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ADAPTIVE SIGNIFICANCE OF A SEMILUNAR RHYTHM IN THE TERRESTRIAL CRAB *SESARMA*

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Abstract

Larval release activities of the terrestrial crab *Sesarma* were observed 1.5 km upriver from the sea. The number of *Sesarma haematocheir* and *Sesarma intermedium* females releasing larvae peaked twice monthly, during the full and new moon periods. Larval release, at about dusk, coincided with high water at the nearby seacoast. Larvae of *S. haematocheir* and *S. intermedium* died quickly in fresh water. The semilunar rhythm of larval release gives the larvae, released just after high water of spring tides and around high water on the days following the full and new moons, a better chance of reaching the sea than otherwise. *Sesarma dehaani* did not reveal a clear semilunar rhythm and the time of day of larval release did not coincide well with high water. *S. dehaani* inhabits riverbanks and rice paddies near the sea, and its larvae have the highest tolerance to fresh water. These factors may account for its lack of synchronization with tides.

Introduction

A number of marine organisms exhibit lunar or semilunar rhythms in reproductive activities (Korringa, 1947; Enright, 1975; Naylor, 1976). Several recent works, particularly on the polychaete *Platynereis* (Hauenschild, 1960), the intertidal midge *Clunio* (Neumann, 1966, 1975, 1976, 1978) and the terrestrial crab *Sesarma* (Saigusa, 1980a) studied these rhythms as biological clocks.

The adaptive advantages of fewer of these reproductive rhythms have been reported. Since almost all known lunar and semilunar rhythms are reproductive, it is presumed that they enhance synchronization of the sexes for mating. For species with external fertilization, restricting the release of gametes to a particular time and place enhances the possibility of successful fertilization (Klapow, 1972).

Further insight into reproductive synchrony may be sought for species with internal fertilization. Oka and Hashimoto (1959) reported that the intertidal midge, *Clunio tsushimensis*, emerges at the time of morning low water for a few days before spring tides. According to Neumann (1966), emergence of *Clunio marinus* is synchronized with the time of afternoon low water of spring tides. This synchronization of emergence would assure both mating and suitable substrata for the succeeding egg-laying.

Clunio deposits fertilized eggs onto the exposed substrata. Many other organisms with lunar or semilunar rhythms release larvae. (For example, several *Uca* species have been reported to exhibit semilunar rhythms of reproduction; Christy, 1978; Zucker, 1978.) When such animals inhabit estuarine flats or banks where tidal excursions are fairly large, families might have to release their larvae during the most favorable tides. Therefore, the sexes might have to synchronize mating (Naylor, 1976), or females might have to synchronize egg-laying (*i.e.*, attachment of fertilized eggs to the ovigerous hairs).

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Grapsid crabs of the genus *Sesarma* are mainly found on and near the estuarine shores. They inhabit riverside banks near the sea. Among them, *Sesarma (Holometopus) haematocheir* (de Haan), *Sesarma (Sesarma) intermedium* (de Haan), and *Sesarma (Holometopus) dehaani* H. Milne Edwards are land dwellers inhabiting hillsides and rice paddies beyond estuarine shores (Saigusa, 1978). From June to September, ovigerous females of these species move to the riverside or seashore and release their larvae (zoeae) into water. The author has already reported a semilunar rhythm of larval release in *S. haematocheir* and *S. intermedium*, and briefly referred to the adaptive significance of this rhythm (Saigusa and Hidaka, 1978). The present paper confirms the semilunar rhythm of larval release in these two species on the basis of data obtained in 1975, and further reports a larval release rhythm of *S. dehaani*. In addition, this paper presents evidence indicating that the phase relationship between larval release rhythm and the semilunar cycle of tides is an adaptation to help zoeae released into a stream reach the sea as soon as possible.

Materials and Methods

Observations were carried out from June–September 1975 and from 10 July–24 September 1976 on the riverside in the southern end of Izu Peninsula, about 1.5 km upriver from the sea (Saigusa, 1980b). The author sat on a rock close to the stream every evening and counted the number of females that released larvae into the stream. With the aid of an electric torch (4.8 V midget lamp), counting was done in a 5-m reach along the water's edge. Despite daytime searches many times from June to July 1975, almost every day from 1 July to 13 August 1976, and sometimes after that I never observed release of larvae during daytime. All-night observations 9–10 June and 22–23 July 1975, and 28–29 August 1976, made it clear that females did not release larvae in the early morning. Therefore, except on the days just cited, counting started about 30 min before sunset every day and finished around 24:00 at the latest in 1975 and around 1:30 at the latest in 1976. Further details and behavior of ovigerous females upon larval release have been described elsewhere (Saigusa, 1980b; Saigusa and Hidaka, 1978).

