Short Communications

Sand moisture as a factor determining depth of burrowing in the oniscid isopod *Tylos granulatus* Krauss

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Tylos granulatus, a sandy-beach isopod, prefers an environmental moisture range exceeding 3,4% but less than 13%. The depths to which the animals burrow are, at least partly, determined by the moisture gradient in the sand. They are, however, incapable of burrowing into totally dry sand. Animals alter their position in the sand in response to changes in moisture content so as to ensure exposure to suitable conditions.

Tylos granulatus, 'n sandstrand isopod, verkies 'n omgewingsvogtigheidsgraad wat 3,4% oorskry maar minder is as 13%. Die dieptes waartoe die diere grawe word, minstens gedeeltelik, deur die vogtigheidsgradient in die sand bepaal. Hulle is egter nie in staat om in 'n heeltemal droë sand te grawe nie. Die organismes kan hulle posisie in die sand verander met 'n verandering in vogtigheid, om so, blootstelling aan geskikte toestande te verseker.

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It has frequently been suggested that depth of burrowing in a number of sandy-beach, semi-terrestrial invertebrates, including *Tylos*, is related to the moisture content of the substratum (Hayes 1969; 1974; 1977; Kensley 1974; Garthwaite, Hochberg & Sassaman 1985; Brown & Trueman 1994). Brusca (1966) came to the same conclusion for the fully terrestrial oniscid *Alloniscus perconvexus*. Holanov & Hendrickson (1980) tested this hypothesis with regard to *Tylos punctatus* inhabiting sandy beaches in the Gulf of California. Day-time distribution within the substratum was determined, as well as the moisture content of the sand column at intervals of 5 cm. Their results indicated that *T. punctatus* burrows downward until it reaches sand with a moisture content of between 1,5 and 2%, regardless of ambient temperature. These authors further showed that animals held in sand with a moisture content of 1,1% at 33°C for 12 h all survived, whereas 14 of 25 animals held at a 0,1% moisture content, at the same temperature and for the same length of time, died.

The evidence from the above observations was largely circumstantial and we decided to conduct more critical experiments in the laboratory to test a possible relationship between depth of burrowing and substratum moisture content in *Tylos granulatus* Krauss, a species which is typical of the South African west coast. The general biology of this species has been reviewed by Kensley (1974) and more recently by Brown & Odendaal (1994), while the mechanism and cost of excavating the burrows have been investigated by Brown & Trueman (1994).

Animals were collected from Yserfontein (33°22'S; 18°19'E) during May and July 1992. Only adult *T. granulatus* were used (mean size: 21,9 ± 1,9 mm maximum width, n =140). Three series of laboratory experiments were performed at ambient temperatures (16–19°C).

1. To ascertain the preferred moisture conditions, a series of sand-filled PVC columns (20-cm diameter; 120-cm height) were prepared. The moisture gradient in each ranged from *c.* 1% on the surface to 20% at 1-m depth. A small volume of sea-water was placed in a holding tank at the base of each column to ensure maintenance of the moisture gradient. Groups of 7–9 animals were placed on the surface of each column and left for 72 h to allow them to burrow and establish themselves in the columns. Pieces of fresh kelp (*Laminaria pallida*), upon which the animals could feed, were left on the surface. The columns were then excavated and the depths of the animals noted. About 100 ml of sand was collected from the surface and at 5-cm depth intervals, weighed, oven-dried (12 h at 90–100°C) and reweighed. The difference in moisture content was calculated and expressed as a percentage. Seven such experiments were performed and no animal was used more than once. Results indicate a mean value for selected moisture content of 7,2% (SD = 2,5; range = 3,4–13%; n = 56). Animals placed on totally dry sand did not burrow, or were not successful in their attempts, and took refuge under kelp fronds on the surface.

2. To determine if the depth to which *T. granulatus* burrows reflects its selection of a particular moisture level, three experiments were performed. Animals were collected on three separate days by excavating a 1-m^2 area of beach to a depth of 0,6–1,0 m (below this, a layer of coarse gravel occurred). Sand samples were collected at 5-cm depth intervals for moisture content determination. Animals encountered during the excavation were numbered on the dorsal surface of the pleon with a waterproof pen, and their relative depths recorded. In the laboratory, the animals (n = 7, 6 & 7) were transferred onto experimental columns in which a specific moisture/depth gradient had been established. Animals were allowed 72 h to establish themselves before being excavated. Their depth, and the moisture content of sand samples were determined as previously described. The animals were transferred to a second column, with a different moisture/depth profile. The procedure was repeated five or six times for each group of animals. In each of Figures 1A–C, field conditions (F) are shown, together with results from subsequent reburrowing, numbered accordingly. Mean moisture values for animals in the field ranged from 5,8% (±0,9) to 6,8% (±0,9), and mean depths from 32,9 (±7,0) to 60,7 cm (±7,9). Moisture levels selected by the animals in the laboratory tended to be slightly higher than those selected in the field, all, nevertheless, falling within the range recorded in (1) above. Depth of burrowing, on the other hand, covered a very wide range (10–93 cm), depending on the moisture profile presented.

