Oecologia (Berl.) 37, 163–176 (1978)

*Oecologia*


# Semilunar Rhythm in the Zoea-Release Activity of the Land Crabs *Sesarma**

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**Summary.** The number of the land crabs *Sesarma* which released zoeae in a river was counted and recorded for 2 years. The number of crabs releasing zoeae reached a maximum at around every syzygy and decreased to a minimum at around every half moon, showing a semilunar rhythm (Fig. 2). This semilunar rhythm, when examined temporally, showed a peculiar pattern accurately synchronized with the lunar cycle. On the day of and during 4–5 days prior to the syzygy, the peak of zoea-release activity came just after sunset. A few days later, the peak gradually shifted to later in the evening and became flattened until temporal concentration was no longer observed. About 2 days after the half moon, the peak appeared again just after sunset (Figs. 3, 4 and 5). It is not likely that the tide itself affects the semilunar rhythm of *Sesarma*, but it is supposed that the lunadian factor is involved in it. The adaptive significance of this semilunar rhythm may be interpreted to mean that zoeae released in the river just after the time of spring high tides will succesfully arrive at the sea and that the lunadian modification of the peak in the temporal structure will also ensure that the zoeae will be released at the time of high tides and will have a better chance of arriving at the sea than they would otherwise do.

## Introduction

A biological rhythm may be defined as showing lunar or semilunar rhythm if the maxima and minima of the rhythmical process appear once or twice respectively in every lunar month. Many cases have been found in field studies, both by occasional observations and by statistical analysis of repeated observations (Fox, 1923; Korringa, 1947; Caspers, 1951). Many lunar periodic processes are connected with reproduction.

*Sesarma haematocheir* and *S. intermedium* are land crabs which inhabit lowland valleys never influenced by tides (Saigusa, 1978). Their larvae, however,

* Contributions from Shimoda Marine Research Center, The University of Tsukuba, No 331

0029-8549/78/0037/0163/$03.40

develop in the sea, and adult crabs return to water which flows into the sea in order to spawn (release of zoeae). A remarkable semilunar rhythm is observed in the zoea-release activity as briefly reported by several authors (Shimoizumi and Tanemura, 1951; Hashimoto, 1965; Saigusa, 1976).

Some experiments have demonstrated the presence of rhythms with a lunar or semilunar period in *Platynereis* (Hauenschild, 1956, 1960), *Dictyota* (Bünning und Müller, 1961; Müller, 1962; Vielhaben, 1963) and *Clunio* (Neumann, 1966, 1968, 1976). It is, however, much debated on what basis a lunar or semilunar rhythm is controlled.

Hypotheses on the mechanisms explaining lunar or semilunar thythm can be summarized in the following three categories:

1. "Beat" caused by the interaction of daily and tidal rhythms (Brown et al., 1953; Bünning und Müller, 1961).

2. Existence of an endogenous rhythm with a long period of about 15 days or 1 month, which can be entrained with moonlight as a Zeitgeber (Neumann, 1969).

3. Coaction of two tidal rhythms with circa-lunar amplitude modulation (Enright, 1972).

For the understanding and explanation of the nature of lunar and semilunar rhythm, a detailed examination of the temporal structure or pattern underlying the rhythm is necessary.

The present paper reports the temporal structure of the zoea-release activity rhythm of land crabs.

## Methods

In the summer of 1975 and 1976, zoea-release of *Sesarma haematocheir* (de Haan) as well as of *S. intermedium* (de Haan) was observed at a field station in the southern end of Izu Peninsula. A site along a river (Ōgamo River) (Fig. 1) was selected, and the zoea-release activity of the two species was recorded in the breeding season lasting from early July to late September.

The station for observation lay about 1.5 km upriver from the sea. At this site, the river was about 7 m wide and became a shallow stream of about 20 cm deep at the low water of both spring and neap tides. The bottom was partially exposed and the release of zoeae, when it occurred at this period, was performed in a pool remaining along the shore or in a shallow stream.

At the high water of the spring tides, the river rose to 50–60 cm deep and was slow-flowing, and the variation in water level due to tidal influence reached 200 m upriver from the observation site. During this period, the release of zoeae was performed at the riverside shore. But the level of high water at the neap tides was hardly different from that of low water at the spring tides. Therefore at the observation site, fluctuation of the water level at high and low waters is regarded as being between 0–40 cm. Salinity of the water at the site was no different from ordinary fresh water regardless of tidal situation. The time of high and low waters at the observation site was much the same as in Figs. 3, 4, and 5 which are based on the data at Shimoda in the Tide Tables of the Japan Meteorological Agency.

Observations were made on a riverside rocky shore about 1 m high. Many crabs of *S. haematocheir* and *S. intermedium*, usually living in burrows along the hills behind (Saigusa, 1978), come down and swarm on the shore for release of zoeae.

