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ORIGINAL ARTICLE

Relationships between bioturbation by *Tylos spinulosus* (Crustacea, Isopoda) and its distribution on sandy beaches of north-central Chile

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Conflict of interest
The authors declare no conflict of interests.

Abstract

The semi-terrestrial isopod, *Tylos spinulosus* Dana, is a common inhabitant of the upper shore levels of sandy beaches of north-central Chile (ca. 26–30°S). During daylight hours, this isopod remains buried in the sand, while during the night emerges for feeding on stranded organic detritus, leaving exit holes on the beach surface. After feeding, isopods return to dig in their burrowing zones leaving surface irregularities such as cone-shaped mounds of sand. The burrowing preference of *T. spinulosus* was studied in the field, by: (i) releasing 30 isopods on artificially prepared sand circles (2 m diameter) having exit holes and mounds similar to those left by the isopods and on circles without holes and mounds, and (ii) counting active and buried isopods 15 min after their release in the experimental arenas. The circles had two densities of holes and mounds: treatments 1 and 2 had 100 and 200 holes, respectively, while treatments 3 and 4 had 100 and 200 mounds, respectively. Other 30 isopods were released on sand circles without these holes and mounds (treatment 5). A significantly higher number of isopods buried in circles with holes and mounds (either inside or outside them), compared with experimental arenas without such structures. These results show that the beach surface heterogeneity resulting from holes and mounds would be one of the processes explaining the patchiness of *T. spinulosus* and thus, its zonation on the intertidal zones of sandy beaches of north-central Chile.

Problem

The semi-terrestrial isopods of the genus *Tylos* (Oniscoidea) are typical inhabitants of the sandy beach macroinfauna, inhabiting the upper-shore levels of mid-latitude sandy beaches around the world (Hamner *et al.* 1969; Kensley 1974; Imafuku 1976; Hayes 1977; Brown & McLachlan 1990; McLachlan & Jaramillo 1995; Odendaal *et al.* 1999; Jaramillo *et al.* 2001). Similar to other upper beach arthropods, such as talitrid amphipods and tenebrionid insects, tylid isopods usually remain buried in the sand or underneath algal wrack deposits during daylight hours, while during the night they emerge for feeding on stranded organic detritus, leaving exit holes on the beach surface (e.g. Kensley 1974; Brown & Odendaal 1994). After feeding, isopods return to dig in their burrowing zones, which are located close to the high water line and leave surface irregularities such as cone-shaped mounds of sand (Kensley 1974; Hayes 1977; Odendaal *et al.* 1999). The species of *Tylos* show across and along shore spatial variability. The first one has been analysed in terms of changes in the location of the drift line and variability in physical factors such as beach face slope, grain size and water content of sands (e.g. Kensley 1974; Imafuku 1976; Hayes 1977; Holanov & Hendrickson 1980). Their along shore variability, which results in aggregations of the isopods mainly around the high water mark, has been related to the location of algal wrack deposits (Kensley 1974; Brown & Odendaal 1994), differences in the penetrability of the substratum (Brown & Odendaal 1994) and location of existing burrowing holes (Odendaal *et al.* 1999).

Tylos spinulosus Dana, the only species of the genus found on sandy beaches of the long Chilean coast is restricted to sandy beaches of north-central Chile (ca. 26–30°S). This isopod is a common inhabitant of the upper shore levels of sandy beaches where it coexists with the talitrid amphipod *Orchestoidea tuberculata* Nicolet and the tenebrionid insect *Phalerisida maculata* Kulser (Jaramillo 1987, 2001; Jaramillo *et al.* 1998, 2001, 2003). Despite the fact that *T. spinulosus* is quite a common species along this area of the Chilean coast, its biology and ecology remain almost unknown. Thus, while this species has been mentioned on studies on the zonation of the whole sand beach macroinfauna of the Chilean coast (e.g. Jaramillo 1987, 2001), there are just two studies dealing with biological and ecological aspects of *T. spinulosus*. Jaramillo *et al.* (2003) analysed on a sandy beach of north-central Chile (El Apolillado, 29°10′S, 71°29′W) the locomotor activity and interspecific interactions of this isopod and that of *O. tuberculata* and *P. maculata*, the other two species, which form the scavenger guild on those beaches, finding that the mean hourly zonation of the night locomotor activity of *T. spinulosus* was similar to that of *P. maculata* but different from that of *O. tuberculata*. These results did match with that of laboratory experiments, where the survival of *T. spinulosus* was affected by the presence of *O. tuberculata*; thus, Jaramillo *et al.* (2003) concluded that differences in time/space partitioning of surface locomotor activity would allow coexistence of scavenger arthropods on the same beach. Jaramillo *et al.* (2006) also studied at the beach El Apolillado, the population abundances of *T. spinulosus* under algal wrack deposits and nearby bare sands, finding up to nearly 24 times more abundances underneath the stranded macroalgae.

