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Tidal Adaptation of a Circadian Clock Controlling a Crustacean Swimming Behavior

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ABSTRACT—Cumacean *Dimorphostylis asiatica* exhibits an endogenous swimming rhythm, free-running period of which spontaneously changes from circa 12-hr to circa 24-hr in the laboratory. Administration of a 4-hr pulse of hydrostatic pressure stimulus and a 4-hr light pulse confirmed that the circa 12-hr rhythm is circatidal and the circa 24-hr rhythm circadian, with respect to the phase setting characteristics. The activity records provide evidence of a "splitting" phenomenon, which suggests that these two types of rhythms are governed by (an) identical pacemaker(s). This species appears to have acquired tidal synchrony by making use of flexibly coupled circadian pacemakers, accompanied by expansion of their subtidal habitat to shallow, tide-affected area.

INTRODUCTION

Diurnal vertical migration (DVM) of marine zooplanktonic crustaceans has been reported for several taxonomic groups such as copepods (Enright, 1977), a shrimp (Pearcy, 1970) and cumaceans (Corey, 1970). This behavior is predominantly based on nocturnal swimming, which is largely governed by circadian rhythm (Enright and Hamner, 1967).

In the Seto Inland Sea of Japan, a cumacean, *Dimorphostylis asiatica*, exhibits a temporal pattern of DVM modified by tidal cycles: the animals swimm up to the water surface at nocturnal high tides (Akiyama and Yoshida, 1990). The endogenous swimming rhythm of freshly collected animals is circatidal but not circadian (Akiyama, 1995). Compared with the generally noisy, less persistent circatidal activity pattern of intertidal organisms (Neumann, 1981), the free-running rhythm of *D. asiatica* is highly precise and persistent, which is rather a common feature of circadian rhythms. In addition, unaccountable change in the free-running period from circa 12-hr to circa 24-hr occurred within several days of recording in most of the specimens (Akiyama, 1995). One plausible explanation is that the "circatidal" rhythm of *D. asiatica* spontaneously changes into a circadian rhythm in the laboratory.

An effective method to discriminate circatidal rhythms from circadian rhythms is the administration of rhythm-specific agents: circatidal rhythms are phased by some tidally caused stimulus such as mechanical agitation (Enright, 1965; Hastings, 1981), temperature (Williams and Naylor, 1969), salinity (Bolt and Naylor, 1985), or hydrostatic pressure (Morgan, 1965; Northcott *et al.*, 1991a, b), but circadian rhythms are predominantly entrained by light. In this study, phase responsiveness of the circa 12-hr and the circa 24-hr rhythms of *D. asiatica* to a 4-hr pulse of hydrostatic pressure stimulus and a 4-hr light pulse were compared.

MATERIALS AND METHODS

Adult males of *Dimorphostylis asiatica* were collected at night along the coast of the Seto Inland Sea at Ushimado, Okayama Prefecture, using electric torch lamp (100 V, 200 W) and a hand net. Each freshly collected specimen was transferred to an air tight cylindrical recording aquaria (3 cm in diameter, 7.5 cm in height) containing 20 ml sea water and 1 mm layer of boiled mud substratum. The aquaria were kept under constant darkness in light tight incubators. The activity of the specimens was monitored using photoelectric switches and personal computers (NEC PC-8800). The double plotted actogram for each specimen was illustrated using another personal computer (NEC PC-9800).

A 4-hr hydrostatic pressure stimulus equivalent to 3 m of water was made using an electric air pump (100 V, 100 W; IWAKI Co.), which was connected to the recording aquaria. The intensity of the stimulus was controlled by a hand made air bulb and tightly packed wool which also eliminated high frequency air vibration. A 4-hr light pulse (approximately 1000 lx) was given using cool fluorescent lamps (100 V, 20 W). Water temperature was kept at 15°C and 20°C for the circa 12-hr rhythms, and 10°C and 15°C for the circa 24-hr rhythms, depending on seasonal changes of ambient sea water at the collection site.

