hippa adactyla*, is more abundant around the horns (McLachlan and Hesp, 1984) where there is coarser sand (Dye *et al.*, 1981). Donn (1986) and Donn *et al.*, (1986) found macrofauna and bivalves of the genus *Donax* occurring in higher numbers on flat as compared to steep Namibian and eastern Cape sandy beaches. McLachlan (1990)

showed that beaches towards the dissipative end of the morphodynamic spectrum support a more abundant and species-rich fauna than beaches nearer the reflective extreme. This phenomenon may manifest on a small scale as well, i.e. in a mega cusp system.

The differential concentration along a cusp system could be a reflection of the preferences for different sand particle sizes (Jones, 1970 ; Bally, 1983 b) or food availability (McLachlan & Hesp, 1984) or reflect the effects of currents (Cubit, 1969 ; Dillery & Knapp, 1970). However, in this study the top 10 cm of sand, where the highest numbers of isopods occurred, did not differ visibly between the different transects. Finer food particles may accumulate on horns, which could explain the preference for horns by scavengers during calm conditions (McLachlan and Hesp, 1984). All three species in this study are highly mobile scavengers, being able to burrow into the sand within 2 seconds, yet they seemed to avoid the horn. Since food availability or sand particle size are not likely to explain the differential distribution of these isopods along cusp systems in this study, currents and differential surf energy is suggested as a cause for this phenomenon.

#### CONCLUSIONS

The vertical zonation pattern of the three cirolanid isopods on Sundays River Beach corresponded generally to those described by Bally (1983 a, b) on west coast beaches and McLachlan *et al.* (1981) on south coast beaches of South Africa. If Sundays River Beach is taken as representative of sandy beaches on the south-eastern coast, then by comparison with other studies the conclusion may be drawn that a similar vertical zonation pattern occurs on all exposed sandy beaches around the South African coast where these species occur together.

As expected on beaches with more than one cirolanid species, differences with Dahl's, Salvat's and Trevallion *et al.*'s schemes existed at Sundays River Beach. In view of the apparent differences in zonation both in the present study and the literature, the use of cirolanid isopods as indicators of zones is questionable. Environmental factors are suspected to be more important than biological interactions as cause for the observed zonation patterns of the three species, but more work is needed on this aspect. Although not conclusive, this study suggests longshore distributional differences in the cirolanid isopod populations both on a large scale along a log-spiral bay and on a small scale along a mega-cusp system. Seasonal changes in distribution seem to occur in all three species. In addition, *E. natalensis* exhibits semilunar zonation changes.

The flexible zonation patterns exhibited by the cirolanid isopods on Sundays River Beach may be due to the low tidal amplitude (1.6 m) and the high wave energy (1-6 m waves) in this location as compared to beaches in Europe where the tidal amplitude is in the order of 5-10 m for a wave height of 1-2 m. The weak zonation patterns exhibited here may be an adaptation for survival in the dynamic, unstable conditions of a high energy, microtidal beach.

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