The number of animals which released zoeae within a 5 m reach along the riverside was counted at 5 min intervals. Since preliminary all-day observations extending over half a lunar month had made it clear that practically all the release of zoeae occurred before 3 o'clock in the morning and never at dawn nor in the daytime, observations were mainly continued from

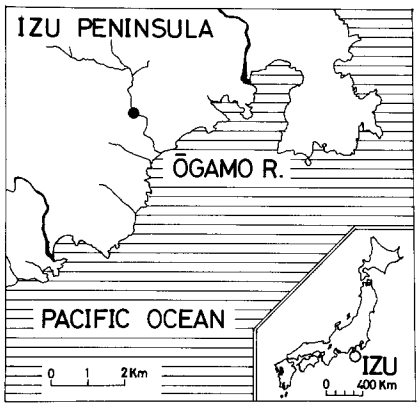



**Fig. 1.** Location of the observation site (●)

evening to 3 o'clock in the morning. The two species were counted separately. Counting was made with the aid of a very dim hand light. Crabs released zoeae quite normally under such conditions without showing any sign of being disturbed.

## Results

### *1. Behavior of Crabs upon Zoea-Release*

Late in the afternoon, around the full and the new moon (syzygy), ovigerous female crabs (with zoea in the egg) position themselves along the river bank. The bank often appeared red because of the number of swarming crabs. All the crabs dwelling along Ōgamo River appear to release zoeae in the main stream and not in its tributaries. Release of zoeae seems to take place on any site of the main riverside where access to water is possible for the crabs.

As evening falls, ovigerous female crabs positioning themselves on the riverside slowly approach the water. At sunset, almost all of them concentrate on the shore within 50 cm above the water level. Just at the time when crabs are invisible to the naked eye (the "dusk", probably less than 1 lux), they begin to release zoeae.

Release of zoeae proceeds as follows. An ovigerous female crab steps into the water, immerses half of her body in the water and turns directly or obliquely toward the open water surface. She stretches 2–4 pairs of her posterior pereiopods for support, fixes her chelae onto the ventral side of the cephalothorax while fanning up and down with the abdomen half opened to release zoeae. The release finishes in 3–4 s. The behavior pattern of zoea-release is identical in the two species. Almost all crabs release zoeae within a short time span of about 1.5 h and retreat to the shore.

Around the first or last quarter of the moon only a few crabs gather on the riverside, and zoea-release occurs sporadically until midnight without being concentrated in the period just after sunset. In this case, some crabs release zoeae as soon as they come to the waterside, but other crabs, wandering about the riverside or going out of and returning into the spaces among rocks, do not easily release zoeae.

Most ovigerous female crabs finish the release of zoeae at one time, but some crabs perform a second release a little later. This second release lasts only 1–2 s and released zoeae are few in number and hardly observable in the water. The second release can therefore be easily distinguished from the first one and has not been counted in recording.

After having released zoeae, some crabs still fan their abdomens in the water, but most of the crabs soon return to the shore, spread their abdomens and clear them with the chelae. Crabs after release of zoeae eventually leave the riverside. The second incubation of eggs will soon start (July-August) (Saigusa and Hidaka, unpublished).

## 2. *Semilunar Rhythm*

Figure 2 shows the number of *S. haematocheir* and *S. intermedium* which released zoeae every day from July 10 until September 24, 1976. In both species, the number of animals releasing zoeae reached a maximum at around every syzygy and decreased to a minimum at around every first and last quarter of the moon (half moon), showing a remarkable semilunar rhythm. Peak-to-peak intervals appeared to be about 11–14 days in *S. haematocheir* and 10–15 days in *S. intermedium*. The following features which have not generally been referred to in discussions on semilunar rhythm were also noticed:

There were some days when the number of animals releasing zoeae suddenly increased, for example, August 5 and August 7, in *S. intermedium* and August 30, in *S. haematocheir*.

There were some cases, especially in *S. haematocheir* in July, where the maxima deviated from the syzygy. Similar facts were observed with the minima. For example, a peak was found between the full moon and the last quarter of the moon (July 13–18), and a minimum between the last quarter and the new moon (July 30).

In both species, the maxima and the minima of the number of animals releasing zoeae seemed to gradually synchronize with the phase of the moon through July to September.

In *S. haematocheir* in August, two peaks were clearly observed at around the full moon (August 10).

Comparison with the record of everyday weather (shown in Fig. 3) demonstrated no dependency on weather conditions of the number of crabs releasing zoeae.

The water level of the observation site was influenced more by rain than by tides. However, even when the water rose more than 30–50 cm above the level of high water following heavy rain (↑ in Fig. 2), no influence on the number of crabs was observed.

For *S. haematocheir*, the number of animals releasing zoeae during a 2-week period around the full moon far exceeded that around the new moon. The same tendency was observed also for *S. intermedium*.

