

From the University Zoology Laboratory, Madras, India

PERSISTENT TIDAL AND DIURNAL RHYTHMS  
OF LOCOMOTORY ACTIVITY AND OXYGEN CONSUMPTION  
IN *EMERITA ASIATICA* (M.-EDW.)

By

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With 13 Figures in the Text

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The adjustment of one or the other of the physiological processes in littoral animals to the phases of the habitat tidal cycle has long been known. The emergence and disappearance in sand of *Convoluta roscoffensis* (BOHN 1903; GAMBLE and KEEBLE 1903, 1904) during low and high tide respectively even when this flatworm was held under the constant conditions of the laboratory, was about the earliest description of a persisting tidal rhythm of activity. BOHN (1904) also described such rhythms in the activity of a polychaete *Hedistes diversicolor* and a snail *Littorina rudis*. Subsequent to these early observations, several instances of tidal rhythms were reported in the rate of oxygen uptake, colour change and locomotory activity of a number of littoral invertebrates. The literature in this field has been reviewed by FINGERMAN (1960). More recently a tidal rhythmicity in the oxygen consumption of an intertidal isopod *Naesa bidentata* (WIESER 1962) and in the swimming activity of another sandy beach amphipod *Synchelidium* sp. (ENRIGHT 1963) has been reported. Rhythms of approximately 15 and 30 days duration — lunar rhythms — have also been observed in several animals, predominantly marine, as closely being associated with rhythms of tidal frequency (CLOUDSLEY-THOMPSON 1961; HAUENSCHILD 1960). In addition to periodicities of tidal and lunar frequencies phenomena corresponding with the 24-hr. day (circadian rhythms) have been reported from time to time. The reviews of HARKER (1958), WEBB and BROWN (1959), ASCHOFF (1963), the monographs of BÜNNING (1963) and CLOUDSLEY-THOMPSON (1961) and reports of recent symposia (Cold Spring Harbor Symp. Quant. Biol. 1960; WOLF 1962) all summarize our knowledge in this field and indicate the growing interest biological rhythms have come to claim.

Increasingly, however, emphasis is being laid on the importance of direct evidence of precise and overtly persistent rhythms of activity as shown by several marine crustaceans and molluscs, to obviate possible

pitfalls consequent upon "statistical extraction" of rhythms from extensive time-series data (COLE 1957). An account is here given of persistent tidal and diurnal rhythms in the swimming activity and oxygen consumption of *Emerita asiatica* (M.-EDW.), a burrowing anomuran abundant in the intertidal strip of the sandy beach at Madras, on the East Coast of South India. The observations were made on solitary specimens (excepting in one series where group metabolism was studied). The rhythms of activity and metabolism so obtained appeared precise and persistent over periods of 3—5 days.

### Materials and Methods

Large numbers of *Emerita* were obtained from the sandy shore 150 yards from the laboratory. These were left in lots of 4 and 5 in large concrete tanks with seawater and a little sand. Non-ovigerous females in the intermoult stage were chosen

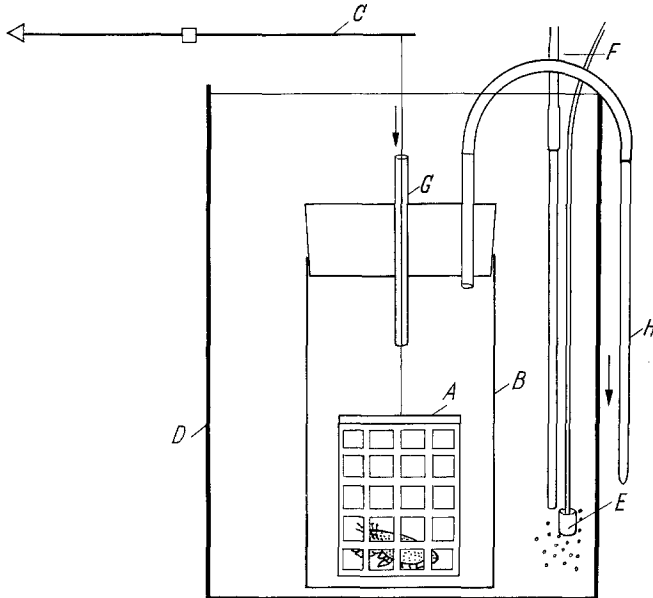


Fig. 1. The vertically moving cage device used to study the locomotory activity of *Emerita*, with the continuous flow arrangement to enable oxygen uptake estimations (A: activity cage, B: animal chamber, C: marking lever, D: constant level trough-not drawn to scale, E: stone aerator, F: from seawater reservoir, G: inlet to the animal chamber, H: flush out of the animal chamber)

