Rhythmic swimming of the isopod Exosphaeroma obtusum (Dana)

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RHYTHMIC SWIMMING OF THE ISOPOD
EXOSPHAEROMA OBTUSUM (DANA)

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ABSTRACT

The tidal swimming rhythm of the New Zealand rocky shore isopod *Exosphaeroma obtusum* (Dana) is described. Peak swimming was on the ebb tide about 2.5 h after high water; the peak in the dark period was 6–8 times greater in amplitude than the daytime peak. Positive thigmotaxis was shown at all other times. The rhythm period in continuous darkness (free-running period) was greater than tidal periodicity, and there was a semi-lunar swimming pattern with peaks at the first and third quarters of the moon. Rheotropic experiments showed that changes in water flow did not initiate the swimming rhythm. The work was compared with the infaunal species *Pseudaega punctata* and the northern *Eurydice pulchra*. It was concluded that infaunal species rely more on endogenous control of the swimming rhythm because of their isolation, when buried, from exogenous Zeitgeber.

INTRODUCTION

The swimming rhythm of sand beach isopods has been well documented (Salvat 1966, Fish 1970, Jones & Naylor 1970, Fish & Fish 1972, Fincham 1973). Little is known of the behaviour of rocky shore isopods. The basic difference in behaviour of animals living on sandy and on rocky shores is put succinctly by Yonge (1949): "Where the animals of a rocky shore confront or circumvent danger, those of a sandy shore burrow to avoid it". More recently Eltringham (1971) reiterated: "With few exceptions, the rocky shore fauna has to endure the atmospheric weather while the animals of the depositing shore avoid it through their burrowing habits". Since the animals of rocky shores are unable to avoid adverse conditions, it is reasonable to suppose that this would be reflected in their behaviour. It is likely that they would be more responsive to exogenous Zeitgeber than their infaunal counterparts, which may rely more on endogenous control of their activity. The present work on the New Zealand rocky shore isopod *Exosphaeroma obtusum* (Dana) was undertaken to test the effect of two exogenous Zeitgeber: light, and tidal flow. Direct comparisons could then be made with infaunal sand-dwelling species such as *Eurydice pulchra* Leach (Jones & Naylor 1970, Fish & Fish 1972) and *Pseudaega punctata* Thomson (Fincham 1973). The relative importance of endogenous and exogenous Zeitgeber for both infaunal and epifaunal isopods could then be assessed.

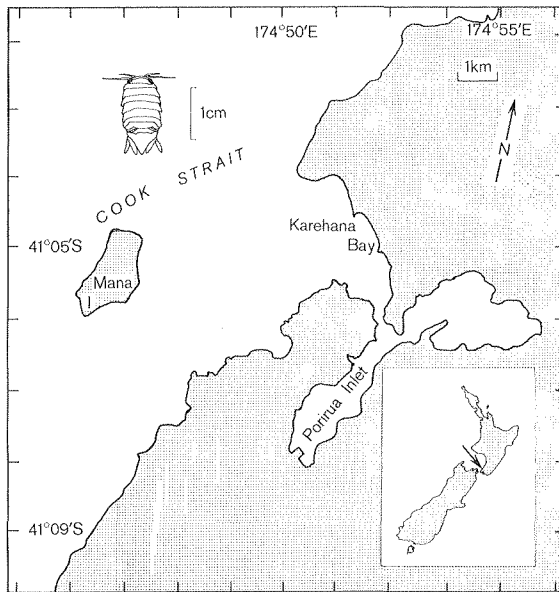**Present address*: British Museum (Natural History), Cromwell Road, South Kensington, London SW7, England.

FIG. 1—Sketch map showing the protected rocky shore at Karehana Bay, North Island, New Zealand, where the isopod *Exosphaeroma obtusum* was collected. Inset map shows the area in relation to the rest of New Zealand.

METHODS

Exosphaeroma obtusum was collected from low shore rock pools at Karehana Bay (Fig. 1), which faces west on to Cook Strait and is protected by Mana Island lying offshore. The swimming behaviour of the isopods was monitored in equipment comprising an observation tank of internal dimensions $2 \times 7 \times 10$ cm with an infrared beam focused through the middle of the end wall of the tank, at a height of 1.5 cm, on to a photo-conductive cell, the latter linked to a digital printout counter via a control unit (Fincham 1972, 1973). A time switch operated a 100 W bulb fixed 40 cm above the tank; the light period chosen in different experiments coincided with the day length at the beginning of the experiment. The equipment was used in a controlled temperature cabinet held at 16 ± 1°C.

