TIDAL AND DIURNAL RHYTHMS OF LOCOMOTORY ACTIVITY IN *CARCINUS MAENAS* (L.)

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INTRODUCTION

Since the early observations of tidal rhythms in *Convoluta* (Gamble & Keeble, 1903, 1904) and in *Actinia* (Bohn, 1906) much experimental work on rhythms of behaviour in intertidal animals has been concerned with such phenomena as oxygen uptake and colour changes. Gompel (1937) demonstrated tidal rhythms of oxygen consumption in *Patella*, *Mytilus* and *Haliotis* and similar rhythms have been shown more convincingly in several other organisms by F. A. Brown and his co-workers. Superimposed tidal and diurnal rhythms of oxygen consumption are described in *Littorina littorea* and *Urosalpinx cinereus* (Sandeen, Stephens & Brown, 1954), and in *Uca pugnax* and *U. pugilator* (Brown, Bennett & Webb, 1954), and similar rhythms of colour change occur in *U. pugnax* (Brown, Fingerman, Sandeen & Webb, 1953) and *Callinectes sapidus* (Fingerman, 1955). Along similar lines, Rao (1954) has described persistent tidal rhythmicity in the rate of water propulsion by *Mytilus*. Many physiological rhythms of this kind have been reported but, as has been noted by Bennett, Shriner & Brown (1957) several are apparent only after statistical analysis of extensive data.

Despite the fact that it is often more simple to obtain a continuous record of the movement of an animal than of its oxygen uptake there are few published examples of rhythms of locomotory activity in marine animals. Recent demonstrations of tidal rhythms of this nature in *Nassa obsoleta* (Stephens, Sandeen & Webb, 1953) and *Uca pugnax* (Bennet *et al.* 1957) are notable. The present paper describes spontaneous tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.)

METHODS

Two types of apparatus were used, one in which a crab was kept moist in air and another in which it was continuously immersed in sea water. The first type consisted of a box measuring 10 cm. wide × 15 cm. long × 4 cm. high, constructed of thin transparent Perspex and suspended in pivots at the centre of each long side. The inside of the box was moistened with sea water and a single specimen of *Carcinus* enclosed. The box was allowed to tilt slightly when the crab moved across the axis of suspension and a wire stylus attached beneath the box recorded the movement on a rotating drum.

In the second type of apparatus a specimen of *Carcinus* was free to move in a tank of aerated sea water in which a sheet of glass was suspended vertically on copper wire. The glass plate acted as a swinging partition, being large enough to prevent the specimen from passing between it and the walls of the tank. The copper wire passed through a small hole in a piece of copper plate. Whenever the crab moved the glass partition sufficiently, the wire touched the surrounding copper, completing a circuit which made a mark electro-magnetically on a smoked drum. A resistance and a condenser were used in the circuit to prevent the overlap of successive marks on the drum.

For convenience most experiments were carried out at temperatures of between 15 and 20° C. which varied by $\pm 1^{\circ}$ C. over 24 hr., though some were carried out at a more accurately controlled temperature of 25° C. Illumination was constant and dim, usually from a 25 W. red lamp at a distance of 3–4 ft. Animals were not fed during the experiments.

RESULTS

Carcinus *kept moist in air*

Fig. 1 shows a typical trace by a specimen of *Carcinus* in the tipping-box aktograph during the first 24 hr. after capture. Bursts of activity occurred at times corresponding to those of high tide, and activity was greatest at the time of that high tide which occurred during what would have been the hours of darkness outside. The persistence of this rhythm of locomotory activity for a period of 3 days is illustrated in Fig. 2. Activity is plotted as the number of tilts of the box per hour. Peaks of activity occur later each day and they closely follow the succession of tides; this is particularly apparent in the exaggerated night-time peaks.