Linear regression lines of consecutive activity onsets (illustrated as diagonal lines in Figs. 1, 3, 5 and 7) were calculated to determine the phase of the rhythm and the phase shifts. Phase of treatments of the hydrostatic and light pulses was determined as offset time of treatments to activity onsets (circadian time 12), which was calibrated by the free-running periods. For the circa 12-hr rhythms, phase shifts of two conjugated activities were calculated separately (so one or two phase shifts are plotted for each treatment).

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RESULTS

Phase responses of the circa 12-hr rhythms

Figure 1 illustrates the circa 12-hr swimming rhythms of *Dimorphostylis asiatica* exposed to a 4-hr pulse of hydrostatic pressure. As well as phase shifts of the rhythms, the treatment resulted in two types of responses: persistence of the circa 12-hr rhythm after the treatment (Fig. 1A-D) and change of the activity rhythm to a circa 24-hr cycle (Fig. 1E, F). The phase responses to the stimulus are summarized as phase response curves (PRCs, Fig. 2). Although it is unknown whether these PRCs are comparable with the PRCs of circatidal rhythms previously reported (Enright, 1976; Naylor and Williams, 1984; Harris and Morgan, 1984; Northcott *et al.*, 1991b), including the unaccountable change of the activity pattern, the several hours of phase shifts (especially in Fig. 2B) strongly suggests that the circa 12-hr rhythm perceive hydrostatic pressure as an entraining agent.

The circa 12-hr swimming rhythms exposed to a 4-hr light pulse are shown in Fig. 3. Most of the specimens retained the circa 12-hr rhythms after the treatments. The treatments did not cause large phase shifts. The PRC to the light pulses is illustrated in Fig. 4. Phase advances and delays, most of which were within 2 hr, did not relate to the circadian time at which the pulses were given. Thus the circa 12-hr rhythm of *D. asiatica* is a "circatidal" rhythm with respect to the phase setting characteristics.