for the experiments in view of their larger size and suitability for activity studies. Such specimens were isolated from the stock collection and placed in glass troughs with filtered and aerated fresh seawater for over 24 hr. before the commencement of the experiments. It appeared necessary to empty the alimentary tracts of the crabs, so that subsequent oxygen uptake estimations using WINKLER'S method may not be vitiated.

In measuring the oxygen consumption and the locomotory activity of *Emerita*, the simple continuous-flow- and activity-cage set up (shown in Fig. 1) was em-

ployed. This aktograph appeared well suited to record the characteristic vertical-backward swimming movements of this crab. In addition to permitting simultaneous estimation of locomotory activity and oxygen consumption, the set up also ensured constant conditions for the experiments.

The rates of oxygen consumption were estimated as follows: The volume of water flushing through the respiration chambers was calculated every 2 hr. period immediately following the collection of sample for oxygen content estimation. The initial oxygen concentration of water gaining entry to the respiration chambers was obtained from water flushing a control chamber, similar in design and details to the respiration chambers (B) save for the absence of the specimen. The flow rates employed were of such magnitudes that the effluent had more than 50% air saturation oxygen in it. Oxygen analyses were by the regular WINKLER method.  $N/_{100}$  thiosulphate standardised against  $N/_{100}$  potassium bichromate was used in all experiments. The stock solution of  $N/_{100}$  potassium bichromate was prepared in quantities sufficient to last through a year.

For activity recording, a single specimen was placed in the activity cage (A) made of plastic,  $2\frac{1}{2}$ " in diameter and  $4\frac{1}{2}$ " high with numerous closely arranged windows cut out on all sides. The water in the cage and that surrounding it was thus confluent. The cage was attached to a lever (c), so counterpoised that when the animal rested the cage just touched the bottom of the animal chamber (B). The plastic cage rose up when the animal executed a brief spell of swimming activity. This ascent of the cage was checked by its bottom coming into contact with the swimming crab and descended to its original position when the animal ceased locomotory activity. These spurts of activity were registered as vertical markings on the slow moving kymograph drum, which completed one revolution in 6 hr. The activity cycle through 24 hour periods was recorded at 4 levels on the kymograph. This procedure minimised greatly overlap of quick successive activity bursts. The flow rates employed did not cause or impede the movements of the aktograph-cage. The water in the constant level trough (D) was continuously aerated. Light was precluded by painting the sides of the respiration chambers black. The experiment were performed at temperatures of between  $25^{\circ}$  and  $28^{\circ}$  C, the temperature during any one experiment varying by not more than  $\pm 0.5^{\circ}$  C over 24 hr. The experiments were carried out at different periods of the year between November '61 and March '63. However, in a tropical place such as Madras, the temperature and light conditions are fairly uniform whatever the time of year. In the figures accompanying this paper oxygen consumption is expressed in  $\text{mm}^3/\text{g}/\text{hr.}$  and activity as the number of tilts by the cage per hr. The tidal curves are from data obtained from the Tide Tables annually published by the Geodetical Survey of the Government of India. The average range from lowest level of the sea to the highest was 1.3 metre.

## Results

### A. Tidal rhythms

1. *Tidal rhythm in the oxygen consumption of solitary specimens of Emerita asiatica* (M.-EDW.). Oxygen consumption estimations were made at 2 hr. intervals through 24 hr. periods. The results of a typical experiment are presented here in Fig. 2. The figure here, as also those in later sections, represents the metabolic rates of the crab through a day-night cycle beginning 24 hr. or a little more after capture.

It is evident from the figure, that the rises and falls in the level of metabolism for the crab indicate a definite, recurring pattern in close agreement with the phases of the habitat tidal cycle. Thus the rhythm even as seen in the oxygen uptake of individual subjects is sharply delineated. The relationship of the metabolism to the tidal stages is direct, the rate of oxygen consumption being high during high water and low during the ebb tide 6 hr. later.