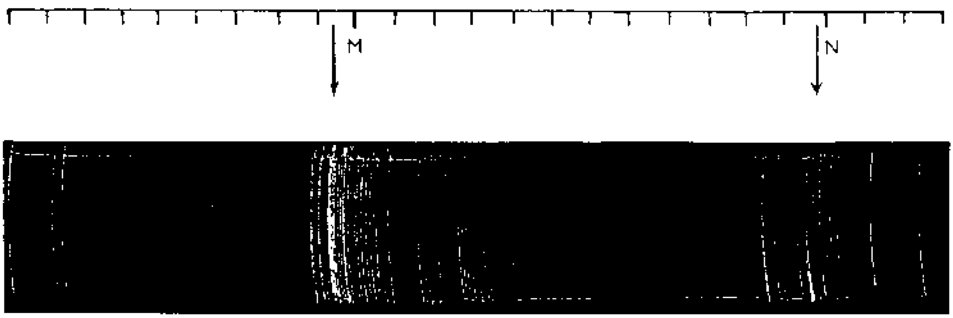

Fig. 1. Typical aktograph trace of the activity of a single *Carcinus* during the first 24 hr. after capture. (Units are hours; M is midnight, N is noon. Arrows indicate times of high tide.)

Such a rhythm persists clearly for up to 3 or 4 days in individual specimens and can be shown to be apparent for longer if the mean activity of a few crabs is considered. Fig. 3 shows the mean activity of three specimens of *Carcinus* from 21 to 23 August and of the two surviving specimens for another 4 days.

Since the activity of *Carcinus* was greater at those times when high tide would have occurred during the hours of darkness, there appeared to be a diurnal component in the rhythm. This is borne out by traces such as that in Fig. 4, which is typical of those crabs collected in summer at a time when they were experiencing both high tides during the hours of daylight. Such crabs showed a third outburst of locomotory activity during what would have been the hours of darkness, even though it would have been low tide at the time. The presence of diurnal and tidal components in the rhythm is further demonstrated in Fig. 5. This represents the summated activity of fifteen crabs, collected on successive days during a semi-

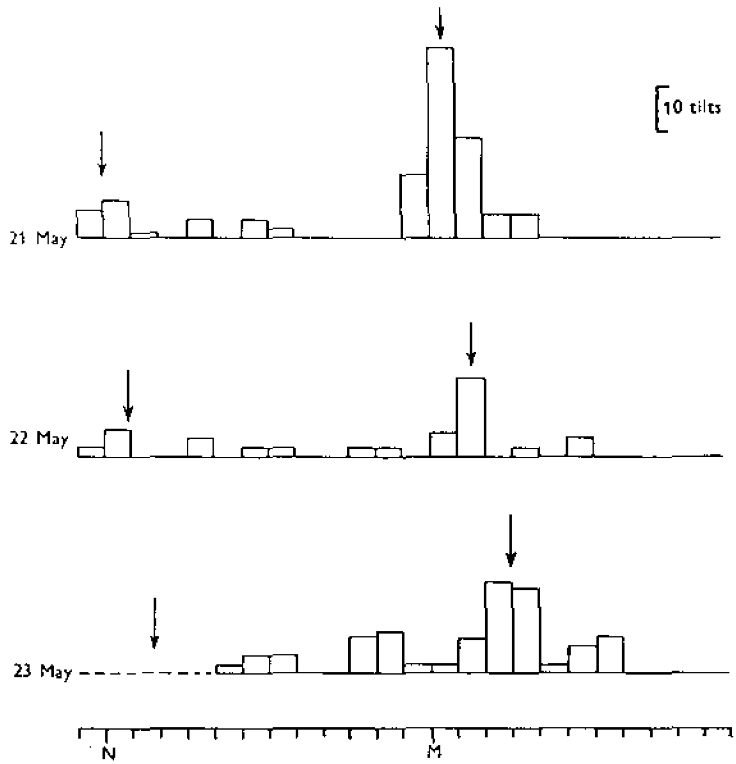

Fig. 2. Hourly activity of a single *Carcinus* from 11.00 a.m. on 21 May 1957, until 11.00 a.m. on 23 May. (Symbols as in Fig. 1; - - - -, indicates no record.)

lunar (15 day) cycle and each tested over a period of 48 hr. The upper histogram (Fig. 5) shows the total activity of all the crabs during each hour of the 48 hr. period irrespective of the times of high tide during each experiment. Since the experiment was over a period of 15 days the times of high tide would be evenly distributed over the whole 48 hr. period. In the lower histogram activity is plotted around the times of the four high tides which occurred during each 48 hr. period, irrespective of the time of day when they occurred. The tendency is for activity to be concentrated within 1 or 2 hr. on each side of high water and, alternatively, during and just before the hours of darkness.