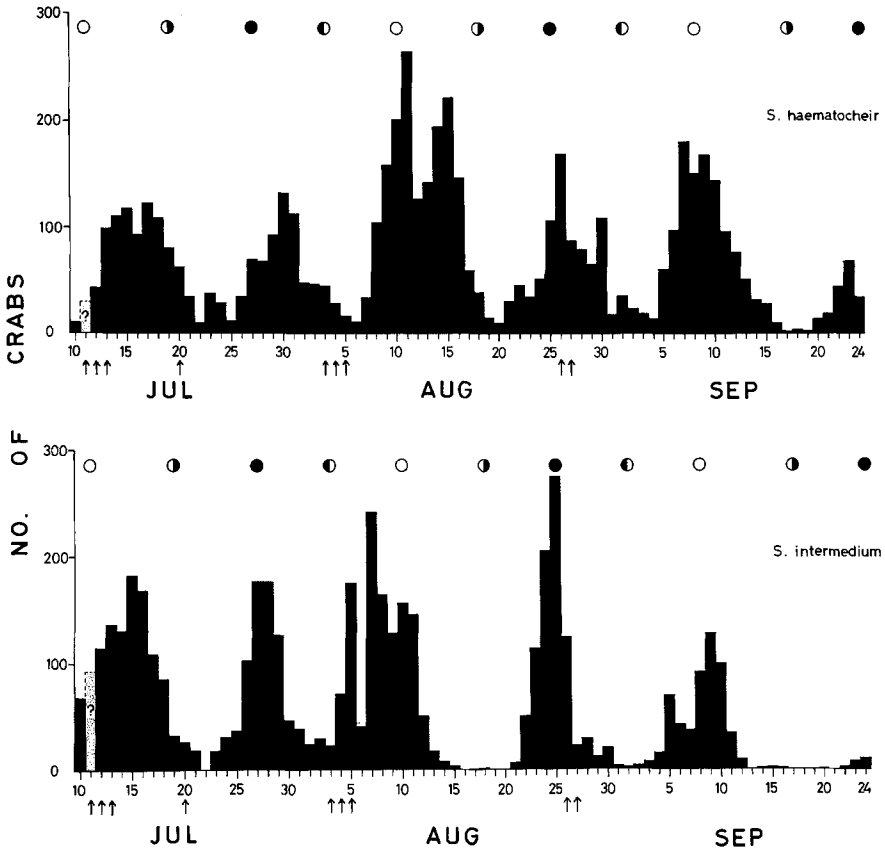



**Fig. 2.** Daily number of *S. haematocheir* and *S. intermedium* which released zoeae from July 10 to September 24, 1976. ?—not examined. *Arrows* show the days when water rose more than 30–50 cm above the high water level of spring tides following heavy rains

### *3. Temporal Structure of the Semilunar Rhythm*

Figure 3 summarizes the record of the zoea-release activity of these two species over 2 lunar month periods in relation to the phase of the moon, times of high and low tides, and times of rise and fall of the sun and the moon.

It is obvious that the zoea-release activity was concentrated around the syzygy. On the day of and during 4–5 days prior to the syzygy, zoea-release took place within about 1.5 h after sunset, with the peak of the activity coming just after sunset. Starting therefrom, however, the peak gradually delayed. Parallel to this delay, the peak became flattened until temporal concentration was no longer observed by the time of the half moon. Around the half moon, the peak was completely lost, zoea-release occurring sporadically during a time span extending before and after the time of the high tide and the time of