The following experiments were intended to determine the tolerance of zoeae to fresh and sea water. Sixteen test tubes (1.7 cm diameter and 15 cm depth, or 3 cm diameter and 20 cm depth) were prepared for each experiment. Ovigerous females of *Sesarma haematocheir, S. intermedium,* and *S. dehaani* were captured on the hillsides fronting Gokasho Bay of Kii Peninsula in 1979 and brought into the laboratory at Kyoto. They were kept in plastic containers. Zoeae released into fresh water at the bottom of the containers were transferred into the test tubes. Three individual zoeae were placed in each test tube and the surviving individuals were counted at intervals of 2–24 h. Spring water (chlorinity 0.02‰; chlorinity = grams chloride ion in 1 kg H_2O) and city water (chlorinity 0.04‰, kept standing for a day) were used as fresh water. Sea water from Gokasho Bay of Kii Peninsula was used after rough filtration. Further experiments examined tolerance of zoeae of *S. haematocheir* and *S. intermedium* to sea water diluted with fresh water in the following ratio: 1:20 sea water and 1:10 sea water. All these experiments were carried out at room temperature.

The time needed for zoeae released at the observation site (Izu Peninsula) to reach the sea was estimated by floating corks down the river. A small lead was suspended from each cork by a string 10–20 cm long. Five corks were thrown into the river at the observation site 1 h after high water of spring tides (at 6:15 on 28

May 1979) and at low water (at 12:00 on 27 May 1979), respectively. When stagnant pools or dead trees, etc., captured corks, they were picked up and re-thrown into the middle of the stream, or new corks were thrown in.

RESULTS

At the observation site, the river was about 7–10 m wide. It was a shallow stream about 20 cm deep at low water, rising about 50–100 cm at high water and on rainy days. Since I saw no zoeae released into tributaries, I concluded that females inhabiting hillsides along this river move to the main stream. Figure 1 shows a chlorinity gradient in the river at high water and low water on 24 August 1980 (2 days before the full moon). At high-water periods, tidal influence reached 1.7 km upriver from the sea, but chlorinity was not different from fresh water more than 1.25 km upriver from the sea (0.03–0.04‰).

From mid-June to September, ovigerous females of *Sesarma dehaani* moved to the riverside and released larvae into water. *S. intermedium* females released larvae from late June to September, *S. haematocheir* from early July to September.

Figures 2A and B show the observed number of females releasing zoeae every night for *S. haematocheir* and *S. intermedium.* (Since no data were collected for several days between 21 July and 8 August, data obtained in 1976 for corresponding lunar phases were substituted.) Zoea-release activities in *S. haematocheir* and *S. intermedium* peaked twice monthly during both the full and new moon periods—thus, they had a semilunar rhythm. The number of *S. intermedium* females releasing zoeae during the full moon was about the same as the number during the new moon (Fig. 2B). This was also seen in 1976. More *S. haematocheir* females were seen during the full moon than during the new moon (Fig. 2A). The populations observed in 1976 also demonstrated the full moon periods for larval release activities.

Figure 2C shows the number of *S. dehaani* females observed releasing larvae every night from 21 June to 9 July and from 21 July to 8 August 1975, and from 10 July to 13 September 1976. The number of females revealed no concentration of larval release activities in *S. dehaani* about each full and new moon.

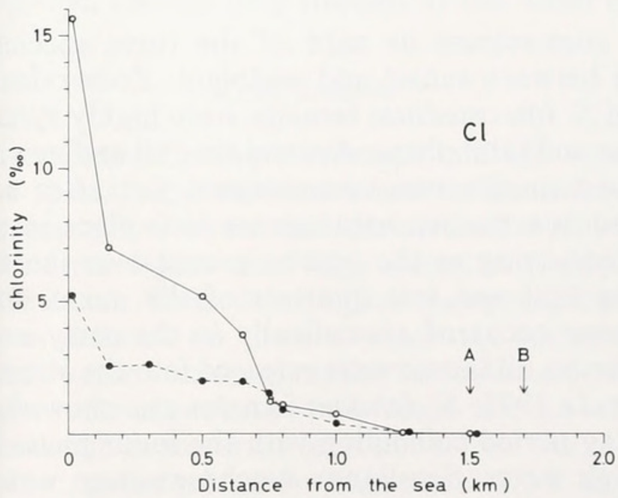

FIGURE 1. Chlorinity (content of chloride ion in NaCl) gradient in the river during low water (broken line) and high water (solid line). Water was sampled from 9:50 to 10:35 and 17:00 to 17:40 on 24 August 1980 (2 days before the full moon). Chlorinity was calculated by titration with $AgNO_3$. Arrows show the locations of the observation site (*A*) and the end of tidal influence (*B*).