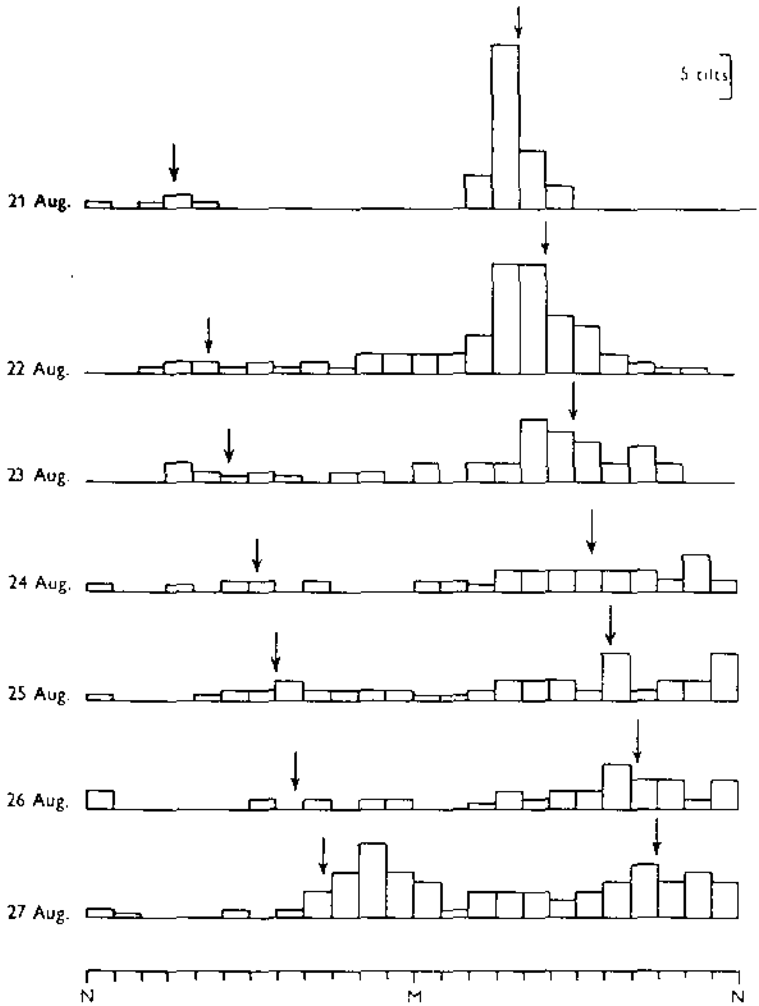

Fig. 3. Mean hourly activity of three *Carcinus* from noon on 21 August until noon on 23 August (when one specimen died), and of the two surviving *Carcinus* from noon on 23 August until noon on 27 August. (Symbols as in Fig. 1.)

Most experiments were carried out at temperatures which showed slight variations of ± 1° C. over a period of 24 hr. and it remained to determine whether such conditions were sufficiently constant. For this some of the experiments were repeated in a more accurately controlled constant temperature room. Of ten specimens tested at 25° C. all showed a persistence of the rhythm for a period of 3–4 days.