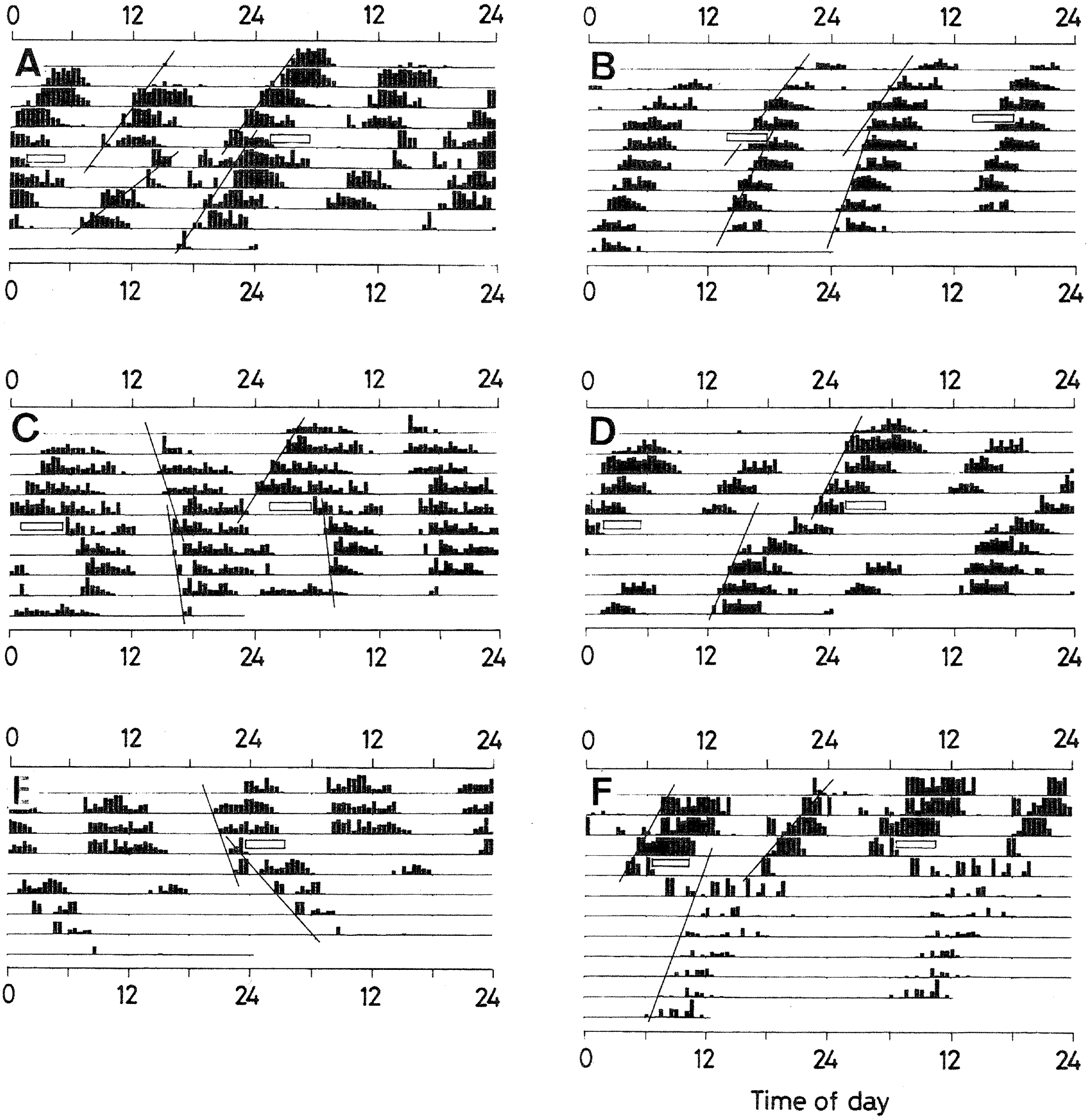

Fig. 1. The circa 12-hr swimming rhythms of individual *Dimorphostylis asiatica* exposed to a 4-hr pulse of hydrostatic pressure. Rectangles indicate the times of treatment. Diagonal lines indicate the linear regression lines of consecutive activity onsets.

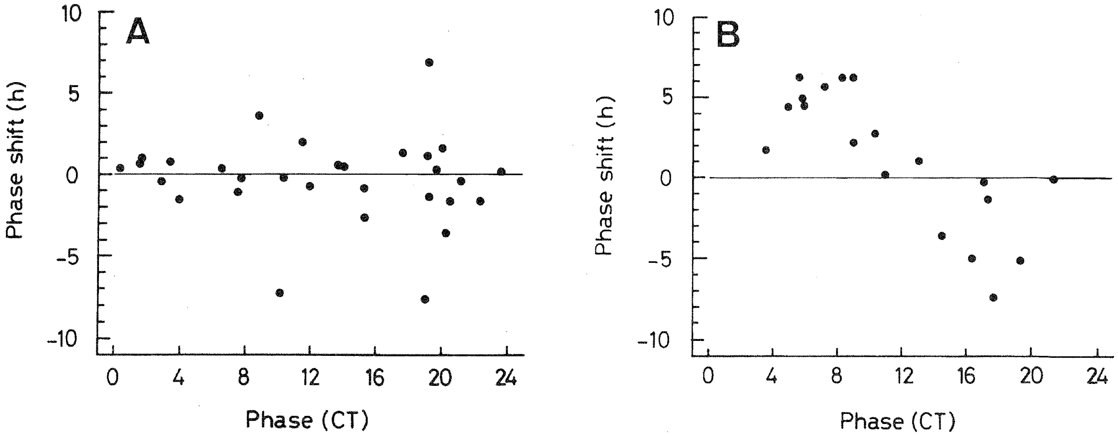

Fig. 2. Phase response curves (PRCs) of the circa 12-hr swimming rhythms exposed to the hydrostatic pressure pulses. (**A**) PRC of the specimens which retained circa 12-hr rhythms after the treatments (20 specimens). (**B**) PRC of the specimens whose activity rhythms changed to the circa 24-hr rhythms after the treatments (19 specimens). Classification of the phase responses into these two types summarized in (**A**) and (**B**) depended on the activity pattern on fourth and fifth days after the treatment. For example, the case shown in Fig. 1D was classified into (**A**) and the case in Fig. 1E into (**B**).