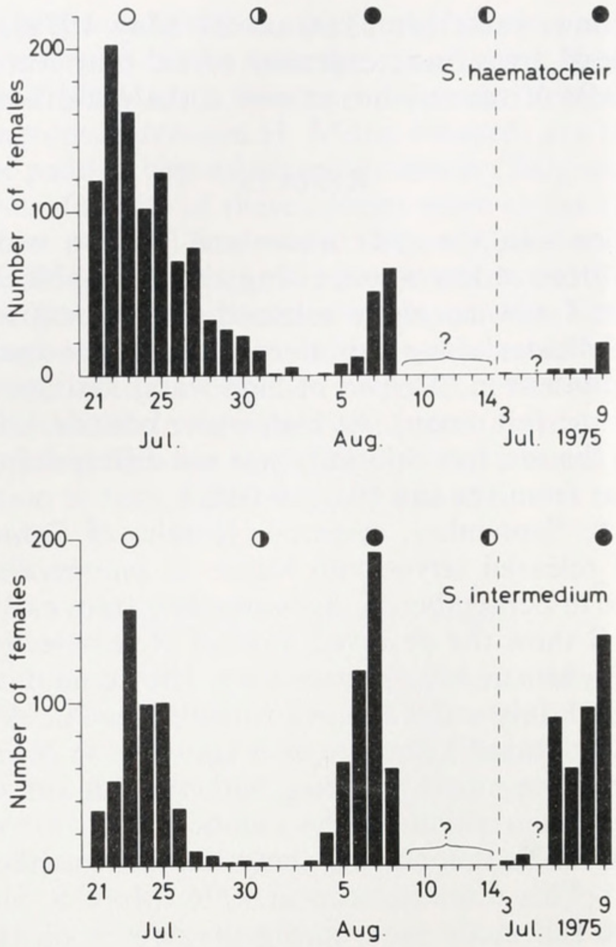

FIGURE 2A. (Above) Number of *Sesarma haematocheir* releasing larvae per night 21 July–8 August and 3 July–9 July 1975. Data from 25, 27, 29, and 31 July and 1 and 3 August replaced by data obtained on 10, 12, 14, 16, 17, and 19 September 1976, respectively; each lunar phase of the former days was identical with the lunar phase of the latter days.

FIGURE 2B. (Below) Number of *Sesarma intermedium* releasing larvae per night 21 July–8 August and 3 July–9 July 1975. For days when observations were not carried out, data obtained on 10, 12, 14, 16, 17, and 19 September 1976 (identical lunar phases) were substituted.

Figure 3 shows zoea-release by each of the three species. All these species released their larvae between sunset and midnight. Zoea-release activities in both *S. haematocheir* and *S. intermedium* females were highly synchronized and timed to coincide with lunar and tidal phase. Around the full and new moons, zoea-release activities in these two species was concentrated just after sunset. On the days following the full and new moons, zoea-release took place in accordance with the time of high water occurring at the nearby seacoast or the time of moonrise or moonset. Around the first and last quarters of the moon, few females released zoeae, and zoea-release occurred sporadically in the early evening. As shown in Figures 3A and B, almost all larvae were released into the stream within 2.5 h after afternoon high water. In 1975, *S. dehaani* females also showed a weak zoea-release rhythm, with a 15-day period coinciding with the lunar phase but only slight synchronization with high water. Semilunar synchronization was more distinct in *S. haematocheir* and *S. intermedium*, which inhabit higher land than *S. dehaani*.

The survival curves of zoeae are shown in Figures 4 and 5. Fresh water severely affected *S. haematocheir* and *S. intermedium* zoeae. Within 6 h of treatment, 5–15% of *S. haematocheir* zoeae died. All died within 48 h. Within 4 h of treatment,

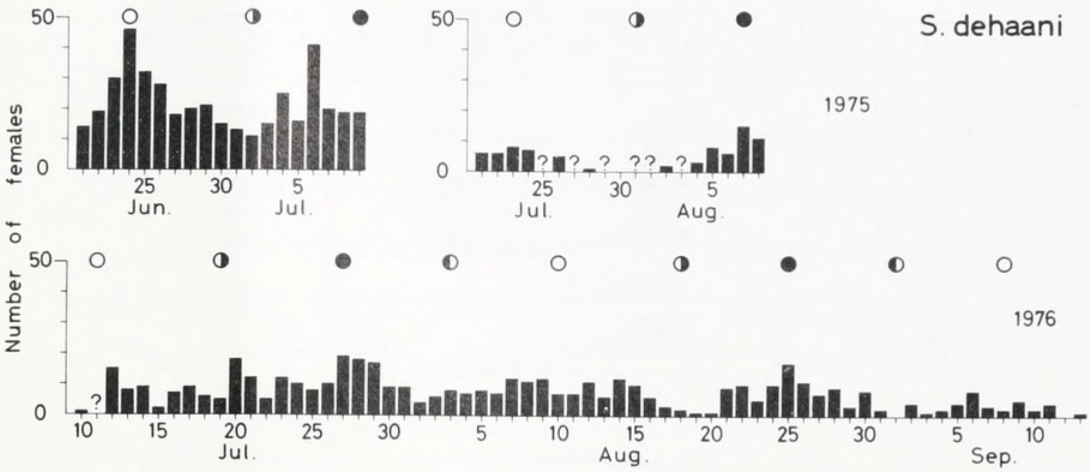

FIGURE 2C. Number of *Sesarma dehaani* releasing larvae per night 21 June–9 July and 21 July–8 August 1975; and 10 July–13 September 1976. Observations not carried out on 26, 27, and 30 June and 1, 2, and 5 July 1975. Each day of no observations was substituted by superposing data of 2 days examined in 1976; phase of larval release rhythm can be regarded as identical (26 June replaced by 14 and 28 July; 27 June by 15 and 29 July; 30 June by 18 July and 1 August; 1 July by 19 July and 2 August; 2 July by 20 July and 3 August; and 5 July by 23 July and 6 August 1976, respectively. See Fig. 3C).