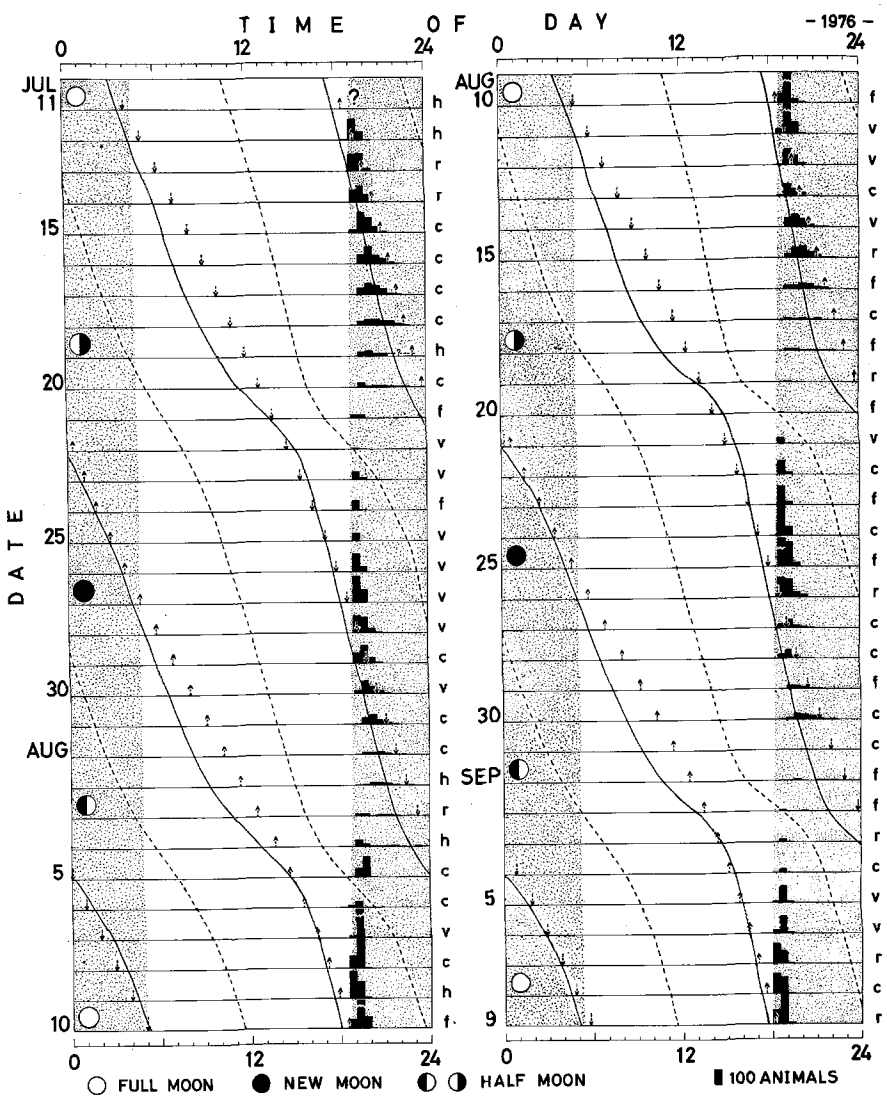



**Fig. 3.** Temporal pattern of the zoea-release activity in *S. haematocheir* and *S. intermedium* as shown by the number of animals per 30 min record over 2 lunar month periods in relation to the phase of the moon, times of high (*solid diagonal lines*) and low (*broken diagonal lines*) tides, and times of rise and set of the sun and the moon. The tidal data in Figs. 3–5 are related to the sea coast. The time of high and low water at the observation site was much the same as the data. Consecutive days run from top to bottom. The *stippled area* shows dark periods between sunset and sunrise. *Upward and downward broken arrows* indicate times of moonrise and moonset respectively. ?—not examined. Weather during the observation: very fine (*v*), fine (*f*), cloudy (*c*), rain (*r*), heavy rain (*h*)

moon-rise or moon-set. A few days thereafter, however, the new, though small, well-concentrated peak appeared just after sunset. As stated before, the zoea-release activity practically never extended beyond midnight.

Thus, when examined temporally, the zoea-release activity was shown to follow a peculiar rhythm which synchronized very accurately with the lunar cycle.

The time of sunset advanced daily by 0.5–2 min in this period, shifting more than 1 h earlier from July until September. When the temporal pattern showed the conspicuous peak, the peak shifted in accordance with the time of the sunset.

At around every syzygy, crabs begin to release zoeae just at "dusk". As the time of "dusk" at the observation site depended on the weather condition of the day ($16 \pm 4$ min after sunset on fine days, $11 \pm 4$ min on cloudy days and only $6 \pm 3$ min on rainy days), it is supposed that the timing of the peaks of zoea-release activity is determined by the time of dusk. However, when observed data were rearranged in temporal relation to the time of dusk, this assumption was not fully supported (Fig. 6a and b). For example, the peak for *S. haematocheir* on August 9 and September 7, which should be much advanced in time because of earlier dusk (Fig. 4a), actually was delayed in relation to the time of dusk (Fig. 6a).

With regard to the zoea-release activity in the period ranging from a few days after the syzygy to the half moon, it was no longer possible to discuss its dependency on the time of dusk.

## Discussion

Long-term examination over 2 years of the zoea-release activity in the land crabs showed that the temporal structure of the semilunar rhythm has a quite exact synchronization with the lunar cycle (Figs. 4 and 5).

The rhythm observed here (Figs. 2, 4, and 5) may be regarded as an example of the combination of the semilunar rhythm of the daily number of individuals and the daily rhythm of the time of the event, as proposed by Neumann (1966, 1969, 1975, 1976) in the case of *Clunio*. The speciality of *Sesarma* seems to be a modification of the daily rhythm to the tidal rhythm during succeeding days.

Many authors have reported endogenous rhythms showing daily and tidal patterns in the activity of littoral organisms (Naylor, 1958; Palmer, 1964; Palmer and Round, 1967; Barnwell, 1966; Honegger, 1973). In view of these works, the case of *Sesarma* (Figs. 4 and 5) may be interpreted as taking the pattern of daily rhythm close to the syzygy and gradually shifting thereafter to the pattern of tidal rhythm. It is difficult, however, to explain the recurrence of the daily-rhythm pattern a few days after every half moon in accurate synchronization with the lunar cycle.

It is not likely that tides themselves are related to the rhythm of *Sesarma* because 1) the water level of the Ogamo River is more influenced by rain than by tides; 2) these crabs live on hillsides far from the main stream (Saigusa, 1978) and adult female crabs approach the river only for the release of zoeae.