2. *Rhythm in the oxygen consumption of 4-5 Emerita huddled together.* Attention has been drawn to grouping of animals in a test

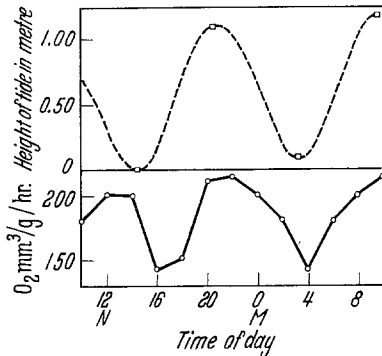


Fig. 2

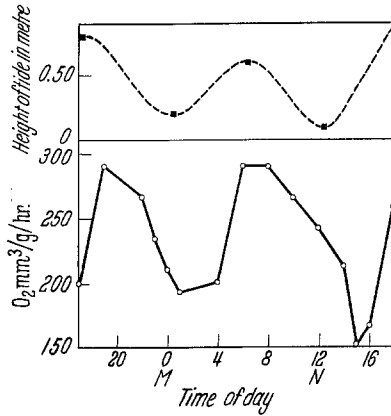


Fig. 3

Fig. 2. Illustrating the rate of oxygen consumption of *Emerita* in relation to the tidal stages, through 24 hr. (M = midnight; N = noon)

Fig. 3. Illustrating the average rate of oxygen consumption of a group of 5. *Emerita* huddled together in relation to the tidal stages

chamber and the consequent effect on oxygen consumption (SCHUETT 1933; SCHLAIFER 1939) and locomotory activity (JOB 1954). The following experiments were performed to observe the resultant effects of grouping *Emerita* on the pattern of the rhythms in oxygen consumption.

Fig. 3 illustrates the data obtained from one such experiment. The experiment was with second year adult berried specimens (eggmasses removed). The figure clearly indicates that the pattern and periodicity of the fluctuations in the average metabolism of the group of sand crabs bear much the same relationship to the phases of the habitat tides as did those of solitary specimens. The subjects touching one another appears not to affect the rhythmicity. The mutual positioning of the phases of the endogenous rhythms by the individuals of the group also appears to be perfectly synchronised.

3. *Persistence of the rhythm in newly moulted Emerita.* Several investigators have induced moulting in Crustacea by the extirpation of

the eyestalks and studied the metabolism (ABRAMOWITZ and ABRAMOWITZ 1940; ROBERTS 1957). It is well known that crustaceans have a higher and intensified metabolism during moulting. It was tempting to see if any rhythmicity will be displayed in *Emerita* during the period of moulting when its metabolism would be geared up to a high level. Owing to scarcity of material no studies could be made on crabs in the proecdysis stage of moulting. Two sets of experiments were performed. One on newly moulted crabs 8—10 hours after ecdysis, and the other on crabs held in the laboratory 2—3 days after ecdysis.

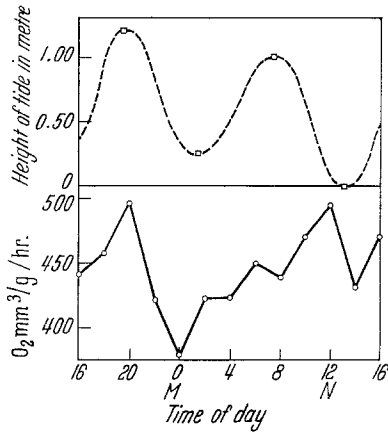


Fig. 4

Fig. 4. The rate of oxygen consumption of newly moulted *Emerita* through 24 hr. starting approximately 8 hr. after ecdysis

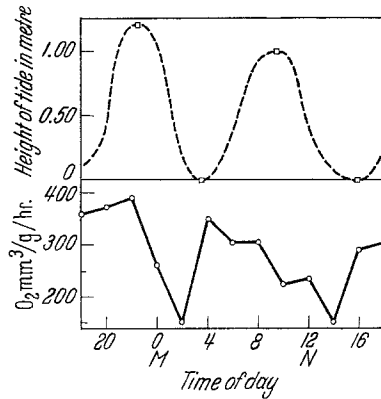


Fig. 5

Fig. 5. The rate of oxygen consumption of a post-moult *Emerita* through 24 hr. starting 78 hr. after ecdysis

Newly moult *Emerita* may be collected during high tide. They lie quiescent along the fringe of the wave line in moist sand, covered and uncovered by the breakers.