5–45% of *S. intermedium* zoeae died and all died within 70 h. *S. dehaani* zoeae had the highest tolerance of fresh water among the three species. However, a dead zoea was found 17 h after the treatment and all died within 96 h. Survival times grew longer as salinity increased (Fig. 5). Zoeae placed in natural sea water all lived at least 4 days, except one *S. haematocheir* zoea. Thus, zoeae released in fresh water are exposed to immediate danger of death. This may be particularly true for zoeae of *S. haematocheir* and *S. intermedium*.

During low water, the river ran very slowly. Mud flats, stones, and dead trees were exposed to the air. Stagnant pools were common, and soon collected all corks; new or re-thrown corks soon entered another pool. At 150 m from the sea, they were borne upriver by the rising tide. However, during high water, stagnant pools were scarce. Two corks took 3 h 20 min and 3 h 30 min, respectively, to reach the sea with the receding tide, though they stopped at the water's edge several times.

DISCUSSION

At the observation site, zoeae were released in fresh water (chlorinity 0.03–0.04‰). As Figure 4 shows, their survival would be immediately threatened. The capture of corks released at low water, and the successful journey to the sea of two corks thrown into the stream just after high water, may apply to zoeae released at the observation site. Zoeae released during low water would soon get into stagnant pools. It would be very difficult for them to reach the sea or even brackish water until the following high water, receding, carries them downriver. On the other hand, zoeae released at high water may successfully reach the sea with the receding tide. High and low waters occur at intervals of about 6.2 h. Corks took about 3.5 h to reach the sea. Therefore, zoeae released within about 2.7 h after high water would have a chance of reaching the sea with the receding tide.

Figure 3 shows that almost all zoeae of *S. haematocheir* and *S. intermedium* were released into the stream within 2.5 h of high tide. They thus might successfully reach the sea with the receding tide. Larvae released just after the time of high