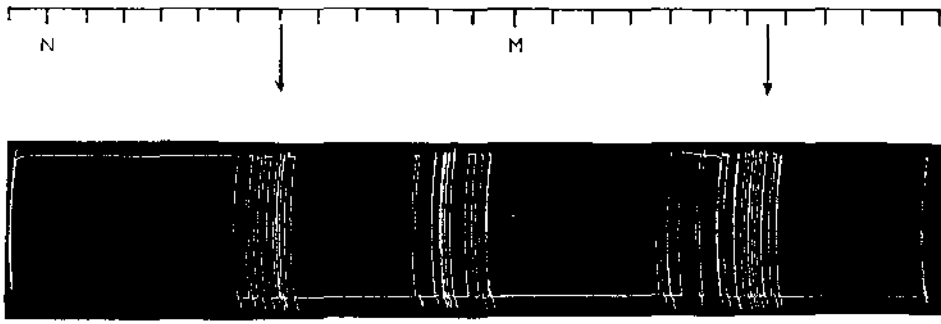

Fig. 4. Aktograph trace of a single *Carcinus* collected at a time in summer when it was experiencing both high tides during the hours of daylight. (Symbols as in Fig. 1.)

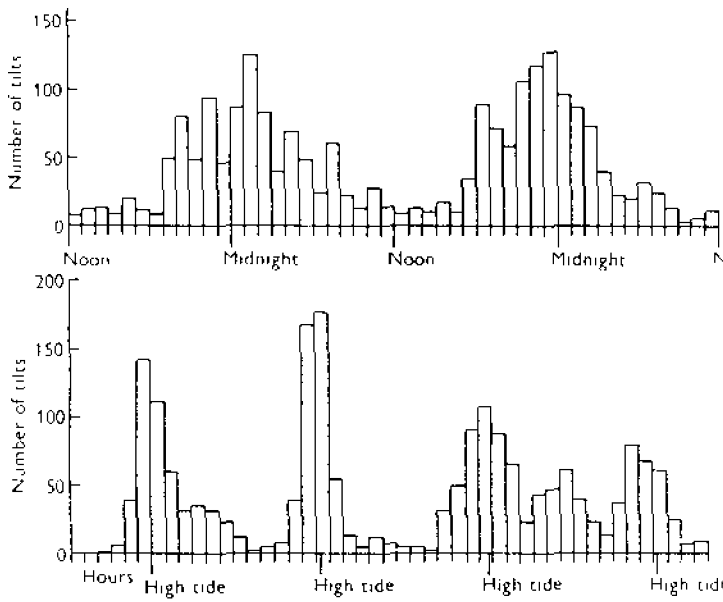

Fig. 5. Total activity of fifteen *Carcinus* collected on successive days over a semi-lunar period and each tested for 48 hr. Upper histogram shows total activity during each hour of the 48 hr. periods, irrespective of the times of high tide. Lower histogram shows total activity per hour plotted around the times of the four high tides which occurred during each 48 hr. period irrespective of the time of day when they occurred.

Carcinus *kept continuously immersed*

Experiments carried out with crabs which were continuously immersed in sea water in the second type of apparatus gave results similar to those already described. Since the apparatus is different the data obtained are comparable only qualitatively, but it is clear from Fig. 6 that both tidal and diurnal rhythms persist for 3–4 days in a crab which is continuously immersed.

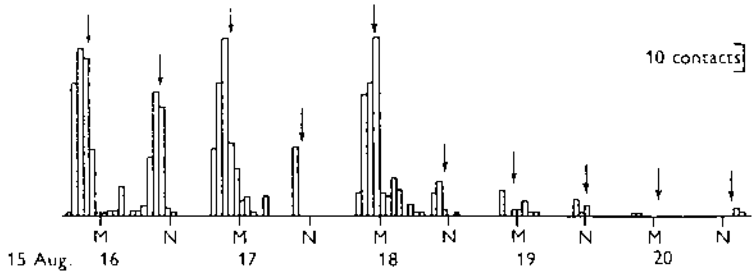

Fig. 6. Hourly activity of a single *Carcinus* kept continuously immersed in sea water from 5.00 p.m. 15 August until 5.00 p.m. 20 August. (Symbols as in Fig. 1.)