Data obtained on a newly moult form, which moulted approximately 8 hr. prior to the start of the experiment are presented in Fig. 4. Here also the rhythmic fluctuations in the metabolic rates may be made out. On the basis of 24 hr. averages of metabolic rates in this case the metabolism appears to be very intense compared to such average metabolic rates of instances cited in the earlier sets. The oxygen consumption of post-moult crabs, i.e. held under laboratory conditions 2—3 days after ecdysis shows (Fig. 5) a staggering in the peaks and phase relations with the tide are not very clear.

4. *Rhythms in locomotory activity and oxygen consumption in solitary forms.* Most fluctuations in the metabolic rate, periodic or aperiodic are known to arise from differential activity, that persists even in the absence of excitatory stimuli. The experiments discussed in this

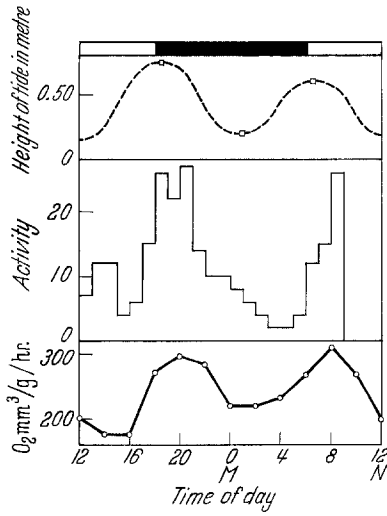


Fig. 6

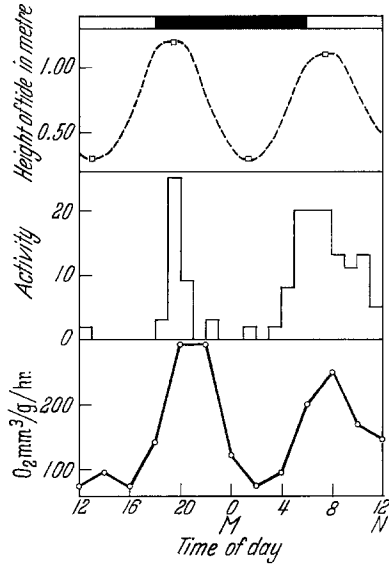


Fig. 7

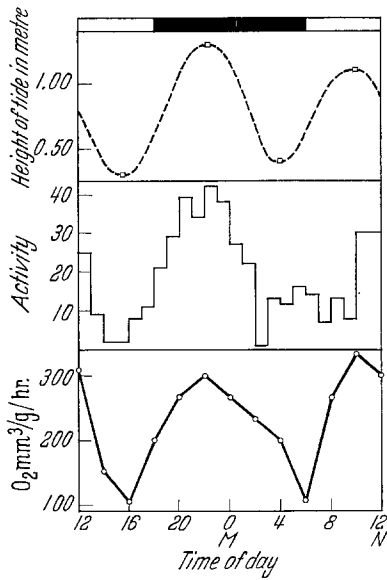


Fig. 8

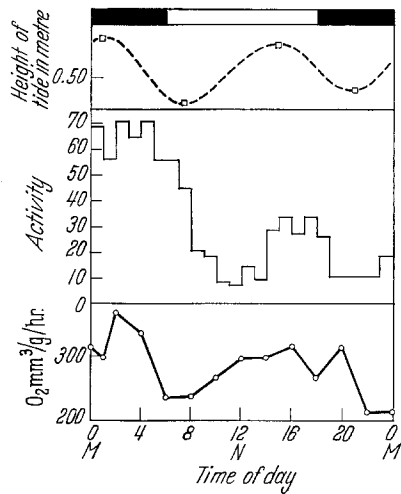


Fig. 9

Fig. 6—9. The rate of oxygen consumption and spontaneous locomotory activity of *Emerita* in relation to the tidal stages. Both activities estimated simultaneously on individual specimens. (Shaded bars indicate hours of darkness in the habitat)

section shed further light on the tidal rhythms characterising the metabolic rates of individual intermoult, grouped and moulting *Emerita*. Moreover, it was felt that results from period measurements of a

very variable parameter such as metabolism should be further confirmed by continuous measurement of some other physiological process.