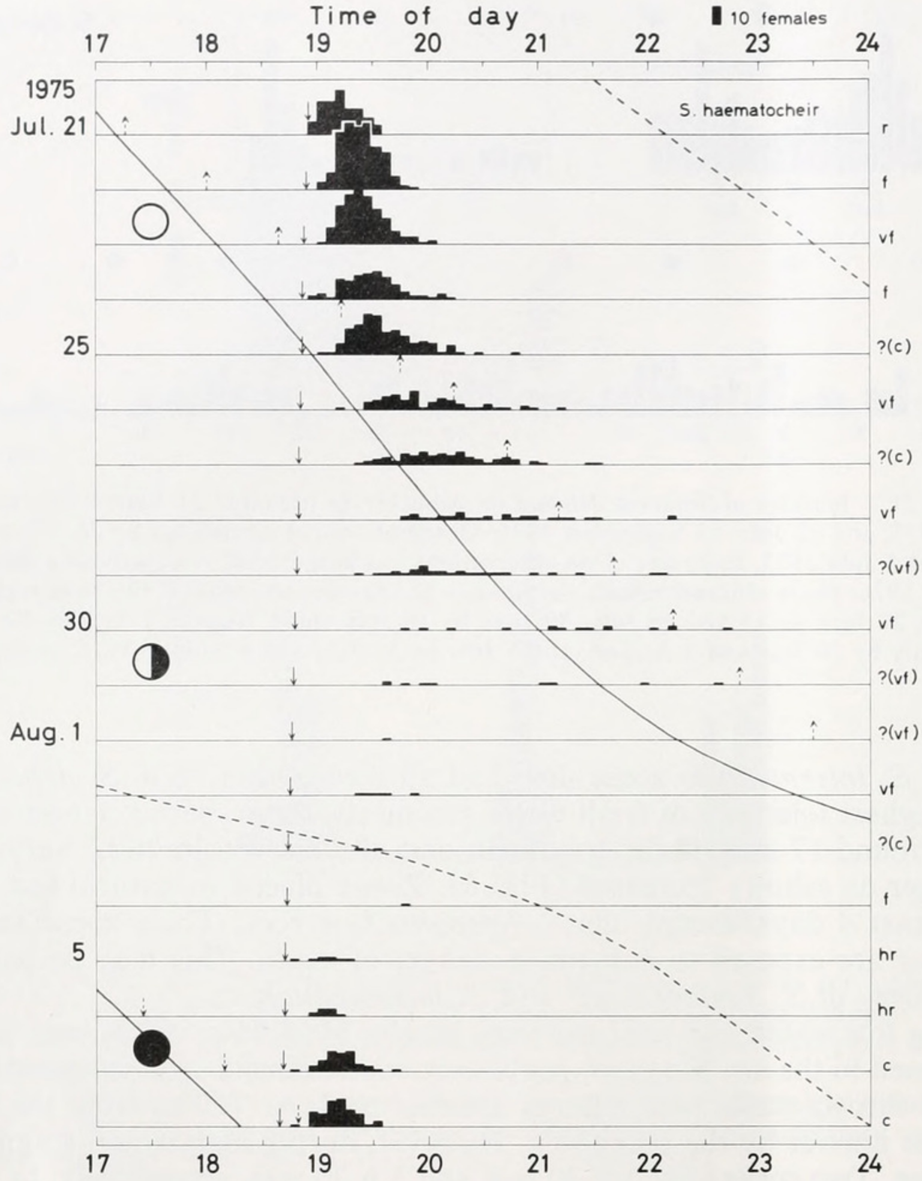

FIGURE 3A. Time of day of larval release in *Sesarma haematocheir* 21 July to 8 August 1975, shown by number of females observed per 5 min in relation to lunar phase, times of high (solid diagonal lines) and low (broken diagonal lines) tides occurring at the nearby seacoast, times of sunset (downward solid arrows) and times of moonrise (upward broken arrows) and moonset (downward broken arrows). Weather during observations: very fine (vf), fine (f), cloudy (c), rain (r), heavy rain (hr). As explained in Fig. 2A, substitute data was used for field observations not carried out on 25, 27, 29, 31 July and 1 and 3 August. Sunset times also substituted on these days.

water of spring tides might have the best chance of reaching the sea and larvae released at the time of high water on the following days would have a better chance of reaching the sea than during other tidal phases.

Larval release activities in *S. dehaani* showed no clear semilunar rhythm (Fig. 2C), and were not well synchronized or timed to coincide with high tides occurring after sunset (Fig. 3C). The zoeae of this species have the highest tolerance of fresh water among three species. Even released at ebb tide, they would live in fresh water until the following receding water carried them downriver. In addition, distribution of this species was limited to bottomlands near the sea (Saigusa, 1978). Many crabs were found in the riverside banks and rice paddies downstream from the observation site. Thus, females may release their larvae into brackish water.

