BEHAVIOURAL ADAPTIONS OF THE ISOPOD *TYLOS GRANULATUS* KRAUSS

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ABSTRACT

The importance of a postulated lunar-day rhythm and a semi-lunar month rhythm in controlling the behaviour of the isopod *Tylos granulatus*, is discussed. It is proposed that this rhythmicity contributes largely to the success of the species. Factors which could possibly influence this rhythmicity are mentioned.

During the course of an investigation into the ecology of the oniscoid littoral isopod *Tylos*, on the coasts of South Africa, several interesting facts emerged concerning the behavioural adaptations of the genus. The following brief report must be regarded as being of a preliminary nature; confirmation or alteration will be given when the investigation is completed.

The genus *Tylos*, containing 15 species, is represented in South Africa by *T. granulatus* Krauss and *T. capensis* Krauss. The former is found on the west coast from northern South West Africa to the west coast of the Cape Peninsula, the latter from False Bay to the Eastern Cape. There is no overlap in the ranges of the two species.

Some brief biological observations are necessary for an appreciation of the adaptations of the isopods to their environment. In all cases, adult *T. granulatus* is the species reported on.

HABITAT

As *Tylos* is a burrowing animal, it is found only on sandy beaches. In all cases these are beaches exposed to direct wave action. Up to a 2 mm diameter, the grain size does not appear to be a factor limiting distribution. The slope of the beaches on which the animals were found ranged between 1 in 7 as at Blouberg in the Cape to 1 in 100 as at Stormvogelbucht near Lüderitz, South West Africa.

BURROWING

The animals burrow into the sand to a depth of up to 40 cm. When entering the sand, the helical burrowing action results in a small pile of sand at the surface. The spread of these piles of sand often gives a good indication of the spread of the population on the beach (Fig. 1, top). The majority of animals in a population enters the sand at or near the high tide mark. As the tides approach neaps, the high tide mark moves down the beach, and with it, the *Tylos* population. This would suggest that *Tylos* is able to orientate on the beach and indeed Hamner *et al.* (1969) demonstrated that the Californian *Tylos punctatus* was able to respond to slopes of as little as 1° from the horizontal.

The population at times may spread over a continuous band along the beach. Similarly, as the tides approach springs, so the population as a whole moves up the beach.

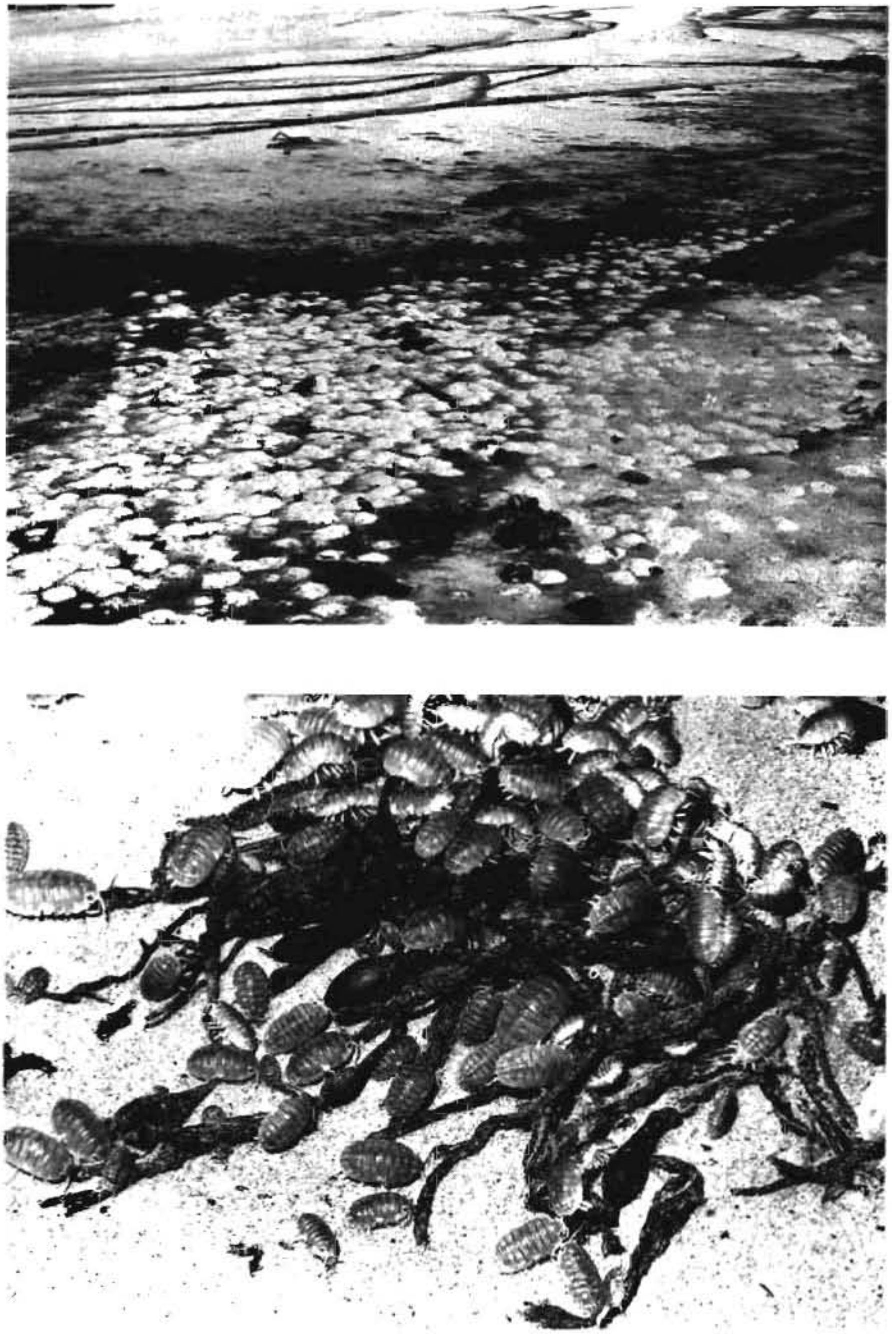

FIGURE 1

Top: Sand mounds made by burrowing *Tylos*. In this case, the isopods entered through a thin layer of polluting crude oil.