The spontaneous locomotory activity of a crab was recorded by placing it in the cage aktograph and tracing the movements on a smoked drum. Its oxygen consumption was also estimated simultaneously at intervals of 2 hr. Such experiments were repeated on a number of crabs on different days. The results show (Figs. 6—9) that the activity levels also closely follow the stages of the habitat tides. As may be expected muscular or motor activity and metabolic rates are closely associated with each other, the latter perhaps being the consequence of differential levels of locomotory activity. Differences, however, in the pattern of activity between individuals are discernible. Whereas all of them show unmistakable tidal rhythms of activity and metabolism, the maximal and minimal levels in these indices do not very precisely coincide with the exact hour of low or high water. This, indeed, is the case in the earlier figures presented in this paper.

#### *B. Diurnal rhythms of activity in Emerita asiatica*

The results of activity experiments showed that activity of this crab was higher during the night than during daytime (see activity curve in

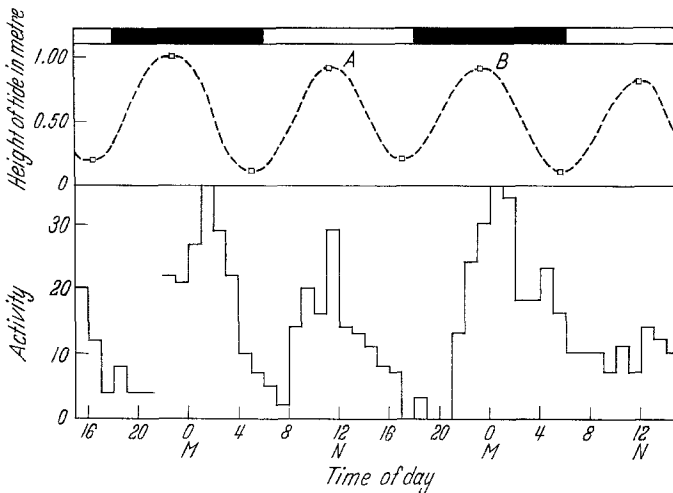


Fig. 10. Illustrating the diurnal rhythm in the locomotory activity of an *Emerita* recorded through 48 hr. when day (A) and night (B) high tide were of equal height (0.9 metre) in the habitat. (Shaded bars indicate hours of darkness outside)

Figs. 6—9). During the days these experiments were performed it also happened that the high tide during night was higher than during day. Therefore, it was not clear whether the increased level of activity was a diurnal effect or a function of the height of the tide. Hence activity

recording was performed between 12. 2. to 14. 2. 63, when the high tide at night was predicted to be of the same magnitude as that during daylight (0.9 m). It was found (Fig. 10) that the crab showed an activity level (36 tilts/hr.) clearly higher at night than during the earlier daytime high tide (29 tilts/hr.).

Another experiment was performed when the noontime high tide was higher than that at night. Such an inverted tidal regime was considered ideal to clarify the issue further. The locomotory activity

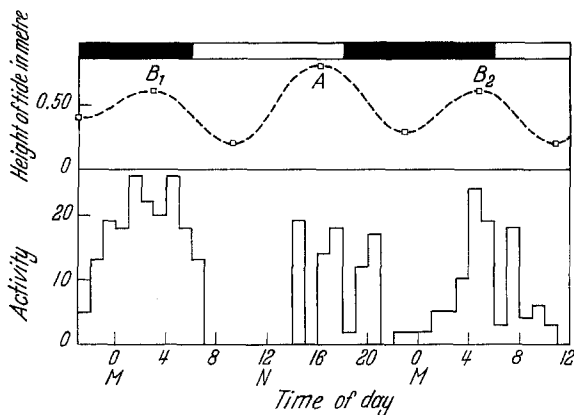


Fig. 11. Illustrating the diurnal rhythm in the locomotory activity of an *Emerita* recorded through 39 hr. when daytime high tide (A 0.8 m) was higher than night high tide ( $B_1 + B_2$  0.6 m) in the habitat. (Shaded bars indicate hours of darkness outside)

of a freshly collected crab (3 hr. before the start of the experiment) was recorded for a continuous period of 39 hours from 9 p.m. 3, March to 12 a.m. 5, March '63. It was again noticed (Fig. 11) that the activity coinciding with night time high tide was more intense (26 tilts/hr. during first dark-hr. high tide and 24 tilts/hr. during the second) than that with daytime high tide (19 tilts/hr.). No quantitative agreement between amplitude of the tide and intensity or degree of activity could be discerned.