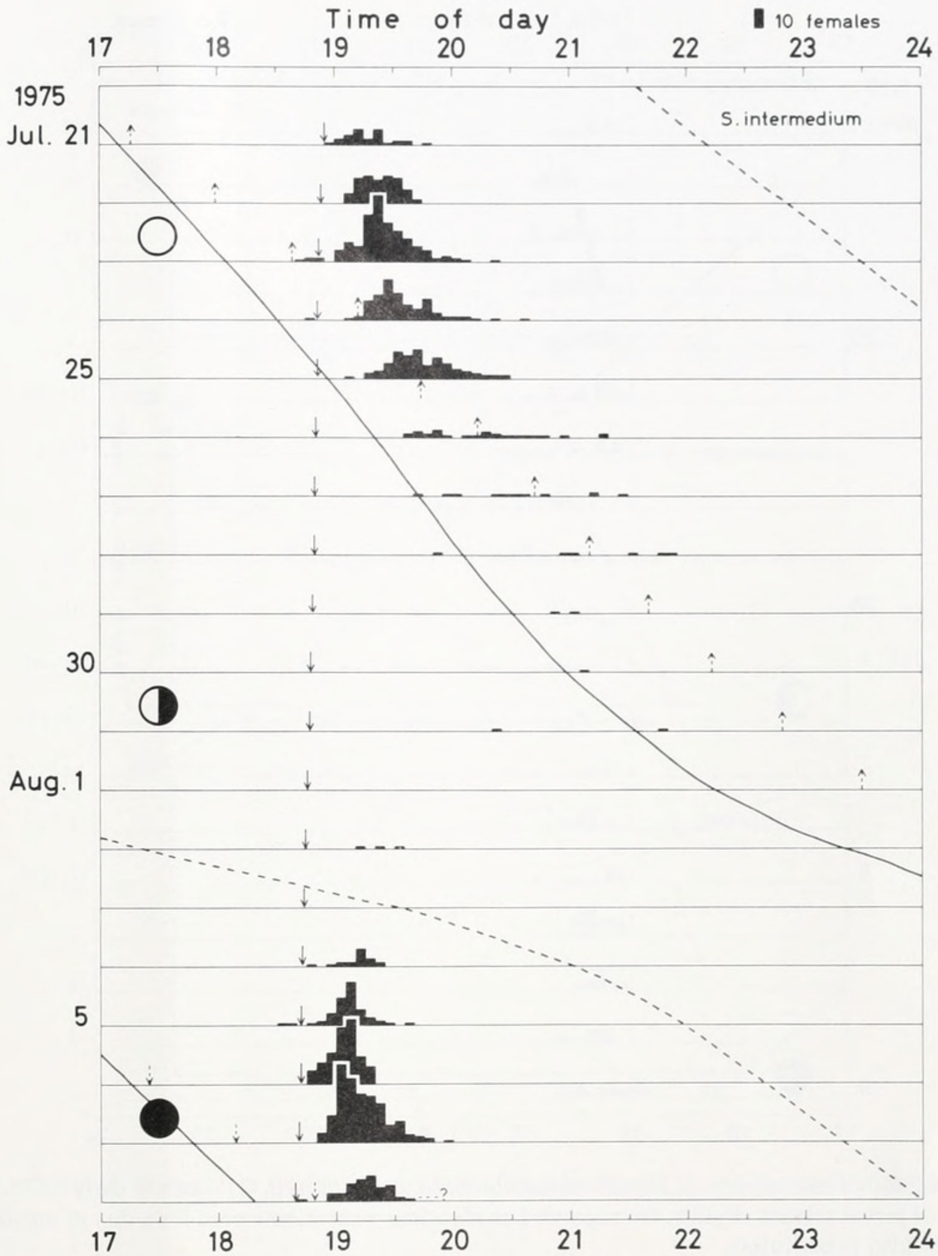

FIGURE 3B. Time of day of larval release in *Sesarma intermedium*, 21 July–8 August 1975. Symbols as in Fig. 3A. For days when observations were not carried out, treatment was as in Fig. 3A.

Larval release in *S. haematocheir* and *S. intermedium* peaked around the full and new moons (Figs. 2A, B). As reported elsewhere (Saigusa and Hidaka, 1978), peaks were often 1–5 days after the full and new moons, at the time of optimal tides (Figs. 3A, B). However, in a few cases the number of *S. intermedium* females releasing zoeae suddenly increased 3–5 days before the full moon: 5 and 7 August and 5 September 1976. Figure 6 shows a case (in September 1975) where larval release in *S. haematocheir* peaked 3 days before the full moon. In these cases, larvae were released at close the time of ebb tide or during the rising tide, making adaptive benefits hard to explain.

As shown in Figures 3A, B, and C, females of the three species released their larvae only in the early half in the night and not in the morning high-water period. One possible explanation is that timing is not determined by a requirement of the larvae, but rather by the females' requirement of moving to the place of larval

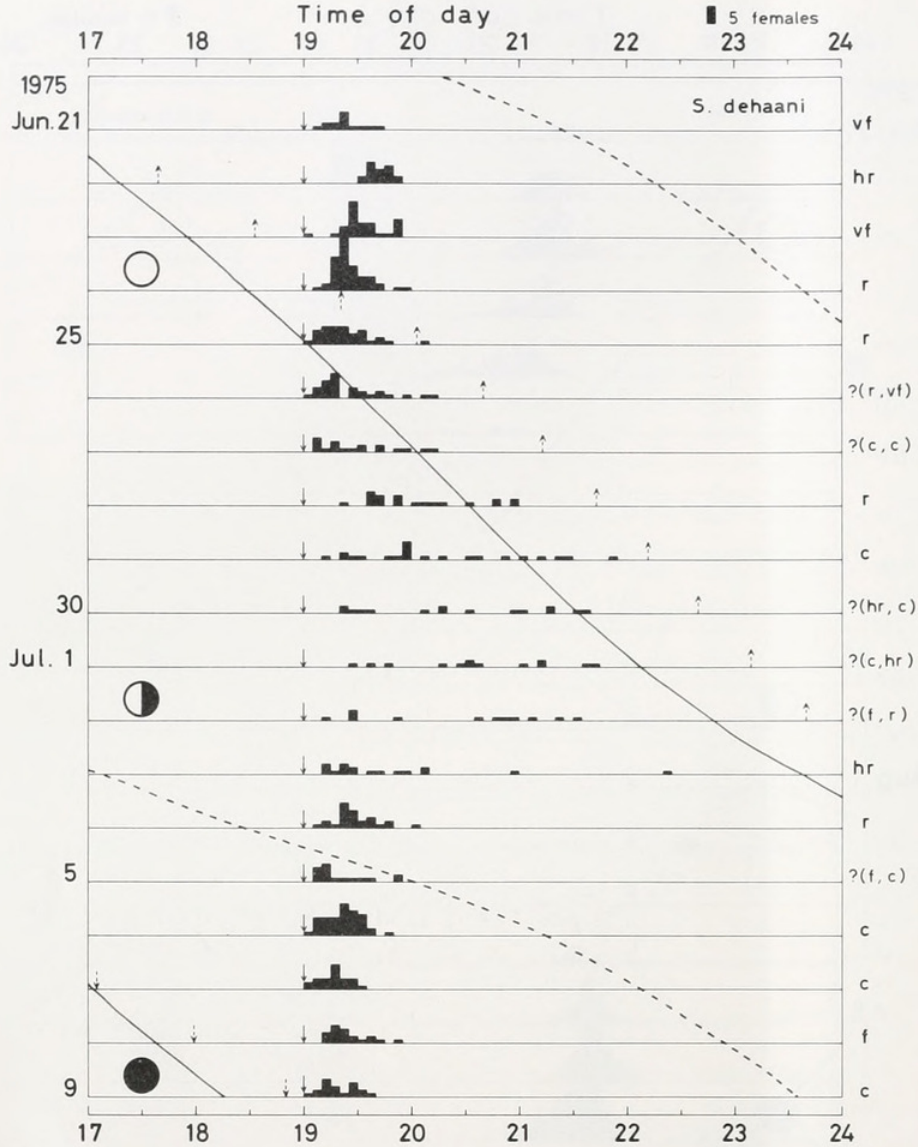

FIGURE 3C. Time of day of larval release in *Sesarma dehaani*, 21 June–9 July 1975. Two days when phase of larval release rhythm are regarded as identical were substituted for a day of no observations. Sunset times also substituted.

release. Ovigerous females move to the shore during the daytime. Around both the full and new moons they release larvae with the onset of night. On the following days, some wait until high water before releasing larvae.