RESULTANT EFFECT OF THE TWO RHYTHMS

During June and July 1957, an extended experiment was carried out to determine the resultant effect of the two rhythms. A fresh crab was collected each day and its hourly activity was recorded during the first 24 hr. after collection. The records for all the 24 hr. periods were then plotted successively (Fig. 7). The result therefore illustrates the hourly activity of representatives of the *Carcinus* population over a period of 18 days. Early in the experiment peaks of locomotory activity were particularly high and particularly low alternately, according to whether the time of high water coincided with darkness or daylight outside. During the middle of the experiment when both high tides occurred during the hours of daylight, the peaks were moderately high and a third nocturnal peak appeared during the time of low

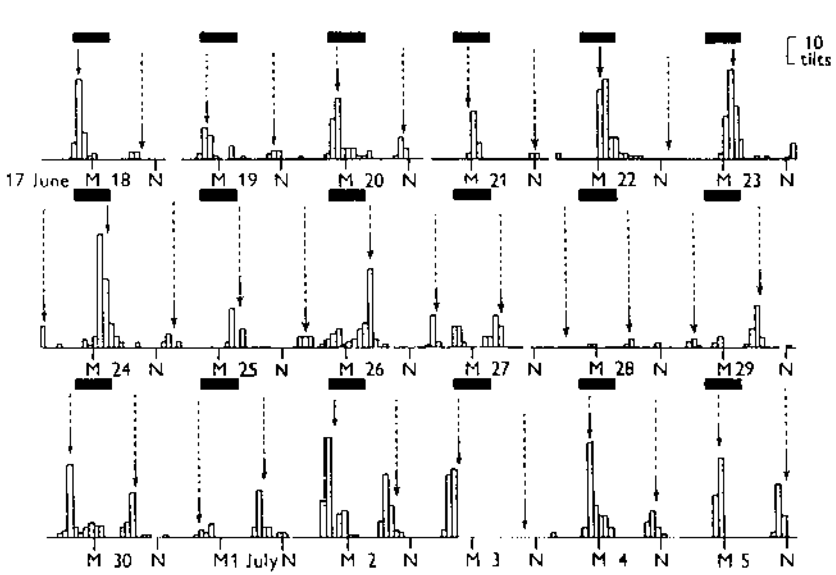

Fig. 7. Hourly activity during the first 24 hr. after capture of eighteen *Carcinus* in box-type aktographs. A specimen was freshly collected on each successive day of the experiment which ran from 2.00 p.m. 17 June 1957 until 2.00 p.m. 5 July. (Symbols as in Fig. 1; shaded rectangles indicate the hours between sunset and sunrise.)

tide. Later, when high tide again occurred in darkness, that tidal peak became particularly well marked.

This is the pattern which would be expected if two rhythms were superimposed, one of the tidal frequency (*ca.* 12·4 hr.) and one of diurnal frequency (24 hr.). Parts of the tidal cycle would become phased with the diurnal cycle every 14 or 15 days, owing to the rate of progression of the tidal cycle relative to the diurnal one. At Swansea the highest activity peaks occur during neap tides, for that is the time when high water occurs in the middle of the night.

Similar experiments carried out at Port Erin, Isle of Man, where high tides occur about 6 hr. later than at Swansea, showed similar peaks of activity, coincident with the times of high tides, and particularly well marked when high tide occurred during darkness, i.e. during spring tides in that locality. It seems probable that the diurnal and tidal cycles reinforce one another, to produce particularly well marked peaks, once a day, during periods which recur with a semi-lunar periodicity, at spring or neap tides or at any time between, depending upon locality.

DISCUSSION

The high-water peaks of activity in *Carcinus* contrast with the pattern in the fiddler crab, *Uca pugnax* (Bennett *et al.* 1957), which shows greatest activity at a time just before low tide. In both species, however, the experimental results appear to reflect the behaviour of the animals on the shore. At high tide, *Carcinus* can be seen moving freely in the littoral zone, and at low tide in daytime, they usually hide beneath stones. Nevertheless, they are sometimes found and successfully attacked by herring gulls, but these are active only during the daytime. At night *Carcinus* can safely move about on the shore during low tide. Fiddler crabs emerge from their burrows as the tide recedes and remain active until the time of low water (Bennett *et al.* 1957). The rhythms of activity in *Carcinus* and *Uca* comply with Kleitman's (1949) definition of a 'physiological rhythm' as a metabolic cycle which is synchronized with external periodicity and which persists when the external periodicity is removed. This phasing of internal rhythmicity with cyclical changes in the environment could well synchronize and facilitate the spread of the behavioural 'moods' discussed by Wells (1957).