The results strongly suggest a diurnal component in the activity appearing superimposed on one of a tidal frequency.

### C. The waning of the tidal rhythms in the activity of *Emerita* in the laboratory

As most experimental studies on tidal or circadian rhythms have to be necessarily conducted in the laboratory, several authors have had occasion to observe and remark on the gradual disappearance of activity rhythms.



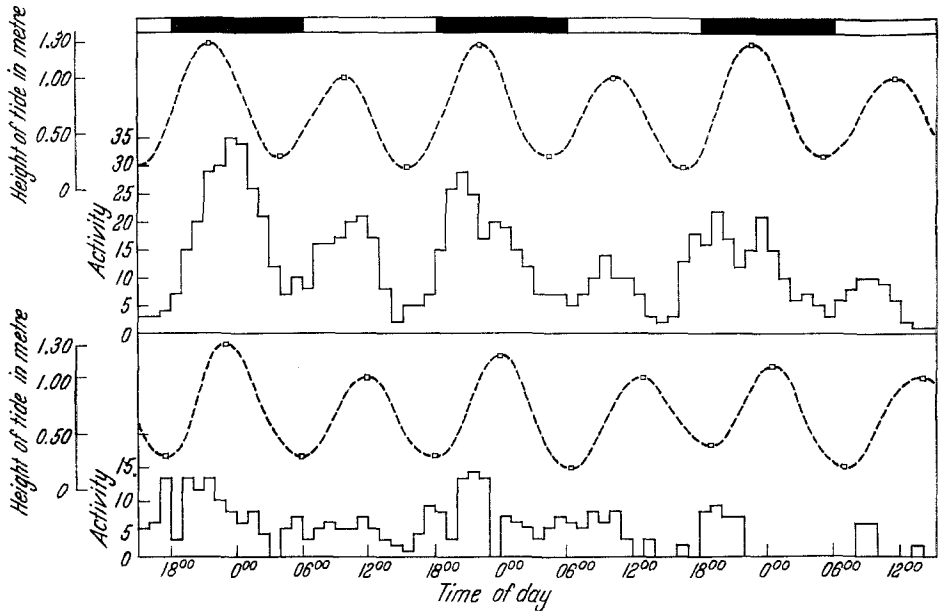


Fig. 12. The waning of the tidal rhythmicity in the spontaneous activity of an *Emerita* recorded through six days. (Shaded bars indicate hours of darkness outside)

The locomotory activity of a solitary specimen of *Emerita* was kymographically traced through six consecutive days. The specimen, a non-berried female in the intermoult stage, was in a healthy condition on release from the activity cage at the close of the experiment. The crab was placed in the aktograph 6 hr. after capture and actual recording commenced 2 hr. later.

The data are presented in Fig. 12. It is obvious that the amplitude and phase of the activity rhythm are in clear agreement for the first 72 hr. of observation. During the 4<sup>th</sup>–5<sup>th</sup> and 6<sup>th</sup> days there is a marked decrease in the level of activity. The amplitude and period are so staggered in relation to the tidal cycle that no rhythm is to be discerned the third day onwards. About the latter part of the sixth day

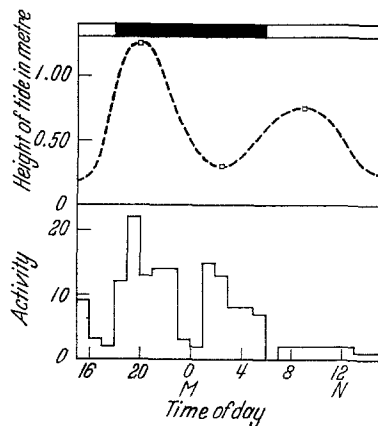


Fig. 13. The spontaneous locomotory activity of an *Emerita* through 24 hr. starting 10 days after removal from habitat. (Shaded bar indicates hours of darkness outside)