On coasts with semidiurnal tides, though the times of high and low waters on days of full and new moons always occur at nearly the same time of day for years, they differ at various locations on the seashore. According to Neumann (1975, 1976, 1978), the time of emergence and subsequent reproduction was correlated with local low waters. The semidiurnal cycle of tides shows time displacements of a few hours along the coasts of Japan, especially in the Inland Sea. It is not known whether larval release activities in *S. haematocheir* and *S. intermedium* are synchronized with such local tidal conditions.

Further insight into adaptive benefits of a semilunar rhythm of larval release may be expected. Christy (1978) recently proposed a hypothesis to explain the semi-monthly release of *Uca pugilator* larvae. He estimated that juvenile crabs would be ready to settle on an intertidal flat about 3 weeks later, i.e., during spring

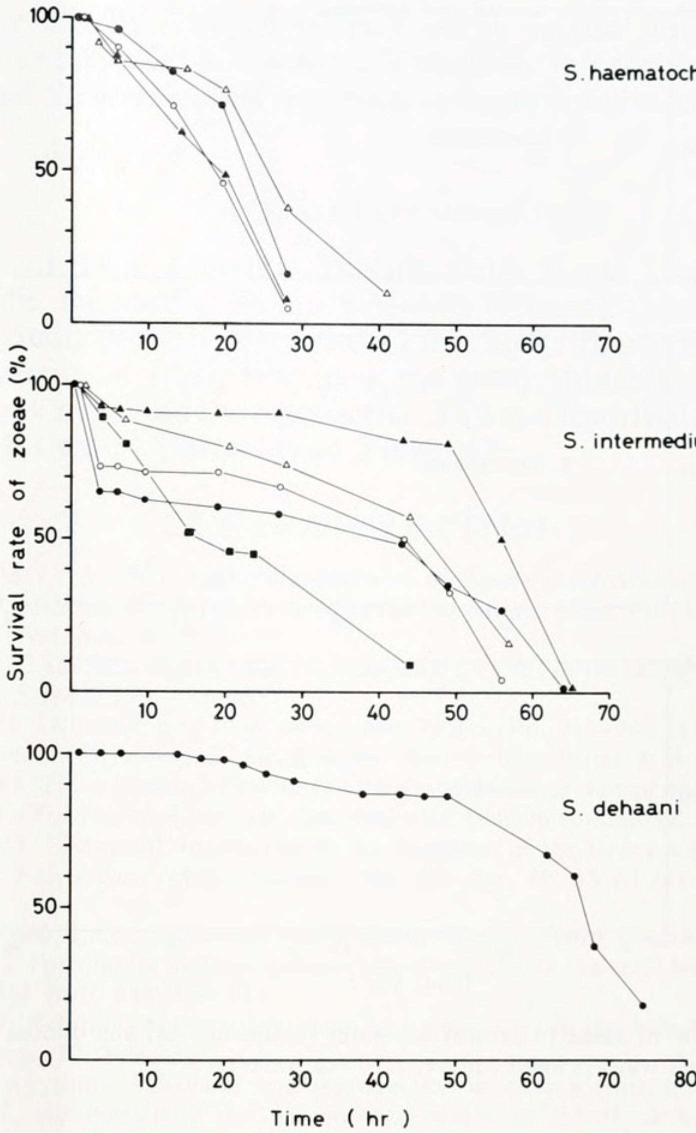

FIGURE 4. Survival of zoeae in fresh water. The ordinate indicates time after the release of zoeae.

tides, and demonstrated that spring-tide currents would help ensure up-estuary transport toward suitable adult habitats. Zucker (1978) suggested that the same might be true for the three tropical *Uca* species, though their courtship activities are displaced a week, from the neap-tide to the spring-tide period.

According to Baba and Miyata (1971), larvae of *S. dehaani* took at least 22 days to become young crabs, passing through four zoea and one megalopa stages. Hashimoto (1968) reported megalops of these three species in river mouths from July to October. This suggests that larvae of *S. haematocheir* and *S. intermedium* return to the river mouth about 1 month after they are released into the river. Megalops which return to the river mouth around spring tides would be able to swim to the most distant riverside from the sea with the rising tide. This might expand adult habitats.