The band, in which the burrowed *T. spinulosus* is found during daylight hours, shifts both across and along shore, a pattern similar to that shown by other species of *Tylos* (Kensley 1974; Hayes 1977; Brown & Odendaal 1994; Odendaal *et al.* 1999). While the across shore variability of the band changes according to the fortnightly tidal cycle, and thus is primarily related to the changing high tide mark (cf. Kensley 1974; Brown & Odendaal 1994), the discontinuous along shore distribution of the burrowing zones of *T. spinulosus* seems to be independent of physical factors, as for example, large-scale beach heterogeneities such as cusps and bays, typical features of intermediate beaches commonly inhabited by this species in north-central Chile (E. Jaramillo, unpublished data). Although population abundances of this isopod are higher in sediments underneath algal wrack deposits (Jaramillo *et al.* 2006), patches of sand bioturbated by *T. spinulosus* are not necessarily found associated with patches of stranded macroalgae found along the coastal line. Thus, other factors are probably involved in the distribution of the burrowing zones of *T. spinulosus*, among them bioturbated sands with holes and mounds produced by the same isopods, as it has been shown for *T. granulatus* in South Africa by Odendaal *et al.* (1999). These authors showed that the presence of beach surface irregularities caused by the presence of the existing exit holes and mounds was important in inducing the patchy distribution of the buried isopods.

Sandy beach organisms usually show a high degree of behavioural plasticity (Chelazzi & Colombini 1989; Colombini *et al.* 1994; Brown 1996; Soares *et al.* 1999; Fallaci *et al.* 1999), which allows them to cope with and adapt to short and long-term variations in their inevitable dynamic habitat. For example, sandy beach Coleoptera show variable locomotor activity in time and space as a response to climatic changes, which may result in tidal variations and sudden stormy conditions (Chelazzi & Colombini 1989; Colombini *et al.* 1994). The differences in the location of the burrowing zone of juveniles of the talitrid amphipod *Talitrus saltator* (Montagu) in sandy beaches of the Mediterranean sea, where they are lower down the beach than the adults, and the French Atlantic coast, where they are higher up the beach, were related to a combination of differences in beach width, beach slope and tidal range (Fallaci *et al.* 1999). For tylid isopods, it has been argued that these sorts of strategies are essential adaptations for survival in continuously changing habitats, such as sandy beaches (Brown & Odendaal 1994). Thus, the aim of this study was to investigate whether the pattern of distribution of *T. spinulosus* is influenced by the location of their exit holes and digging mounds, as it has been proposed throughout the hole-mound hypothesis (Odendaal *et al.* 1999) on the west coast of South Africa. Finding similarities and convergent biotic traits among biogeographical regions with similar physical and biological features constitutes the necessary basis for general models. Both the coast of north-central Chile and that of West South Africa are similar. On both coasts, coldness of the currents, which originate in the West Wind Drift Current circling the Antarctic (Humboldt and Benguela Currents, respectively), has a profound influence on the climate by air passing from the cold sea to the hot land, resulting in arid and desert-like environments (Branch & Branch 1981). On both shores, tylid isopods, talitrid amphipods and tenebrionid beetles make up most of the macroinfauna inhabiting the upper shore levels (cf. Bally 1983; McLachlan 1985; Jaramillo 1987, Jaramillo *et al.* 2001).

Material and Methods

The experimental animals were collected from the sandy beach of Ventanas (29°10′S, 71°29′W), which is included in the Peruvian or Transition Zoogeographic Zone of the Chilean coast (Knox 1960; Dell 1971; Marincovich 1973). This beach is located on the semi-arid coast of Chile and has an annual rainfall close to 110 mm (Brattstrom & Johanssen 1983). The length of the beach is close to 3 km and it is backed by dunes close to 8 m in height. Morphodynamically, Ventanas is an intermediate type of beach (*sensu* Short & Wright 1983). Tides are semidiurnal with an approximate range of 1.4 m.