what was continuous activity before appears broken into spasmodic efforts. Observations were also made on a crab 10 days after removal from habitat. During the 10 days of its detention in the laboratory the crab was left in seawater and sand. Both sand and seawater were replaced daily from the habitat. *Emerita* being an efficient filterfeeder (see MACGINITIE and MACGINITIE 1949), the crab would have obtained its food from the fresh supplies of sand from the intertidal strip for the 10 days. Water was aerated and temperature maintained at 26° C and the light varied on a day-night regime. On the tenth day, when taken up for observation, the crab showed almost continuous activity with peaks and falls (Fig. 13), these, however, bearing no apparent relationship to the habitat tidal stages. From a study of Fig. 13 it would appear that an experimental artifact might have had a role in the unusually low level of activity observed in Fig. 12 for the 5<sup>th</sup> and 6<sup>th</sup> days. But the staggering of the period relative to the tide timings appears to be due to other factors.

### Discussion

The observations presented in this paper permit some conclusions regarding the endogenous nature of the rhythms expressed in the oxygen consumption and activity levels of *Emerita*. That these rhythms are reflections of its adaptations to the habitat correlates is seen when the habits of this anomuran are studied in the field. *Emerita asiatica* (M. EDW.) lives in populous colonies in the narrow intertidal belt in Madras, only 6—8 metre broad and quite steep in profile. This crab occurs close to the water edge and moves up and down the beach during high tide and low tide, thus, always remaining under a few cm of water. Committed to filtering its food through its antennae it may be seen to strain particulate matter from the receding washes during high tide, hopping out of the sand and reburrying with the advent of every breaker. The results of the present studies suggest that the tempo of the metabolic processes of the organism has adapted to the rhythmic events in the habitat and that the periodicity of their migrations, though ecologically phased, persists even after removal from the habitat. The researches of GOMPEL (1937) on *Xantho*, BENNET et al. (1957) on *Uca*, NAYLOR (1958) on *Carcinus*, WIESER (1962) on *Naesa bidentata* and ENRIGHT (1963) on *Synchelidium* sp. all support such an interpretation. The pattern of activity of *Uca* however, is in contrast to that of *Emerita* or *Carcinus*, since the fiddler crabs prefer areas exposed by the receding tide for their feeding ground. But high levels of activity during hours of high water appear to be characteristic of intertidal immersion feeders. It is worthy of note that the metabolism of invertebrate forms can be so varied intrinsically to meet the needs of the environment. It is, however, not always clear whether it is the occurrence of food or

differential temperature, pressure or light intensity, or any one of the periodic stimuli of the ecological complex, that is the chief factor in the phasing of these endogenous rhythms.

The tidal rhythms in group metabolism discussed earlier is interesting in considering the synchronisation of activity by the members of a community. PEARSE *et al.* (1942) observed that "social adjustment" may be so precise in *Emerita* that when a single crab starts moving out of the sand, the rest of the members also do the same, in the course of their tidal migration. Field studies tempt one to believe that the "acoustic shock" generated by the breakers may be the stimulus that sets in motion this migration, as has been suggested by TURNER and BELDING (1957) for *Donax variabilis*. The precision of synchronisation of individual oscillations appears all the more interesting when an otherwise variable and fluctuating parameter of physiology such as the respiratory metabolic rate displays it.

The superimposition of a diurnal periodicity over a tidal frequency of activity in *Emerita asiatica* is reminiscent of the case of colour change of *Uca spp.* (BROWN *et al.* 1953), oxygen uptake of *Littorina littorea* and *Urosalpinx cinereus* (SANDEEN *et al.* 1954) and the activity of *Callinectes sapidus* (FINGERMAN 1955) and *Carcinus maenus* (NAYLOR 1958). It would appear an immediate advantage to *Emerita* to increase activity during the night time high tides when it is darker on the beach and cooler than when it is exposed to the tropical sun and predators. Though initially it appeared that the levels of activity occurred as a function of the amplitude of the habitat tides, as was found by ENRIGHT (1963) for *Synchelidium sp.*, later experiments performed during periods when the environmental tidal amplitudes occurred reversed, proved that the exaggerated nightly activity was controlled by light-dark cycles of the habitat and that the other increases and decreases were phased by the tidal cycle. These two components, however, appear to be inseparably associated and may shift continuously in reaction to each other to result in lunar periodicities. The significance of the merging of these oscillations in the control and regulation of breeding periods has been discussed by earlier workers.