3. We tested whether *T. granulatus*, having burrowed and settled at a specific depth, would alter their positions in response to changes in moisture content. Each experiment

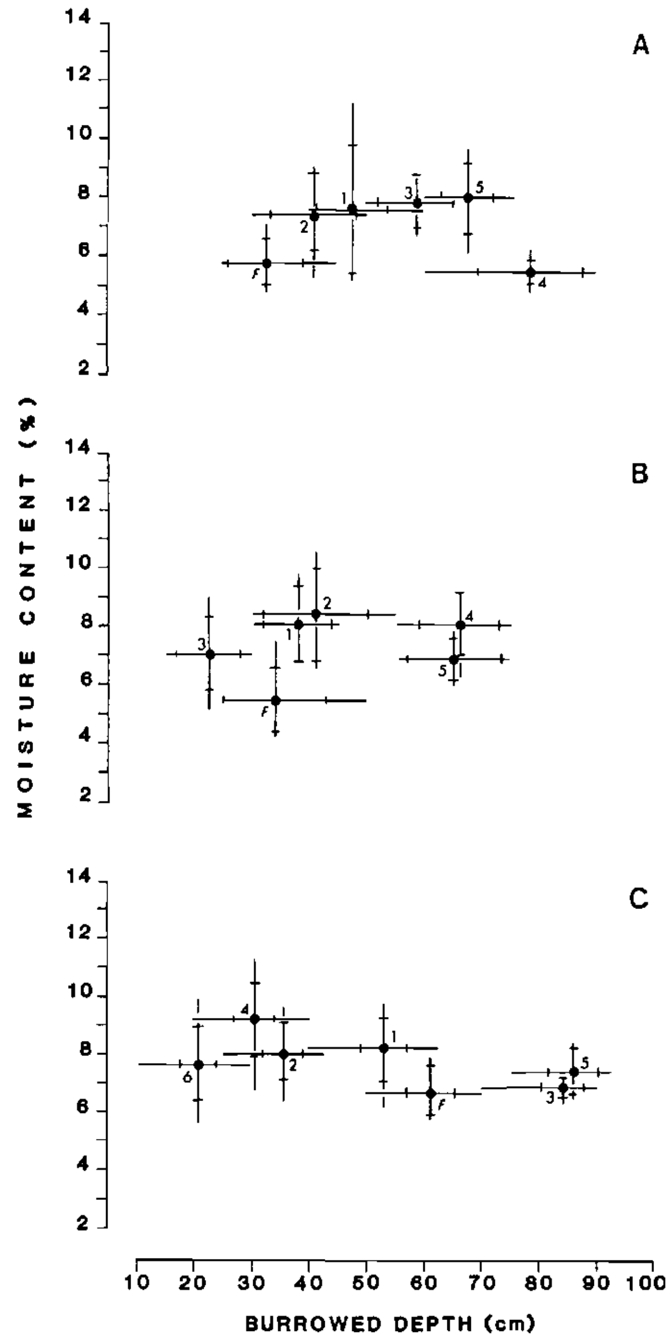

Figure 1 Sand moisture / burrowing depth relationship from three separate experiments (A–C) (n = 7, 6 & 7, respectively). F = field conditions recorded during collection. Numbers 1–6 are consecutive re-burrowing results for each group of animals transferred to columns with different moisture / depth profiles. All results are given as a mean ±*SD* and range.

involved two columns displaying virtually identical depth/moisture profiles. Seven or eight animals were placed on each column and after 72 h one of the columns was excavated. The second column was subjected to a rise in water level by the addition of sea-water into the holding tank, so that the level rose about half way up the column. After a further 6 h this second column was excavated. Four such experiments were conducted and no animal was used more than once. The results (Figure 2) indicate an upward movement of isopods in response to a rising water table. The animals re-established themselves at shallower depths (from a mean depth of 52,7 cm (±11,1) to 25,6 cm (±7,2)), but within the same moisture range as originally occupied (from 7,1% (±2,3) to 8,2% (±3,0)). No animals emerged onto the surface during this period.

Results of our experiments indicate that the moisture content of the substratum is a major factor in determining the depth of burrowing by *Tylos granulatus*, and that the animals adjust their positions in the sand to ensure exposure to suitable moisture conditions. It is clearly important that they come to rest in sand which is neither too dry nor too wet; oniscids show little modification for terrestrial or semi-terrestrial life and lose water rapidly through the integument when exposed to non-saturated air (Edney 1957; Matthewson 1991). They are thus critically dependent on behavioural machanisms to reduce water loss, seeking out microhabitats of high humidity for at least part of every day (Cloudsley-Thompson 1956; Edney 1968; Holanov & Hendrickson 1980). On the other hand, they drown if submerged in water for any length of time (Kensley 1974; Brown & Odendaal 1994).