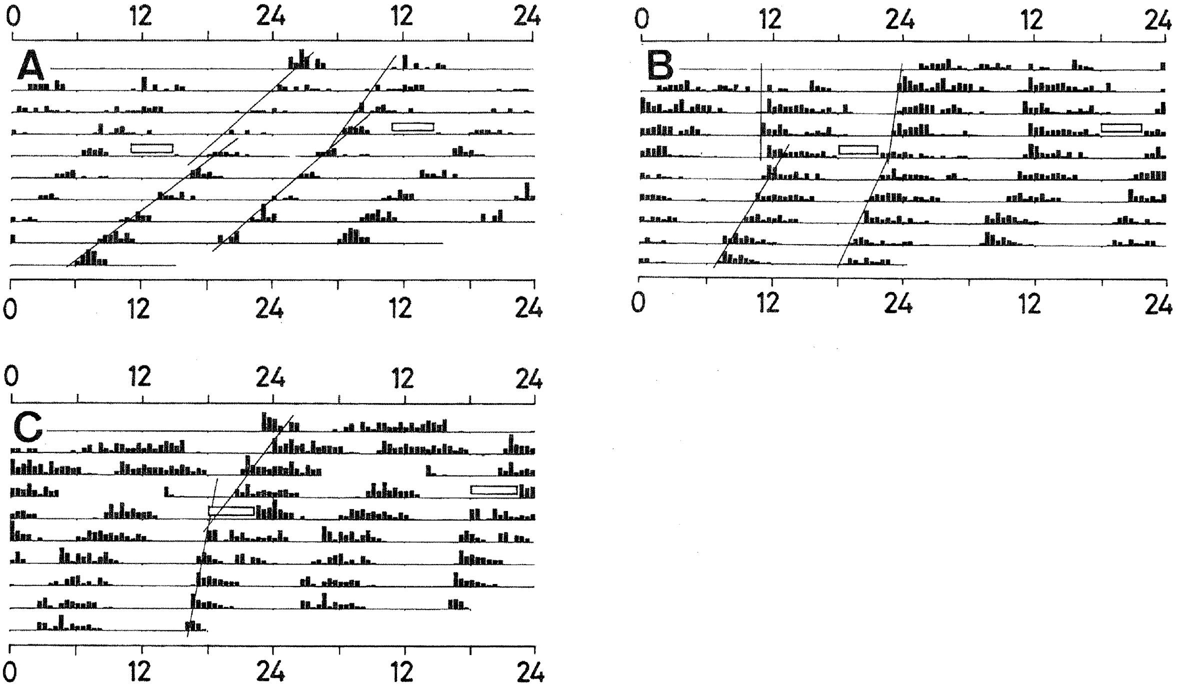

Fig. 3. The circa 12-hr swimming rhythms of *D. asiatica* exposed to a 4-hr light pulses. Rectangles indicate the times of treatment. Diagonal lines indicate the linear regression lines of consecutive activity onsets.

Phase responses of the circa 24-hr rhythms

Administration of the entraining agents to the circa 24-hr rhythm caused a change of phase setting accompanied by a change in free-running periods. Figure 5 shows the representative circa 24-hr swimming rhythm exposed to the hydrostatic pressure pulses, in which small phase shifts were caused by the treatments. The PRC (Fig. 6) indicates that the phase advances and delays, most of which are within 2 hr, did not relate to the circadian time at which the pulse was given. Large phase shifts more than 5 hr, caused by four specimens, appear to lie outside the normal distribution of the phase shifting response.

While the phase response to 4-hr hydrostatic pressure was obscure, the swimming rhythm appeared to be phased by 4-hr light pulses adjusting the activity onsets to the time of light off for each treatment (Fig. 7). The strong rephasing effect of the light pulses was also confirmed by the PRC (Fig. 8). Thus the circa 24-hr rhythm is definitely “circadian”.