The lack of precision of the rhythms after a few days and the diminution of activity in *Carcinus* resembles that described in *Uca* by Bennett *et al.* (1957) and in *Nassa* by Stephens *et al.* (1953). In *Uca* the broadening, warping and diminution of the peaks took place after 7 or 8 days and in *Nassa* the tidal pattern of activity persisted for 24–36 hr. at 21° C. In *Carcinus* it is unlikely that the disappearance of the rhythm resulted solely from the unusual experimental conditions in the box-type aktographs, since a similar falling off took place in crabs which were continuously immersed (Fig. 6). It may be that there are exogenous as well as endogenous components in the rhythms which have not yet been recognized, as has been suggested for *Uca* by Bennett *et al.* (1957). There is evidence for the existence of both components in some aspects of the rhythmicity of fiddler crabs (Brown, Webb

& Bennett, 1955; Brown, Webb, Bennett & Sandeen, 1955). It might of course be of advantage to littoral animals if their rhythmicity was not so well implanted as, for instance, are some diurnal rhythms in fresh-water species (Harker, 1953) and terrestrial species (Cloudsley-Thompson, 1951). Some mayfly nymphs show a reaction to the light-darkness rhythm which may be 'in some measure inherent' (Harker, 1953), and inherited rhythms also occur in *Drosophila* (see Brown, 1957). Since many activity rhythms in shore animals are phased by local tides and since the times of high tide may vary over relatively short distances it might be disadvantageous if an existing rhythm could not be readily modified to suit a new tidal regime. Adult animals might not normally be widely transported, but in those species such as *Carcinus* which have a planktonic dispersal stage selection would no doubt be against an inherent tidal rhythm which could not be modified. Rao (1954) has shown that *Mytilus* transported from Barnstaple Harbour, Cape Cod, to Los Angeles, became adapted to the new tidal cycle after only 7 days. Brown (1954) has gone further than this with oysters. When these were transported to a new locality and maintained in non-tidal conditions, they showed for the first few days a statistical rhythm in phase with tides of the native habitat, but after about 14 days they had reverted to a rhythm which showed maxima at the times of lunar zenith and lunar nadir. Such a rhythm is of a frequency which could readily be phased with the tidal cycle in almost any locality.

A final point which is possibly of wider significance arises from the demonstration of two rhythms of different frequencies in marine animals. In addition to the locomotory rhythms in *Carcinus* diurnal and tidal rhythms of various kinds have been described in *Uca pugnax* and *U. pugilator* (Brown *et al.* 1953; Brown *et al.* 1954; Brown *et al.* 1955), *Ostrea virginica* (Brown, 1954), *Venus mercenaria* (Bennett, 1954), *Littorina littorea* and *Urosalpinx cinereus* (Sandeen *et al.* 1954), and *Callinectes sapidus* (Fingerman, 1955). The resultant pattern of such rhythms is of semi-lunar frequency and it might well be a factor regulating periodic spawning behaviour (Brown *et al.* 1953, 1954, 1955; Brown, 1954; Bennett, 1954) in addition to those which have previously been considered by Korringa (1947), Loosanoff & Nomejko (1951), Knight-Jones (1952) and Fox (1956).

SUMMARY

1. Spontaneous locomotory activity was recorded continuously for several days in *Carcinus maenas* (L.).

2. A complex rhythm was observed which could be analysed into two components, one of diurnal frequency (24 hr.), with peaks of activity during the hours of darkness, and one of tidal frequency (*ca.* 12·4 hr.), with peaks at the time of high tide.

3. The rhythms persist in constant dim light at constant temperatures, whether the crabs are kept moist in air or continuously immersed in sea water.

4. The resultant effect of the two rhythms is to produce particularly high activity peaks during periods which recur with a semi-lunar frequency.

5. Experimental results relate to observed behaviour on the shore.

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