Ten isopods were placed in the observation tank, which contained small stones to a depth of 1 cm collected from the rock pools. Each experiment was preceded by an acclimation period of 24 h. The results have been presented as histograms of total activity either hourly (*see* Figs. 2 *left*, 4 *upper*) or for the dark period (*see* Fig. 5). Other diagrams have also been constructed by averaging activity for each hour before and after high water (HW) over at least four tidal cycles (*see* Figs
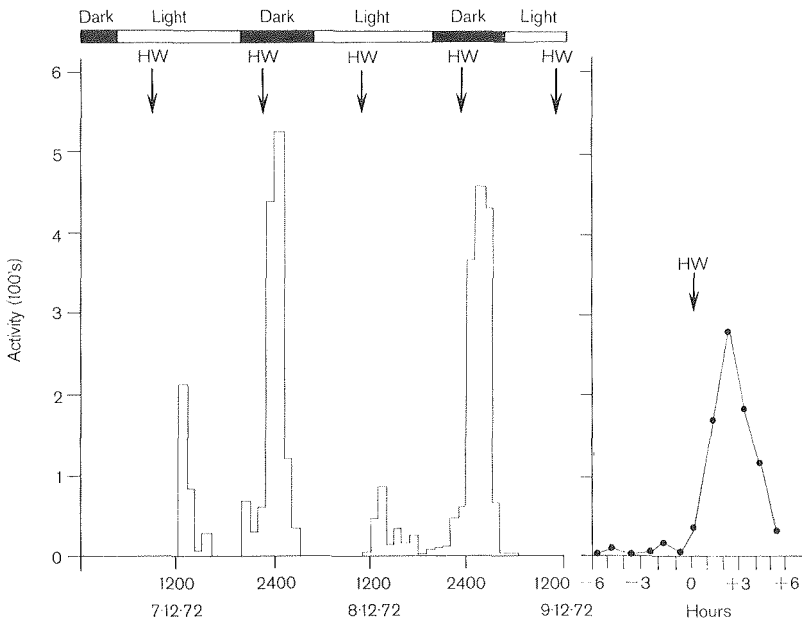
FIG. 2—Swimming activity of 10 *Exosphaeroma obtusum*: *left* – normal summer day and night regime for 7–9 December 1972 (dark period shaded on horizontal bar = 1945–0430 h); *right* – average hourly activity centred around HW (note expanded time scale).

2 *right*, 4 *lower*) or for each hour before and after midnight over 12 days (*see* Fig. 3).

The tank, with an overflow pipe 1 cm from the top, was supplied with running ambient sea water at approximately 15 ml/min in all experiments except for the water flow experiments when sea water was supplied at rates of 20, 40, and 80 ml/min. In this rheotropic experiment, water in the observation tank would be replaced every 5, 2.5, and 1.3 min respectively. Activity of the same ten isopods was monitored for three consecutive periods each of 15 min at the different flow rates (in the order: 20, 40, and 80 ml/min) at 2 h intervals over a complete tidal cycle (0800–2000 h). Water was supplied at 15 ml/min between the test periods.