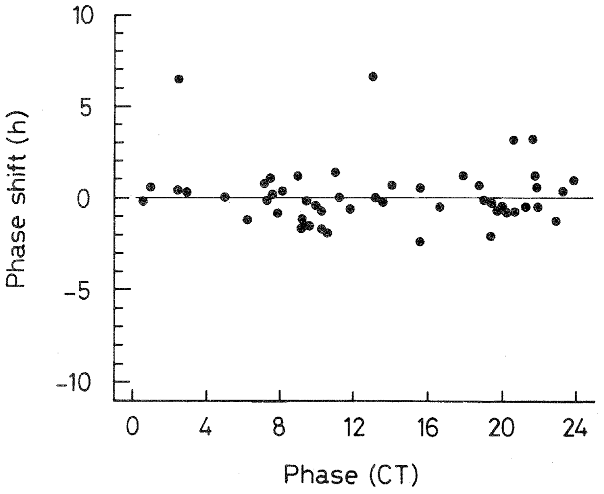

Fig. 4. Phase response curve of the circa 12-hr rhythms exposed to a 4-hr light pulse (32 specimens).

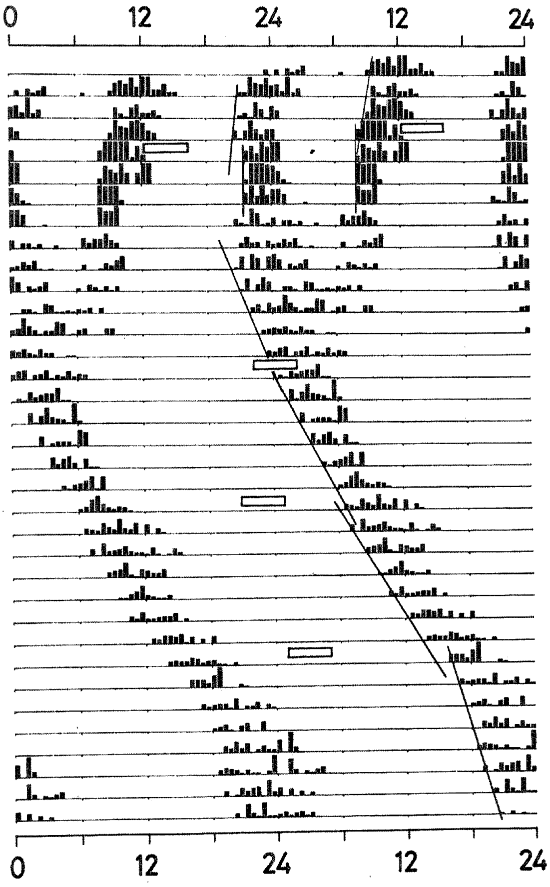

Fig. 5. The circa 24-hr swimming rhythm of *D. asiatica* exposed to 4-hr hydrostatic pressure pulses. Rectangles indicate the times of treatments. Diagonal lines indicate the linear regression lines of consecutive activity onsets.

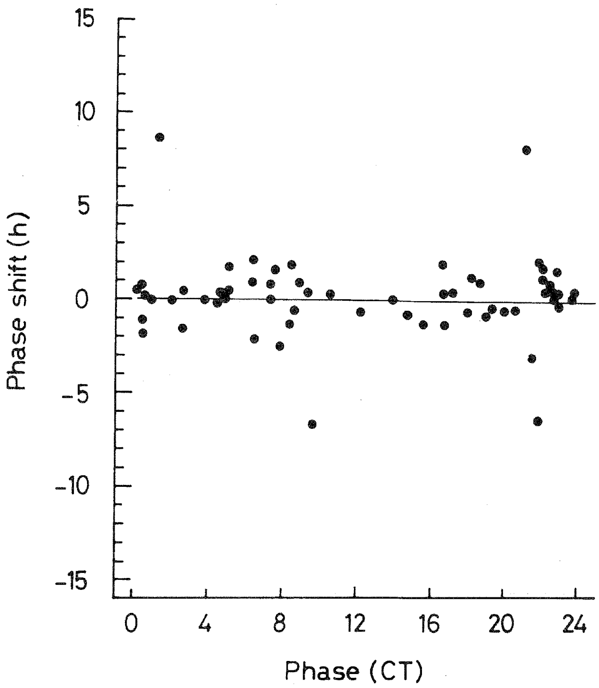

Fig. 6. A phase response curve of the circa 24-hr rhythms receiving a hydrostatic pressure pulses (38 specimens).