The burrowing preference of *T. spinulosus* on different beach surfaces was analysed by the preparation of five types of 2 m diameter circles of groomed sand in the part of the beach where isopods move during the night. These were: (i) 12 circles with 100 artificial holes made with a wooden stick 15 mm in diameter and resembling the exit holes made by *T. spinulosus* (treatment 1), (ii) 12 circles with 200 artificial holes (treatment 2), (iii) 12 circles with 100 mounds around holes (mounds from now on) made by hand and similar to that left by the isopods while digging (treatment 3), (iv) 12 circles with 200 mounds around holes (treatment 4), and (v) 12 circles with no holes and mounds (treatment 5, the control) (see Fig. 1 for a views of the experimental arena). We used two densities of holes and mounds to test whether variations in the number of such structures influenced the burrowing of this isopod. Holes and mounds were roughly evenly spaced in the 0.5 m outer border of each circle. Each circle was limited by a cardboard wall of 12 cm height to avoid escape of experimental animals. The sand circles were cleaned from any wrack and located in beach areas where it was checked that no other scavenger arthropod (*O. tuberculata* and *P. maculata*) was active on the beach surface.

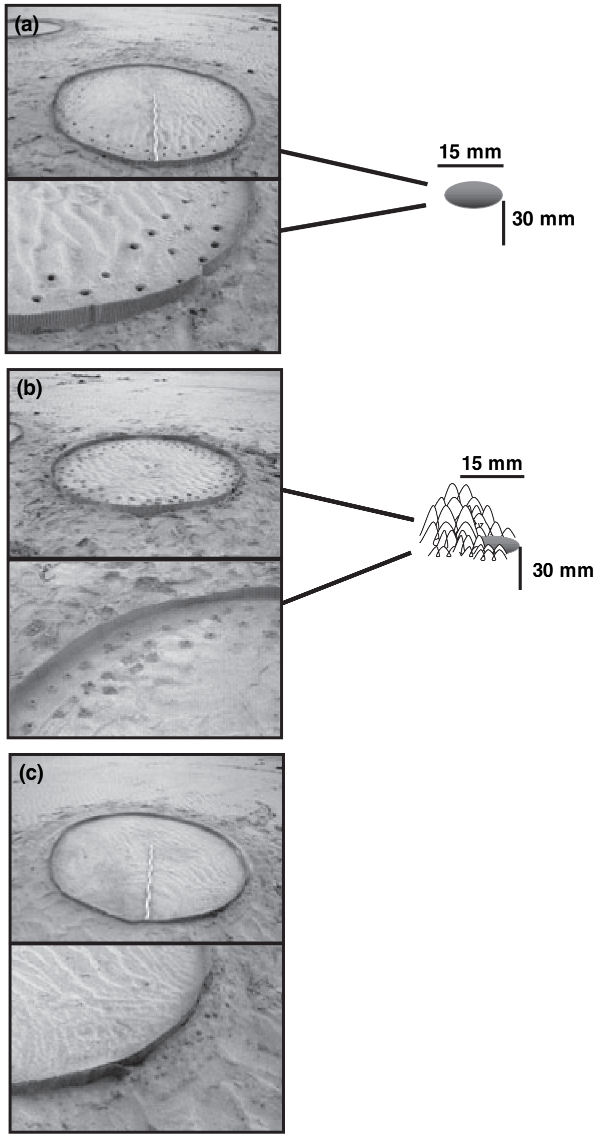

Fig. 1. General and partial views of sand circles with holes (a) and mounds (b) and without those artificial structures (c) (see Material and Methods for details). The scale is equal to 1 m.

At about 20:00 h, before the peak in the locomotor activity of *T. spinulosus* on the beach surface (cf. Jaramillo *et al. 2003*), isopods were randomly collected from excavations (i.e. nearly 30 cm in diameter) located at least 100 m away from the experimental circles. The collected isopods were kept in plastic boxes of 1 l volume with a layer of sands of nearly 5 cm deep. Only adult isopods (i.e. 20–23 mm in body length measured in stretched animals from the tip of the cephalon to the tip of the telson), were chosen to be used in the experiments. Close to the end of the locomotor activity, (around 23:00–24:00 h; cf. Jaramillo *et al.* 2003), 30 isopods were released in darkness at the centre of each experimental circle. After 15 min, the number of active isopods (i.e. those not buried) and that collected manually from inside the artificial holes and mounds of the outer section of each circle were manually collected and counted. Because of shortage of time, it was not possible to count the number of isopods that had buried in the smooth parts of the circles (i.e. the surface located between the holes and mounds of the outer section as well as the inner section) that had artificial structures (T1, T2, T3 and T4). This number was obtained by subtracting the number of active isopods plus the number of animals buried inside holes and mounds from the total number of experimental animals (30). The experiments were carried out during night low tides and during the period 15–21 August 2001 (18 August: new moon). The number of isopods seen over the beach surface was similar on each night. Statistical comparisons were carried out using ANOVA and the *a posteriori* test Tukey HSD (Honestly Significant Difference) (Zar 1999). Assumptions of normality and homocedasticity were tested with the Shapiro–Wilk's and Bartlett's tests, respectively (Zar 1999).