Bottom: *Tylos granulatus* feeding on the brown alga, *Macrocystis angustifolia*. Average size of adults pictured 35 mm.

FEEDING

Burrowing close to the high tide mark is an important behavioural adaptation, as this is where food is likely to be deposited by the tide. This food covers a diversity of materials, as *Tylos* is omnivorous. Thus bits of jellyfish, dead fish and sea-weeds are all consumed. The larger brown algae in particular, such as *Ecklonia* sp., *Laminaria* sp., and *Macrocystis angustifolia,* form the 'staple diet' of the adults (Fig. 1, bottom). Mainly the flattened surfaces of these plants are eaten, the mouth parts having difficulty in cutting into the rounded stipes. A grazing pattern thus emerges on beaches supporting large populations of *Tylos,* with denuded kelp stipes and Macrocystic bladders being prominent.

RHYTHMICITY

This aspect of the biology of *Tylos* is undoubtedly the most interesting, yet also requires much more work before any suitable explanations may be offered.

Observations were made of the same population over a period of 36 consecutive days. The time of high and low tide for these days was noted, as well as the time of the animals' emergence from and re-entry into the sand. (The actual time of emergence and re-entry was determined somewhat subjectively; the former taken when 10 animals could be seen emerging from the sand simultaneously. Similarly, time of re-entry was taken when 10 animals could be seen returning into the sand simultaneously. This problem arises from the very large numbers of animals present in a population, making consecutive observations of selected individuals almost impossible.) From these observations, several facts emerged, the most obvious being that *Tylos* is strictly nocturnal, and seldom emerges less than one hour after sunset.

The average time spent out of the sand for the 36 consecutive observations was 2,0 hours. This time was spent in foraging and feeding. As both the burrows and the food are usually close to the high water mark, this foraging time is kept to a minimum.

It was found that time of emergence almost always coincided with the low tide. Rank correlation tests indicate a strong positive correlation between time of low tide and time of emergence. This emergence at low tide is of survival value, as the chances of being swept to sea by a high wave are reduced.

A trend was observed to emerge later each night. When the time gap between successive emergences was noted, it was found to be always more than 24 hours. The mode of the gaps between successive emergences was 24,7 hours, and it can be stated with reasonable certainty that *Tylos* possesses a lunar day rhythm of 24,8 hours. This is to be expected in an organism living in a habitat whose fluctuations are largely dependent on the lunar cycle.

It was found that occasionally the time of emergence for successive nights remained the same, but in these cases the time of return is always later each night. A possible explanation for this is that not all the same animals emerge each night, and that some emerge later than others and thus return later. It is known that in the intertidal mollusc *Bullia digitalis* only about 12% of the population emerges at any one tidal cycle. (Prof. A.C. Brown, personal communication).

It is obvious that if the animals are emerging later each night, eventually their time of emergence will be at or around sunrise. This would expose them to possible predators. It was found that *Tylos* never emerges in sunlight; thus some sort of mechanism must operate to maintain the nocturnal cycle.

It was observed that about four days before spring tides, when, instead of emerging at about 05.00 in the early morning, the animals emerge in the early evening at the low tide, this was followed by 13-14 days of normal emergence, when again the switch-back to early evening hours took place. This switch-back has been observed on five occasions, and is always 3-4 days before spring tides. It may very tentatively be suggested that this switch-back reflects the operation of a semi-lunar month rhythm of 14½ days, which ensures the maintenance of the nocturnal cycle and also ensures that the chance of being caught by the increasing height of the tide is minimised.

DISCUSSION

From the numbers of *T. granulatus* present on any stretch of beach (estimated at up to 4 000 specimens per 100 metres of beach front), it is obvious that the species is extremely successful. This success must be attributed largely to behavioural adaptations, as amongst isopods *Tylos* is a relatively slow breeder, one ovigerous female producing a brood of less than 50 eggs per year. The rhythmicity controls all other activities and must be the factor which contributes most to the success of the species. Numerous problems remain to be elucidated before the exact role of this rhythmicity can be understood.

It seems probable that the lunar day rhythm of 24,8 hours is an endogenous one, as not all the animals emerge simultaneously, although all are receiving the same external stimuli simultaneously. Further, it was found that when 25 animals were placed in a container of beach sand, away from the sea, and in constant darkness, they maintained the lunar-day rhythm and also switched-back after 14 days. After 29 days, however, some animals emerged during daylight hours, indicating a breakdown of the rhythm.

Whether these rhythms are simple responses to hitherto undetected external stimuli (F.A. Brown 1959; 1961) or, as seems more likely, endogenous rhythms, synchronised and reinforced by external stimuli (see Hardy 1970 for references), is difficult to decide. Several factors could individually, or in combination, play a part in entraining the rhythms displayed by *Tylos*. These include the sinking of water through the sand at high tide and/or the resulting change in temperature. The situation is complicated by the feeding behaviour of the animals, as it would seem that if the isopods have eaten their capacity on one night and the food is retained for at least 24 hours in the gut there is no great stimulus to emerge again and feed. The population effect and the stimulus to one individual by the activity of many other individuals, is also difficult to assess.

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