The waning of the tidal rhythms of activity with time after removal from the habitat firstly suggests that these are phased by the environment variables. An intrinsic rhythm that defies modifiability would seem a disadvantage to littoral organisms, where the tidal cycle itself is subject to irregularities incident upon meteorological changes. ENRIGHT'S (1963) findings show how delicately an intrinsic rhythm may be adjusted to environmental variables. It is also significant that in *Emerita*, in the course of the warping of the activity peaks in amplitude and period, the diurnal component suffers a simultaneous shift and change along with the tidal, indicating the close association of the two. The

staggering of the peaks in oxygen consumption observed in the post-moult form (Fig. 5) is clearly owing to this gradual fading of activity rhythms under constant conditions. BLUME, BÜNNING and MÜLLER (1962) however, observed rhythmic activity bursts in *Carcinus maenas* in diurnal light-dark cycles a long time after removal from habitat. NAYLOR (1960) states that *Carcinus maenas* maintained under non-tidal conditions may yet retain the capacity to exhibit tidal and twice-tidal periodicity.

In the present work no laboratory or field modification of timing was attempted and consequently it is not known whether the lost rhythms may be reinstated with appropriate regimes of imposed stimuli.

The ecological significance of such increases and decreases in the activity of this crab is clear. That even solitary specimens should show clear-cut rhythms in sympathy with the habitat tidal stages, stresses the selection value such adjustment of activity may have in the field. In view of its migratory behaviour within the steep and narrow intertidal belt any asynchrony of activity with the phases of the tide would mean being stranded and inevitable death due to desiccation for the crab.

### Summary

1. The oxygen consumption of the sand crab, *Emerita asiatica*, when estimated employing solitary specimens showed an unmistakable persistent tidal rhythm.

2. Numbers of 4 and 5 crabs even when huddled together in the respiration chambers showed the rhythmicity in their metabolic rates indicating mutual synchronisation of individual oscillations.

3. In newly moult crabs, in spite of the intensified level of metabolism accompanying the process of moulting, the tidal rhythms were displayed in the metabolic rates.

4. Simultaneous estimations of the swimming activity employing a vertically moving cage device and the oxygen consumption of individual crabs further confirmed the persistence of rhythms.

5. The activity of *Emerita* coinciding with the high tide at night was considerably enhanced. It was clear that this exaggerated nightly activity was due to the superimposition of a diurnal rhythm on a tidal rhythm.

6. The rhythms in the locomotory activity waned after the crabs had been in the laboratory for 3—4 days.

7. The behaviour of *Emerita*, as seen in the activity records and oxygen consumption estimations made in the present study, is reminiscent of its behaviour in nature relative to the tide.

8. The adaptive significance of such rhythmic behaviour to the continued existence of littoral animals is evident.

### Zusammenfassung

1. *Emerita asiatica* hat einen deutlichen Gezeitenrhythmus des Sauerstoffverbrauchs, der auch unter Laboratoriumsbedingungen weiterläuft.
2. Werden mehrere Individuen in Gemeinschaft gehalten, so zeigt sich eine gegenseitige Synchronisation hinsichtlich dieser Stoffwechschwankungen.
3. Frisch gehäutete Individuen zeigen, trotz des verstärkten Stoffwechsels während der Häutung, diese Gezeitenrhythmik ebenfalls.
4. Gleichzeitige Messung der Schwimmaktivität und des Stoffwechsels bestätigte das Fortdauern der Rhythmik unter Laboratoriumsbedingungen.
5. Zu den Zeiten nächtlicher Flut ist die Bewegungsaktivität erheblich verstärkt. Das beruht deutlich auf einer Überlagerung der diurnalen Rhythmik mit der Gezeitenrhythmik.
6. Nach 3—4 Tagen des Laboratoriumsaufenthaltes zeigt sich bei der Bewegungsaktivität eine Dämpfung der Rhythmik.
7. Das Verhalten im Laboratorium ist sowohl hinsichtlich des Sauerstoffverbrauches als hinsichtlich der Schwimmaktivität eine Fortsetzung des dem natürlichen Gezeitenwechsel angemessenen Verhaltens.
8. Die ökologische Bedeutung dieser rhythmischen Verhaltensweisen unter den Lebensbedingungen an der Küste ist evident.

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