It is tempting to infer from a comparison of our laboratory-based results with the field data of Holanov & Hendrickson (1980), that *T. granulatus* prefers a higher moisture content than does *T. punctatus*. Such a conclusion would not be justified, however, as different sands have different grain sizes and are hence saturated by different water contents. How the animals detect moisture content has yet to be investigated but it seems likely that relative humidity or, more probably, saturation deficit is the principal cue involved. Stenton-Dozey & Webb (in prep.) have examined scanning electron micrographs of *T. granulatus* and have identified structures which may well be sensitive to the dryness of the interstitial air. Brown (in Brown & Odendaal 1994) has reported that *T. granulatus*, deprived of sand in which to burrow, moves up a humidity gradient in the laboratory.

Despite the clear correlation between moisture content and depth of burrowing reported above, we can not claim that no other factor influences this depth. Grain size and its stratification within the beach must also play a role. *Tylos granulatus* has been observed to burrow through a layer of coarse, shelly sand when this occurred close to the surface but to cease burrowing when such a layer was present at a deeper level. It may be noted that the difference in cost to the animal between deep and shallow burial appears to be negligible when compared with total metabolic cost over a 24-h period (Odendaal, Eekhout, Brown & Branch 1994). Burrowing to a depth of 1 m entails a metabolic cost of *c*. 1,5 J in a large adult (Brown & Trueman 1994), compared with a total metabolic expenditure exceeding 58 J over a period of 24 h.

An unexpected discovery was that the animals cannot burrow in totally dry sand, coming to rest just below the surface as the burrow collapses behind them. In the field, this would clearly place them at risk of desiccation and high temperatures. It is therefore not surprising that on dry sand they tend to shelter under debris on the surface. Although such behaviour has not been observed in the field for this

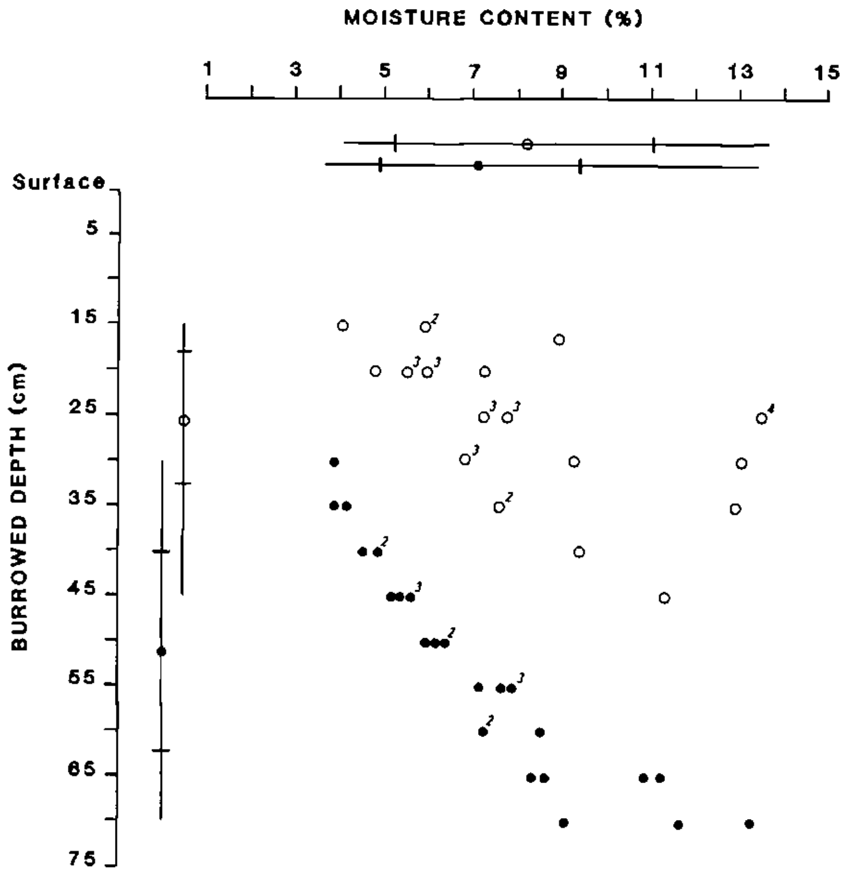

Figure 2 Response of burrowed *T. granulatus* to changes in moisture content in the experimental columns. ● = position of animals in a constant moisture gradient (n = 30); ○ = position of animals following a rise in water levels (n = 32). Depth and moisture content selected by each group are given as mean ±SD and range. Where appropriate, numbers indicate more than one datum point.

species, it is known to occur in *T. punctatus* (Hamner, Smythe & Mulford 1968) and in the Japanese *T. granulatus* Miers (non *T. granulatus* Krauss) (Imafuku 1976).

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