Results

The total number of isopods buried in the circles with holes and mounds (~21–27 isopods, treatments 1–4), either inside holes and mounds or outside them, was significantly higher than number of isopods buried in the circles without such artificial structures (~16 isopods, treatment 5) (Fig. 2a). The total number of isopods buried in circles with 100 holes (treatment 1) was significantly higher than the total number of isopods found buried at the circles with 200 mounds (treatment 4) (Fig. 2a). The number of isopods found buried inside holes and mounds of treatments 1, 3 and 4 (~7–10) was significantly lower than the number of isopods found buried at the circles without artificial structures (treatment 5) (Fig. 2b). Number of isopods found buried inside holes of treatment 2 (~13) differ significantly from number of isopods found buried in mounds of treatment 3 (~7), while were similar ($P > 0.05$) to the number of isopods found buried at the circles without that artificial structures (Fig. 2b).

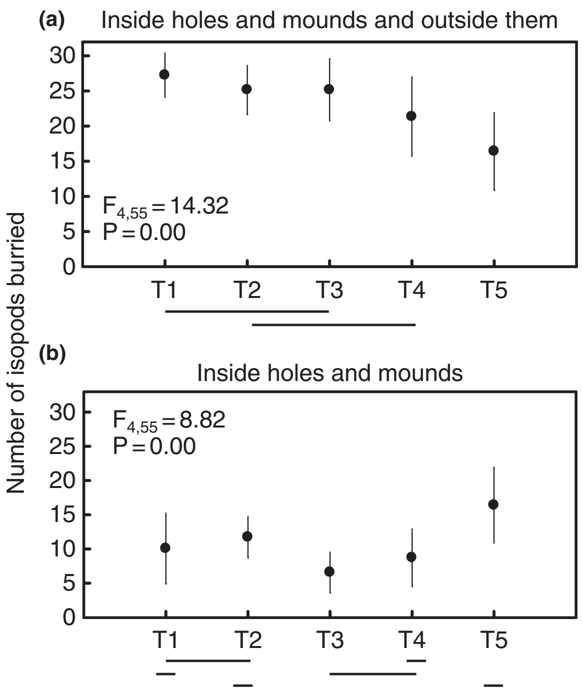

Fig. 2. (a) Total number of isopods found buried in the circles with holes (treatments 1 and 2) and mounds (treatments 3 and 4) and in circles without such artificial structures (treatment 5). (b) Number of isopods found buried inside holes and mounds in the circles of treatments 1–4 and in circles without such artificial structures (treatment 5). Values of F and P resulted from ANOVA. Lines link means not significantly different (results of Tukey's HSD *a posteriori* test).

Discussion

The results of this study show that presence of artificial holes and mounds enhanced burrowing of *T. spinulosus* in the experimental arenas. This conclusion is based on the fact that the total number of isopods buried was higher in those circles with holes and mounds compared with circles with flat sand surfaces. Even when the number of isopods buried outside holes and mounds was not counted, it is worthwhile to mention that presence of mounds in the centre flat areas of circles with such artificial structures was minimal (i.e. the occasions other than digging mounds were observed at those flat areas, which rendered numbers of such structures lower than three). Consequently, we can conclude that most of the isopods buried in the sand areas located within the band of holes and mounds of treatments 1–4. Thus, it seems that beach surface irregularities or visible clues such as holes and mounds *per se* do not act as promoters, but the whole landscape bioturbated by the isopods. Based on the burrowing preferences of *T. granulatus* on the west coast of South Africa, Odendaal *et al.* (1999) developed the hole and mound hypothesis, which states that more *Tylos* will bury in beach areas with higher densities of such features. The preference of *T. granulatus* and *T. spinulosus* to burrow in areas with holes and mounds would result in the aggregated distribution of these species along the beaches of the west coast of South Africa and north-central Chile (cf. Odendaal *et al.* 1999).