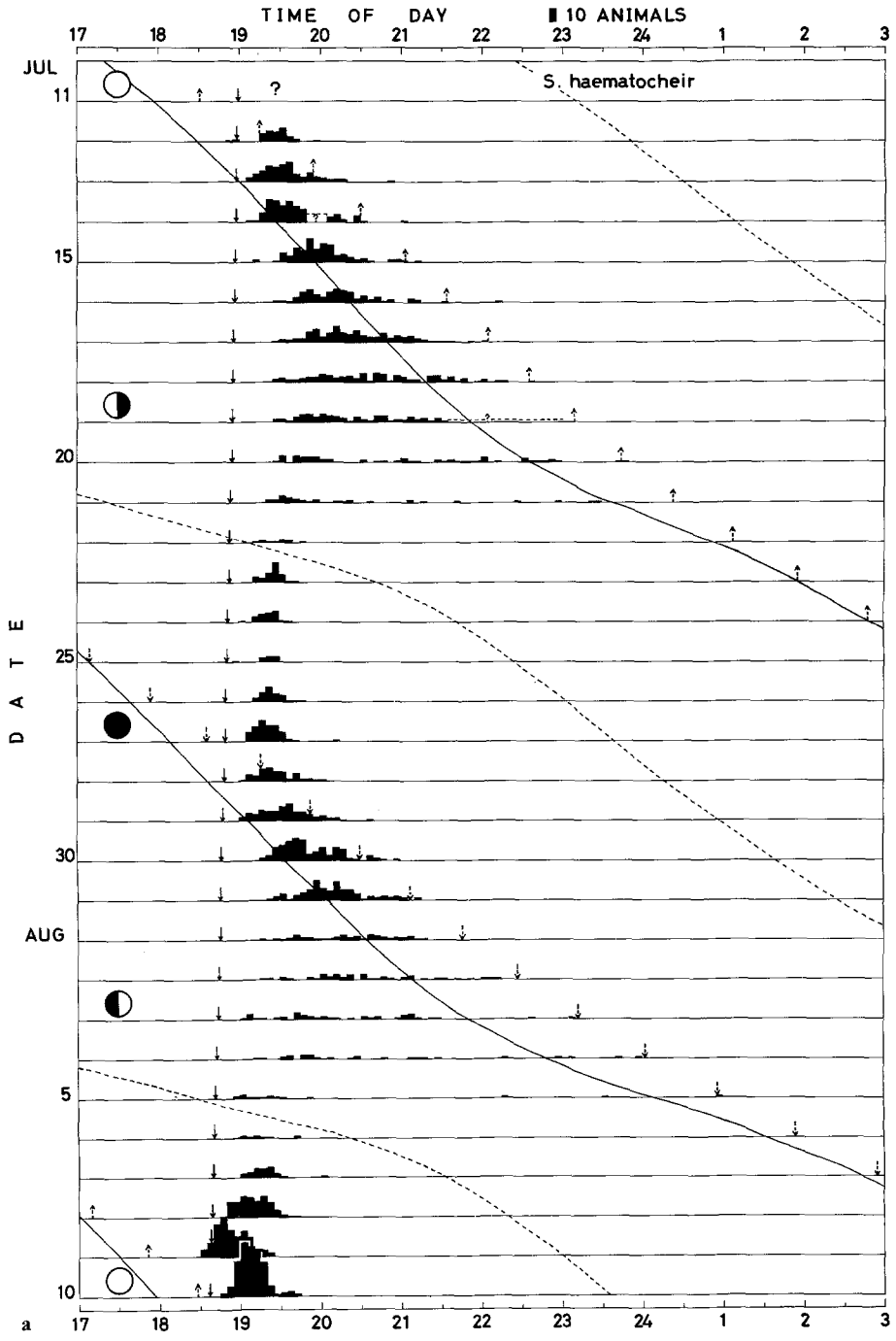
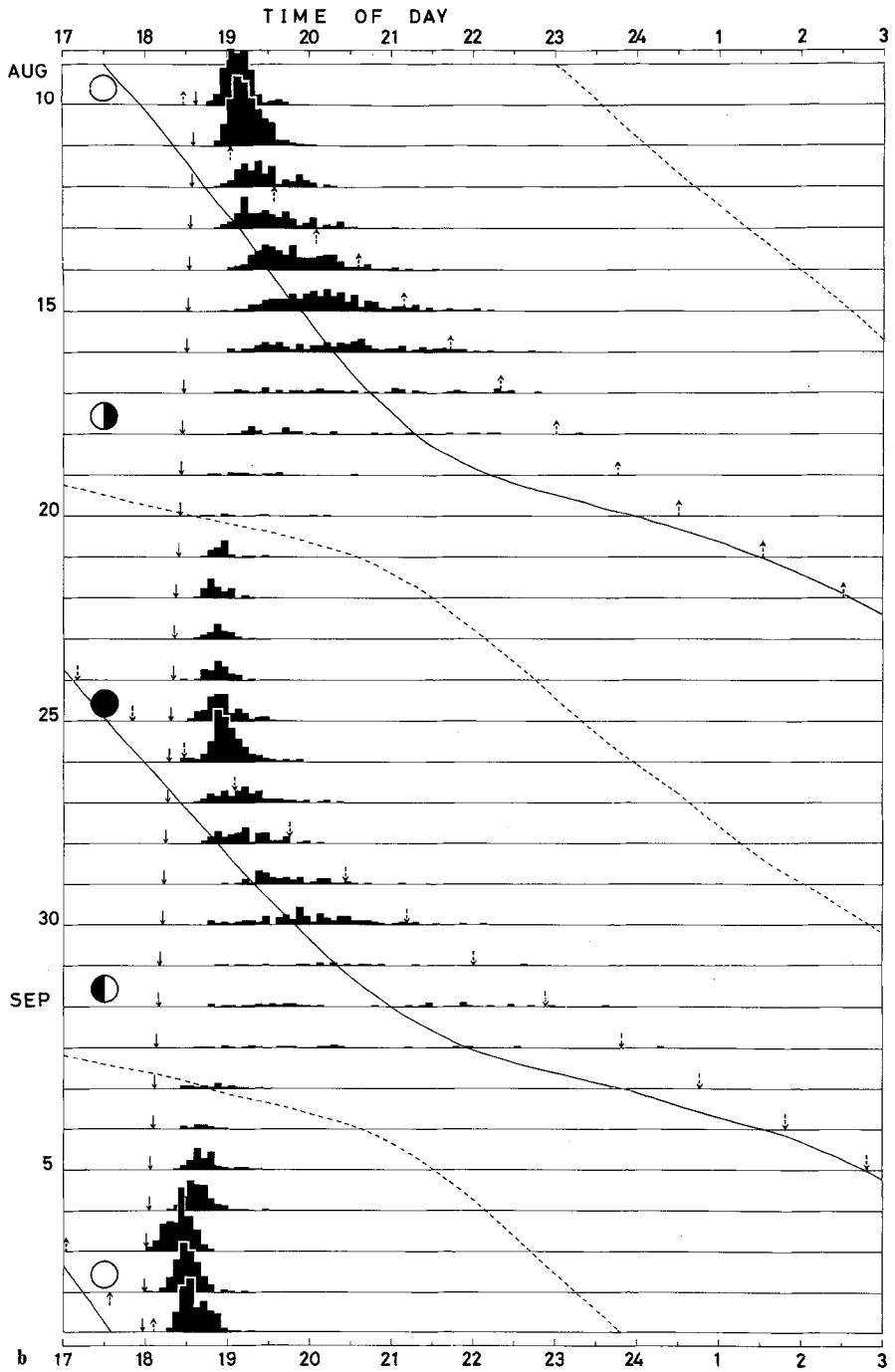