DISCUSSION

The present results clearly show that the circatidal swimming rhythm of *Dimorphostylis asiatica* spontaneously changes to circadian in the laboratory. Now arises a question whether the underlying pacemakers of these rhythms are identical. The activity records of some specimens provide evidence of a “splitting” phenomenon which is informative about the underlying pacemaker(s): 1) two conjugated activities of the circa 12-hr rhythm were occasionally rephased by the pressure stimulus differently (Fig. 1C, D), which suggests that these activities are governed by two or more pacemakers and 2) these two conjugated activities fused gradually to become a single circa 24-hr rhythm (Fig. 7B, C), and rarely re-splitted to revert to the circa 12-hr rhythm (such a tendency is shown in Fig. 7C).

“Splitting” has been reported mainly in vertebrates, including mammals (Pittendrigh and Daan, 1976), birds (Gwinner, 1974), and lizards (Underwood, 1977). Recent studies have documented that splitting is also observed in circatidal rhythms of crab’s locomotor activity (Palmer and Williams, 1986). To explain the splitting, one can postulate the existence of two circa 24-hr pacemakers whose phase angle difference determines whether the split (circa 12hr-period) or fused (circa 24hr-period) activity pattern is displayed (Pittendrigh and Daan, 1976). The circatidal and circadian rhythms of *D. asiatica* also appear to be governed by identical pacemakers but with different phase angle relationships.

Conversion of the activity rhythm in *D. asiatica* is possibly related to their low degree of habitat specialization, which generates various intensity of tidal impact according to the