Notwithstanding the similarity between the burrowing preferences of *T. spinulosus* and *T. granulatus* for beach surface irregularities, the results of this study differ from that of Odendaal *et al.* (1999) in the sense that in circles with the lower density of mounds, *T. spinulosus* preferred to burrow in areas located between mounds rather than inside those structures. In contrast, *T. granulatus* always preferred to bury inside mounds, even in that treatment with lower density of such structures. Another important difference was that while higher density of holes and mounds enhanced the burrowing of *T. granulatus*, the two densities used in our experiments did not generally affect the burrowing preference of *T. spinulosus* when subjected to varying densities of such artificial structures.

Two possible explanations were given by Odendaal *et al.* (1999) to account for the burrowing preference of *T. granulatus*. Both were unrelated to a possible saving of energy, which was dismissed by those authors after several calculations of energy costs for the South African species. As hypothesized by Odendaal *et al.* (1999), the use of existing holes or burrowing in the reworked sediments of the mounds would reduce the exposure time to wave action and thus reduce the possibility of being washed away by incoming waves. Furthermore, the use or burrowing in mounds would allow *T. granulatus* to disappear quickly below the beach surface and thus escape from predators such as the yellow mongoose (*Cynictis penicillata*). Both of these hypotheses would also hold for the burrowing preference of *T. spinulosus* on sandy beaches of the coast of north-central Chile. These beaches are fully exposed to the breaking waves of the Pacific Ocean and so there is indeed a high possibility that isopods moving over the sediment surface can be swept away by the incoming waves. Also, the upper shore levels and foredunes where *T. spinulosus* moves around during the night hours are commonly visited by foxes, which presumably seek to feed on these isopods, as well as the tenebrionid insects, which reach high population densities at the beach studied (Jaramillo *et al.* 2003).

Despite the above-mentioned differences, the general conclusion is that the Chilean species of *Tylos* behaves similarly to its counterpart on the west coast of South Africa in respect of beach surface irregularities such as their exit holes and digging mounds. Therefore, the results of this study provide evidence that despite the behavioural plasticity that seems to be characteristic of tylid isopods (Brown & Odendaal 1994), there are common forms of behaviour in the group that allow these crustaceans to be successful in the rigorous environment of the upper beach levels. Possible variations in behaviour, related either to the neap-spring tidal cycle and seasonal changes in beach morphology and sand storage (and thus, variation in height of the burrowing zone above low water mark) remain to be investigated.

It is also relevant to mention that the results of this study may have direct implications for conservation. Because of the fact that the burrowing zone of tylid isopods is located on the upper beach levels, human activities including walking, use of off-road vehicles, construction of recreational facilities, and beach grooming might well alter or destroy its holes and mounds, and thus the environmental cues that result in aggregation can be lost. As the locomotor activity of tylids over the beach surface occurs within a narrow window of time (Hamner *et al.* 1969; Kensley 1974; Fallaci *et al.* 1996; Odendaal *et al.* 1999; Jaramillo *et al.* 2003), the loss of the aggregated pattern of distribution will surely decrease the chance for mating encounters of reproductive isopods, leading to decreases in population abundances. The awareness that holes and mounds are indeed important in maintaining aggregation may help beach ecologists, for example, to understand breaks in the distribution of these isopods along the Chilean coastline. Thus, the absence of *T. spinulosus* south of 30 °S on the Chilean coast may be related to the fact that human impacts on sandy beaches are far higher to the south of this latitude.

Conclusions

Presence of surface beach irregularities, such as artificial holes and mounds, similar in size and shape to that produced after the tylid isopod *T. spinulosus* leave the sediment and dug into it respectively, enhanced burrowing in experimental arenas set up in a sandy beach of north-central Chile (ca. 29°S). This preference for those irregularities would be one of the processes explaining the patchiness of *T. spinulosus* and thus, its zonation on the intertidal zones of sandy beaches of north-central Chile. The burrowing behaviour of this Chilean beach isopod was similar to that shown by *T. granulatus* on sandy beaches of the west coast of South Africa, suggesting that these responses – which result in isopod aggregations – are general phenomena spanning across different biogeographical regions of the Southern Hemisphere.

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