**Fig. 4. a and b.** Closer examination of the zoea-release activity pattern in *S. haematocheir* as shown by the number of animals per 5 min from July 11 to August 10, 1976 (**a**) and




from August 10 to September 9, 1976 (**b**). *Downward solid arrows* indicate the time of sunset. Other symbols are the same as in Fig. 3

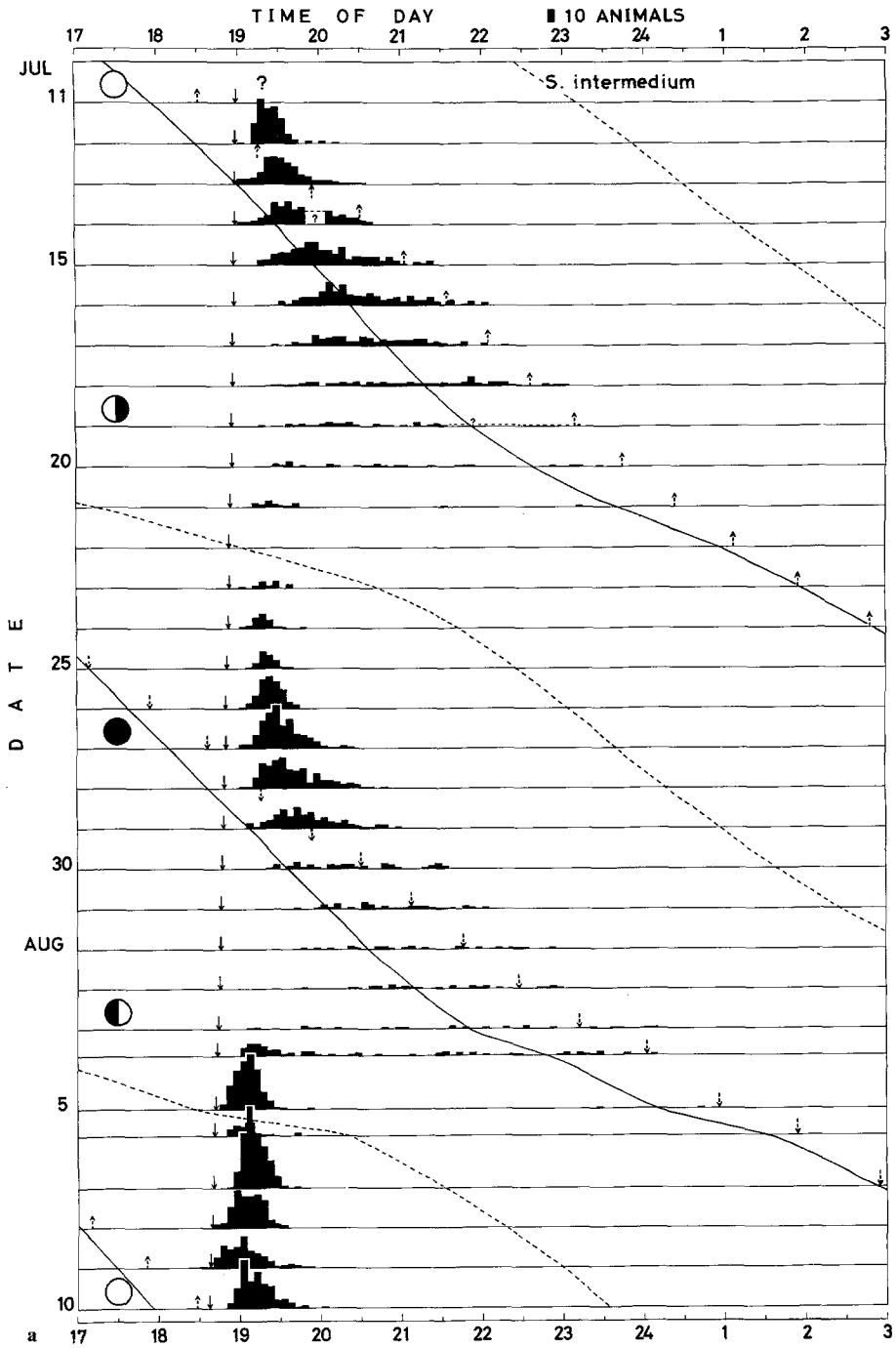
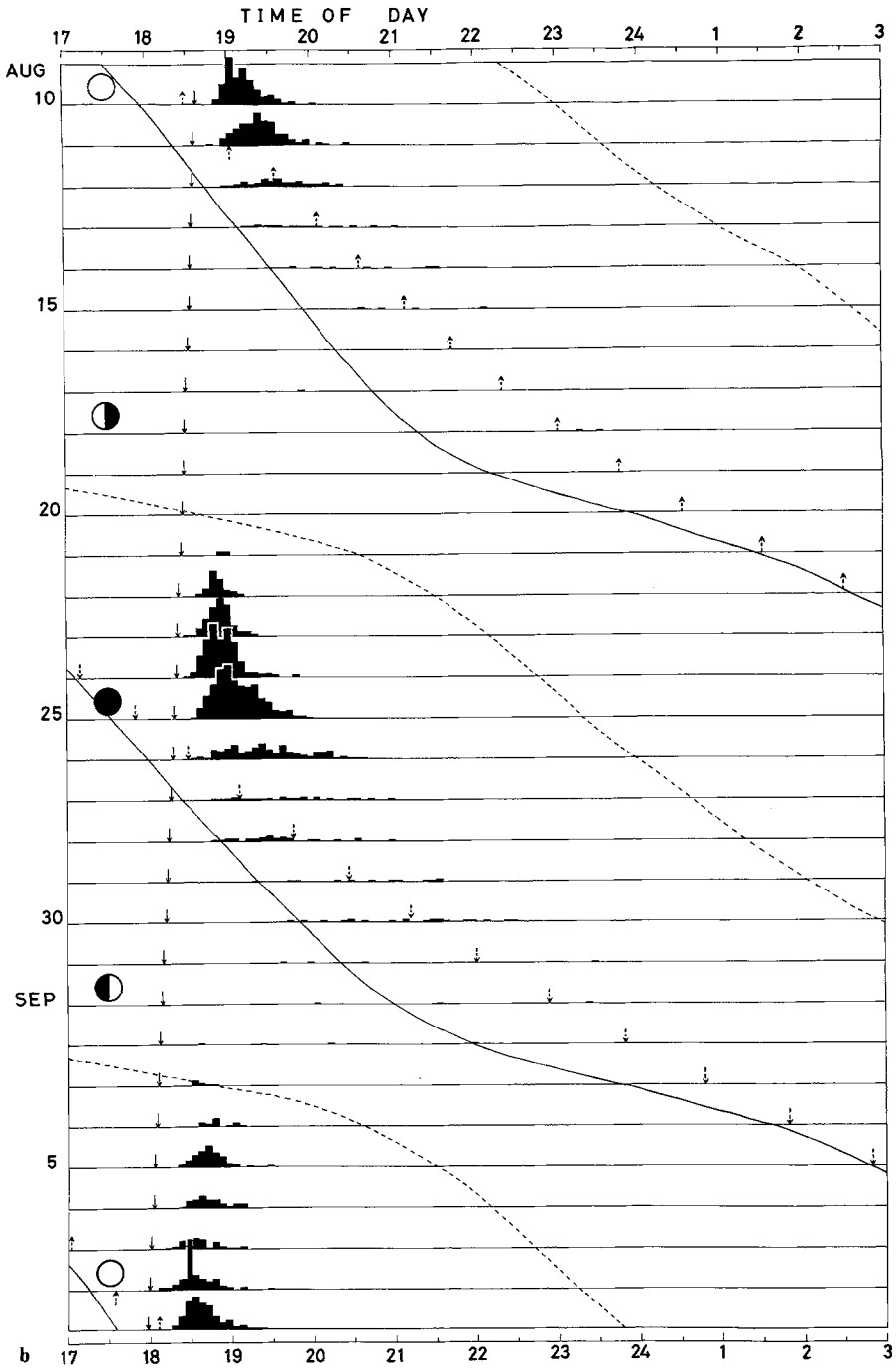



**Fig. 5. a and b.** Closer examination of the zoea-release activity pattern in *S. intermedium* as shown by the number of animals per 5 min from July 11 to August 10, 1976 (**a**) and




from August 10 to September 9, 1976 (**b**)