RESULTS

TIDAL RHYTHM

The normal tidal rhythm of swimming is shown in Fig. 2 *left;* the figure shows the typical pattern during a 2-day period. Each predicted time of high water is accompanied by a peak of swimming activity. The HW in the dark period (1945–0430 h) shows a greater peak than HW in the
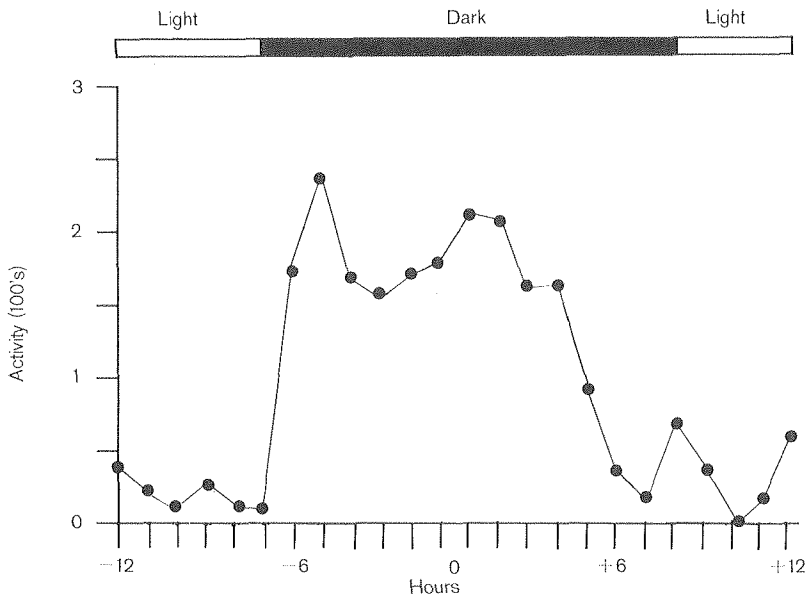
FIG. 3—Hourly activity of ten *Exosphaeroma obtusum* centred on the dark period, averaged from records of 12 days in the period 7 May–3 June 1973.

light period; the ratio of dark to light activity is 6.8 : 1. Average hourly activity (Fig. 2 *right*) centred around HW shows that maximum activity occurs on the ebb tide at about 2.5 h after the predicted time of HW, but only when both the time of HW and the swimming peak are in the dark or in the light period. Regular monitoring over a longer period (*see* 'Lunar Rhythm,) shows that if predicted HW is a few hours before dusk then peak swimming time can be delayed up to 4 h after HW until the dark period begins; conversely, if predicted HW occurs at dawn, peak swimming is brought forward and occurs within an hour of HW.

An hourly activity estimate centred around the dark period (Fig. 3) and derived from figures obtained by monitoring activity for a lunar month (*see* 'Lunar rhythm') shows the increased activity associated with HW in the dark period compared with HW activity in the light period (8.39 : 1). This ratio is higher than the figure derived from the results shown in Fig. 2. This second long-term experiment was carried out in winter (May and June), and consequently the longer dark period (1730–0715 h) contained a higher proportion of the total daily activity.

CONTINUOUS DARK EXPERIMENT

It is clear from the results presented in Fig. 4 that the activity rhythm disappears in the absence of light cues, which must be important Zeitgeber (Ger., time-giver) for maintaining the phase and amplitude
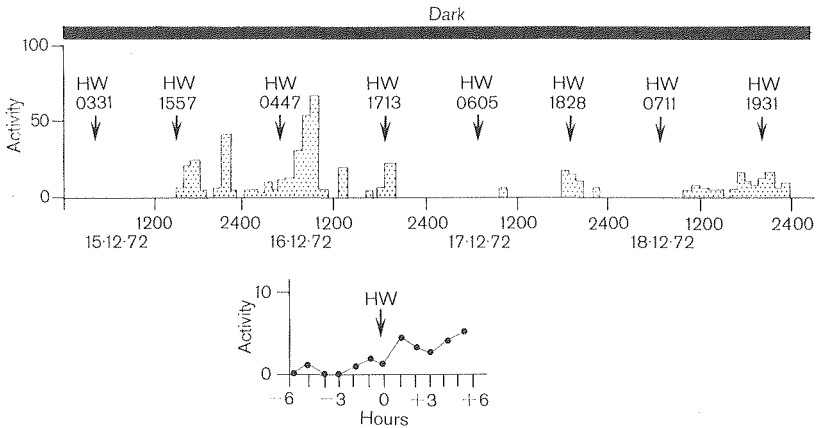
FIG. 4—Swimming activity in continuous dark of ten *Exosphaeroma obtusum*: *upper* – constant conditions maintained from 15–18 December 1972 (temperature 16°C; continuous darkness); *lower* – average hourly activity centred around HW for 15–18 December 1972.

of the swimming rhythm. The experiment was carried out for 4 days in continuous darkness, and there were two obvious effects on the rhythm: typically high levels of activity on the ebb tide were recorded during the 24 h acclimation period (not shown on any of the figures), but amplitude was dampened from the second day onwards. Secondly, the usual timing of the activity peak was erratic, with peak swimming up to 6 h after HW for the 4 days that the experiment was continued at ambient seawater temperatures.