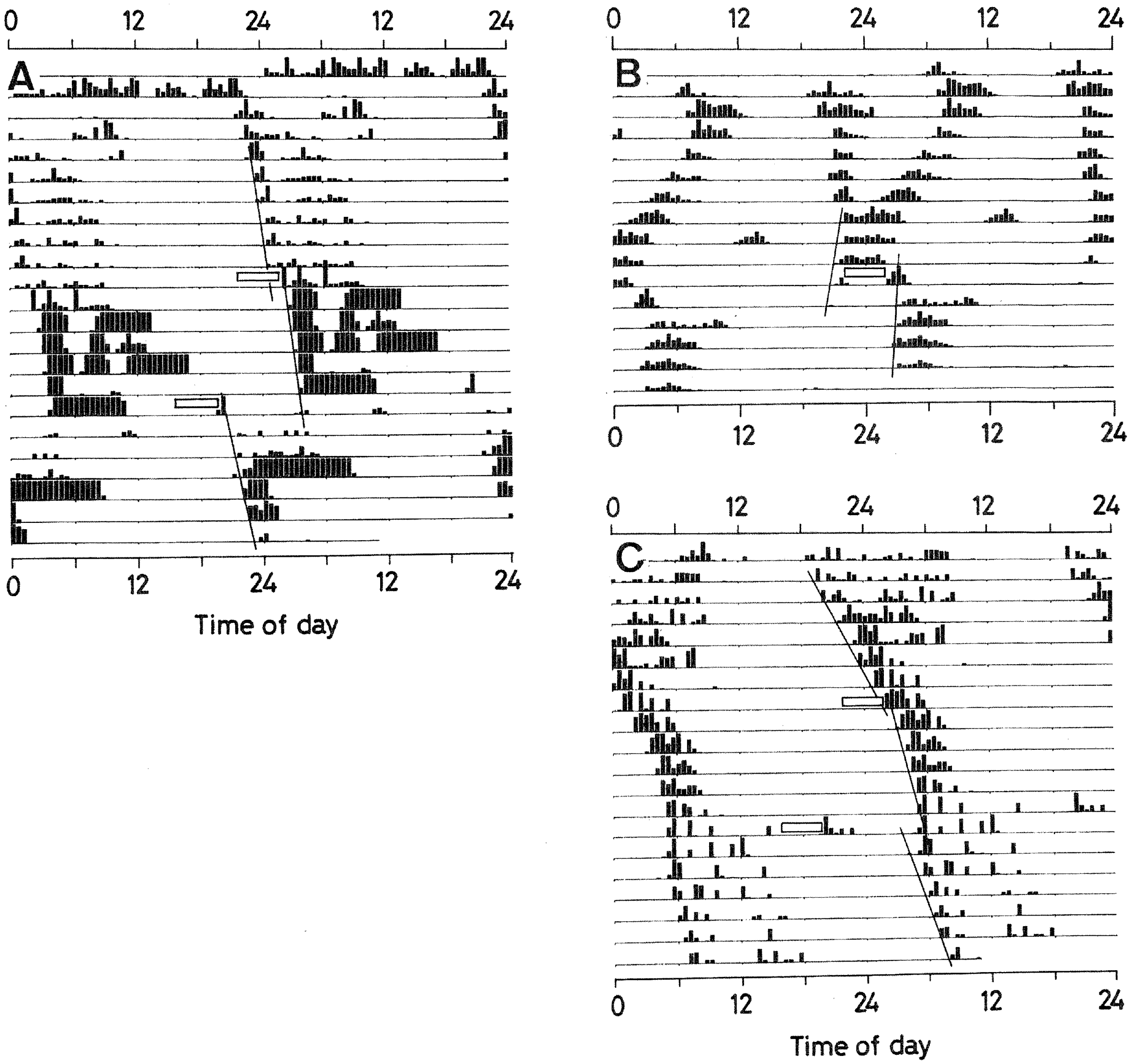

Fig. 7. The circa 24-hr swimming rhythms of *D. asiatica* exposed to a 4-hr light pulse. Rectangles indicate the times of treatment. Diagonal lines indicate the linear regression lines of consecutive activity onsets.

locality. For example, at Shijiki Bay (Nagasaki Prefecture, open to East China Sea), the animals live in muddy substratum in 13-50 m deep, where tidal impact would be small (Azuma, personal communication). In contrast, their habitat in the Seto Inland Sea of Japan (ca. 1.5-3.5 meter tidal amplitude) is situated in shallow water (within a few meters below mean low water spring tide), where there would be considerable tidal impact. It is concluded that, taking into consideration the general cumacean subtidal habitat with little tidal impact, this species would have developed tide-synchronized swimming on the bases of the circadian pacemaker(s) that it originally possessed.

Previous studies have hypothesized that "circatidal rhythms are tidally synchronized circadian rhythms" (Enright, 1976; Rodriguez and Naylor, 1972; Gibson, 1973). However, experimental supports are not sufficient, partly because the circatidal rhythms have been studied in a restricted number of species, most of which are decapod crustaceans such as shore crabs. More extensive studies using a variety of species would reveal the relationship between the circatidal and circadian rhythms.

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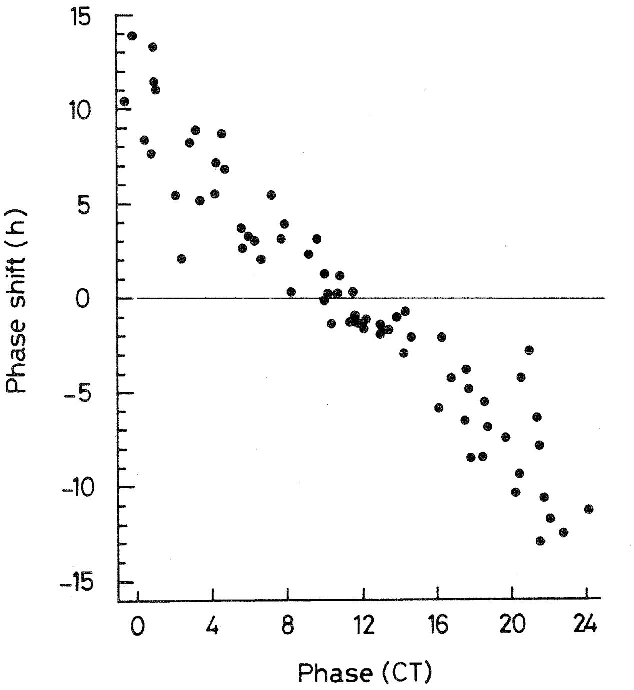

Fig. 8. A phase response curve of the circa 24-hr rhythms exposed to a 4-hr light pulses (51 specimens).

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