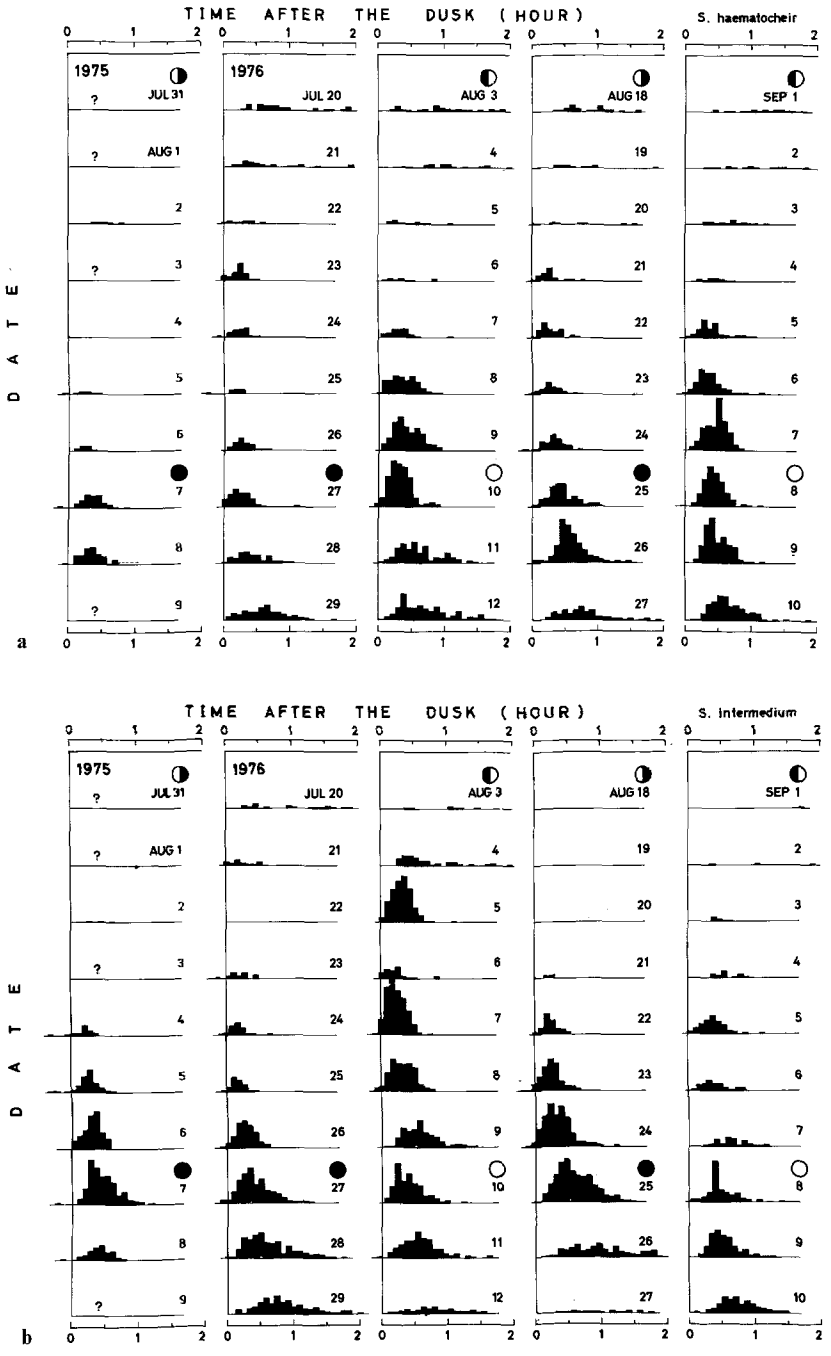



**Fig. 6. a and b.** Shift of the zoea-release activity peak in *S. haematocheir* **(a)** and *S. intermedium* **(b)** in temporal relation to the time of "dusk". ?—not examined

Since the tidal rhythm may be described as the lunadian rhythm, paralleling the moon-rise and moon-set with a period of nearly 24.8 h, it is supposed that a lunadian rather than a tidal factor is involved in the rhythm of zoea-release activity of *Sesarma*.

The problems to be further tested are: Is the temporal pattern of the semilunar rhythm of *Sesarma* of an endogenous nature? If so, what Zeitgeber(s) can entrain it? How are the temporal pattern and the number of crabs releasing zoeae connected to each other?

The adaptive significance of this semilunar rhythm may be interpreted as follows. Zoeae released in the river just after the time of spring high tides will successfully reach the sea. The lunadian modification of the peak in the temporal structure will also ensure that the zoeae to be released at the time of high tides will have a better chance of reaching the sea than otherwise. However, there were a few instances where crabs released zoeae in the river at an unlucky moment. For example, many crabs released zoeae just after the time of low tides on August 5, 1976 (Fig. 5b). There remain therefore some intricate problems. The fact that release of zoeae occurs only in the early half of the night may also have some adaptive significance.

*Acknowledgements.* The authors wish to express their sincere thanks to Professor Hiroshi Watanabe, Director of Shimoda Marine Research Center, The University of Tsukuba, for kindly providing facilities for the work and Dr. Toshiki Makioka, Mr. Keiichi Koike and all other staff of the center for their friendly help. The authors are very grateful to Professor Emeritus Masaru Kato, Kyoto University, for his invaluable advice. Thanks are also due to Dr. Alun M. Anderson, University of Oxford and Kyoto University, for reading the manuscript.

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Received May 29, 1978