LUNAR RHYTHM

In Fig. 5 the histograms represent the total activity during the dark period (shaded areas show the maximum activity in 1 h) on the second night after capture following the usual 24 h period of acclimation. Greatest total activity was recorded on lunar days 2–3 and 20–21, indicating that there is a semi-lunar pattern in the swimming behaviour with peaks at the first and third quarters.

RHEOTROPISM

The isopod is insensitive to water flow at some states of the tide. Activity of ten isopods was monitored for three consecutive periods of 15 min every 2 h for 12 h (0800 – 2000 h) at flow rates of 20, 40, and 80 ml/min. Predicted time of HW was 1004 h and LW 1616 h; the dark period began at 1800 h. At 0800, 1000, and 2000 h no activity was recorded at any of the flow rates. At these times, the isopods were rarely visible and showed positive thigmotaxis, resting beneath the small stones in the tank. Peak swimming was at the predicted time of ebb tide: an

average of 27 movements recorded at 1200 h for the three different flow-rate test periods, with 4.7 at 1400 h and 1.7 at 1600 h. There was an increase to 6.3 at 1800 h at the beginning of the dark period. On average, activity was directly proportional to the rate of flow, with the highest activity of 7.3/15 min recorded during the fastest flow rate periods (7.0 at 40 ml/min, and 2.7 at 20 ml/min). The response, however, was variable, and even at the basal flow rate of 15 ml/min during the predicted time of ebb tide at 1200 h, activity was as high on occasion as that recorded for the fastest rate of flow.

DISCUSSION

The shallow, low-shore rock pools in which *Exosphaeroma obtusum* were collected mitigate the problems of desiccation and respiration normally associated with the rocky shore habitat at low water, but Morton & Miller (1968) point out that 'Pools have ecological hazards of their own'. The swimming rhythm is in phase with the tides, with peak swimming on the ebb tide, but what triggers the swimming is uncertain. There was no clear response to changes in water flow, so it appears that currents do not initiate the swimming. At the time of predicted HW, activity increased, but this was apparently independent of water flow. Light indeed has an effect, as the peak of activity is suppressed when ebb tide occurs during the light period compared with peak activity during the dark period. (*see* Fig. 2). Maintenance of the swimming rhythm in phase with the tides depends on regular alternation of dark and light periods.

Individual isopods can sustain bursts of swimming lasting several seconds, and consequently there is a danger that in swimming the isopod may be swept away from its preferred low-shore habitat. Jansen (1971) found that *Exosphaeroma obtusum* tolerated a wide range of salinities at 10°C, but was restricted to the lower shore by its inability to tolerate high or low salinities at higher temperatures. Resistance to desiccation was also severely limited at higher temperatures. He found that the species was most abundant on moderately exposed shores. Adults occurred mainly in the mid-tide level to low water neap tide zone, with juveniles extending occasionally up to high water neaps. Results from the present work show that swimming is restricted to the late ebb tide, and consequently there is less chance that the isopods would be stranded high upon the shore in potentially dangerous conditions or carried out to sea. Generally, the isopods maintain zonation well, but some are washed further up the shore, and this is probably a result of incomplete development of orientation control in these juveniles when swimming. A relatively large (males up to 17 mm), voracious isopod, it fills an active predatory niche in the economy of the rocky shore.

Jansen (1971) reported densities of 2500 per m², and this gregarious habit would ensure zone maintenance. The isopod swims mainly in the
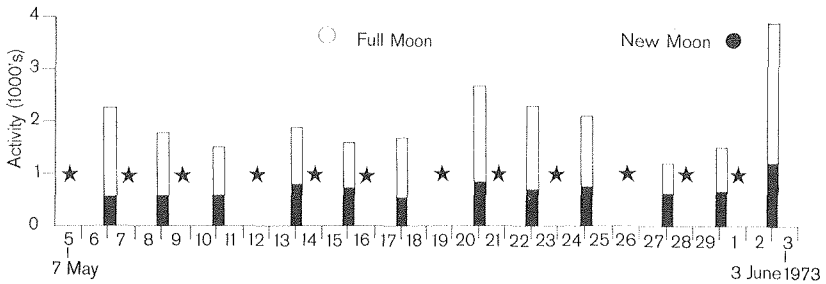
FIG. 5—Swimming activity of *Exosphaeroma obtusum* over a full lunar cycle in a normal winter day and night regime (dark from 1730–0715 h) for 7 May to 3 June 1973. Histograms show total activity of 12 different samples (starred) of 10 isopods in the dark period on the second day after capture and the maximum activity in 1h (shaded).

dark period, and avoids predators which locate their food visually in daylight. The rhythm is sufficiently flexible to allow swimming to be delayed until dusk if HW occurs late in the light period. If HW is at dawn, swimming is brought forward. This degree of flexibility could be achieved by neurosecretory control of the rhythm (Fincham 1973).