Zoeae also are released in brackish and sea water (Saigusa, in preparation), by females inhabiting hillsides where there is no suitable river. According to Hashimoto (1965), in a few cases *S. haematocheir* females release their larvae into tributaries whose water level is not influenced by tides. In such cases, the semilunar rhythm of larval release may have no adaptive significance. However, a large num-

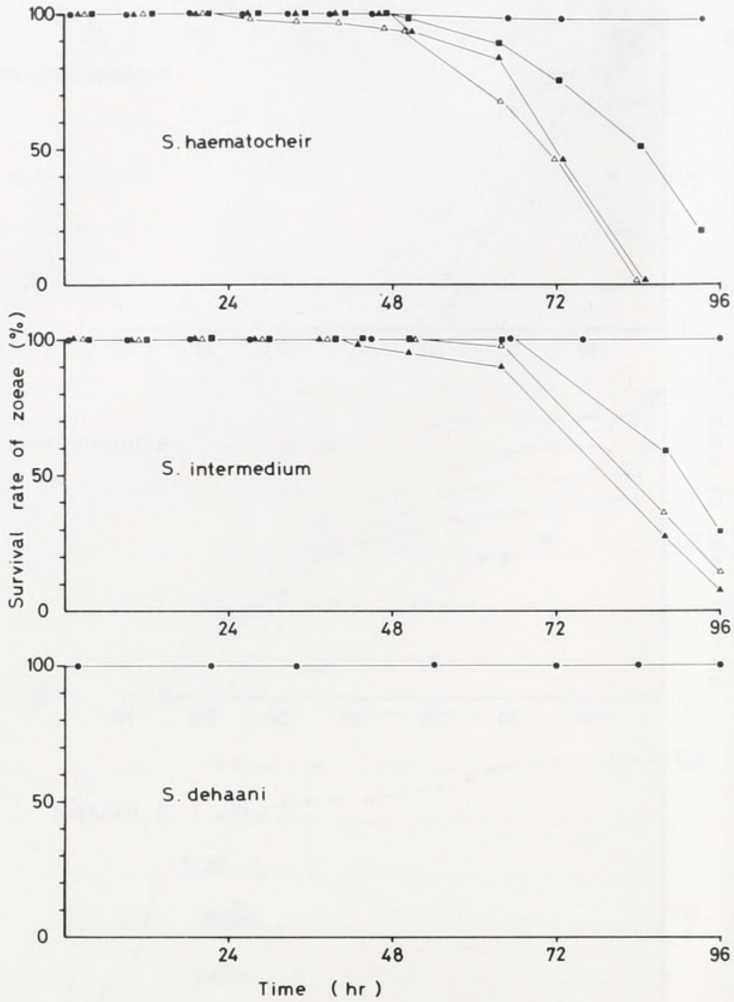

FIGURE 5. Survival of zoeae in natural sea water (closed circles) and diluted sea water (open and closed triangles, 1:20 sea water; closed square, 1:10 sea water).

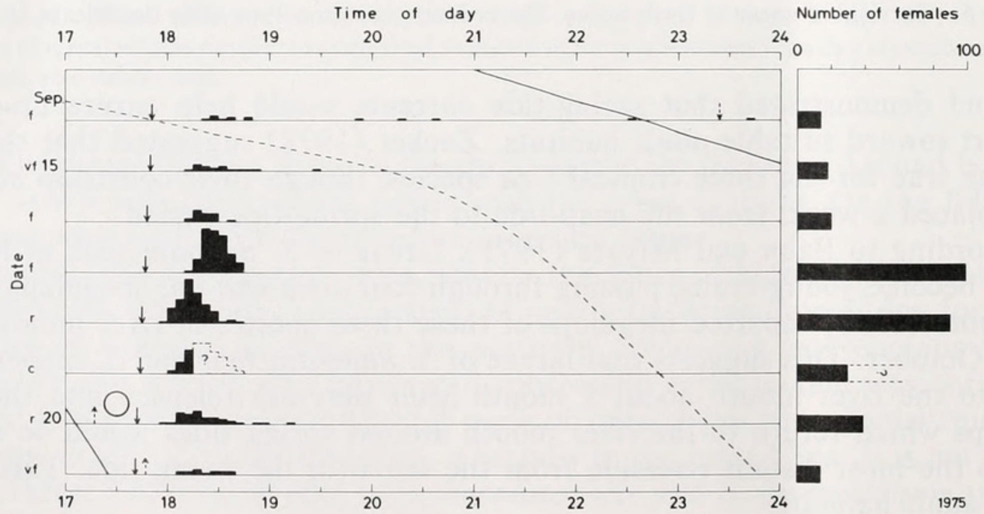

FIGURE 6. Number of *Sesarma haematocheir* females releasing larvae per night (right) and the time of day of release (left) 14 September–21 September 1975. High tide: solid slanted line; low tide: broken slanted line; sunset: downward solid arrow; moonset: downward broken arrow; weather very fine (vf), fine (f), cloudy (c), rain (r), heavy rain (hr).

ber of zoeae are usually released in fresh water; release into a relatively large stream like the one studied is common. Therefore, the semilunar rhythm by *S. haematocheir* and *S. intermedium* females may be regarded as important to survival of their larvae.

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