Reproduction in *Exosphaeroma obtusum* appears to be continuous in the Cook Strait region, where the temperature range (Ritchie 1970) is from $10.0°c$ (August) to $17.9°c$ (January). Jansen (1971) reported continuous breeding at the Kaikoura Peninsula, South Island, New Zealand, with peaks of gravid females in October and January. In Karehana Bay, where the samples were collected, young, and adults in copula, with the larger male clasping the female into its ventral groove, can be found throughout the year. The young are usually found crawling over the adults. Swimming is most likely associated with location of mates and foraging for food.

There was no obvious circadian element to the swimming rhythm, but nevertheless alternation of day and night was essential to maintain the phasing of the tidal rhythm. There was no evidence that water flow was responsible for initiating the swimming. However, a precisely timed ebb tide peak at 2.5 h after HW was maintained in normal day and night conditions. By relying on just one component (tidal) for rhythm phasing the behaviour is more easily adapted in unfavourable conditions in comparison with the dual tidal and circadian components of infaunal species. The strong endogenous component controlling the rhythmic swimming in the two infaunal species *Pseudaega punctata* and *Eurydice pulchra* (*see* Fincham 1973, Jones & Naylor 1970) is not so obvious in *Exosphaeroma obtusum,* because in constant conditions the rhythm deteriorated immediately. The infaunal species normally experience isolation from exogenous Zeitgeber as a result of the burrowing habit, and have probably come to rely more on endogenous control of the swimming rhythm. It would appear, therefore, that the adaptations to

living on a rocky shore where adverse conditions cannot be avoided but have to be endured are:

1. Adoption of the low-shore pool habitat:

2. Less reliance on the endogenous control of the swimming rhythm; and

3. Development of an activity cycle which is geared predominantly to tidal rather than circadian cycles.

ACKNOWLEDGMENTS

LITERATURE CITED

ELTRINGHAM, S. K. 1971: "Life in Mud and Sand". English Universities Press, London. 218 pp.

FINCHAM, A. A. 1972: Rhythmic swimming and rheotropism in the amphipod *Marinogammarus marinus* (Leach). *Journal of Experimental Marine Biology and Ecology 8*: 19–26.

———— 1973: Rhythmic swimming behaviour of the New Zealand sand beach isopod *Pseudaega punctata* Thomson. *Journal of Experimental Marine Biology and Ecology 11*: 229–37.

FISH, S. 1970: The biology of *Eurydice pulchra* (Crustacea: Isopoda). *Journal of the Marine Biological Association of the U.K. 50*: 753–68.

FISH, J. D. & FISH, S. 1972: The swimming rhythm of *Eurydice pulchra* Leach and a possible explanation of intertidal migration. *Journal of Experimental Marine Biology and Ecology 8*: 195–200.

JANSEN, K. P. 1971: Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). *Marine Biology 11*: 262–85.

JONES, D. A. & NAYLOR, E. 1970: The swimming rhythm of the sand beach isopod *Eurydice pulchra. Journal of Experimental Marine Biology and Ecology 4*: 188–99.

MORTON, J. E. & MILLER, M. C. 1968: "The New Zealand Sea Shore". Collins, London & Auckland. 638 pp.

RITCHIE, L. D. 1970: Notes on sea surface temperatures at the Victoria University Marine Laboratory, Island Bay, Cook Strait. *Bulletin of Natural Sciences, Victoria University of Wellington Biological Society, 1*: 1–4.

SALVAT, B. 1966: *Eurydice pulchra* Leach (1815) *Eurydice affinis* Hansen (1905) Isopodes Cirolanidae, taxonomie, éthologie, écologie, répartition verticale, et cycle reproducteur. *Actes de la Société linnéene de Bordeaux T 103, Ser. A*: 1–77.

YONGE, C. M. 1949: "The Sea Shore". Collins, London. 311 pp.