Chapter 2
Circatidal Rhythms and Their Entrainment to the Tidal Cycle in Insects

Aya Satoh and Hideharu Numata

Abstract Some intertidal insects show endogenous activity rhythms that synchronize with the tidal cycle, that is, circatidal rhythms. In this chapter, we collected studies of the circatidal activity rhythms of intertidal insects and the entrainment of the circatidal rhythm to the tidal cycle. Until now, circatidal activity rhythms have been reported in three taxonomic groups: springtails (Collembola), beetles (Coleoptera), and crickets (Orthoptera). The mangrove cricket *Apteronemobius asahinai* is known as the only insect species that shows clear and persistent circatidal activity rhythms. When the inundation cycle with a period of 12.4 h was provided by artificial means, the circatidal rhythm of *A. asahinai* responded to the given periodic inundations in a phase-dependent manner. Furthermore, the molecular mechanism of the circatidal clock of *A. asahinai* is likely to be different from the circadian clock. Advances in studies in *A. asahinai* will lead to better understanding of the circatidal rhythm in insects.

Keywords *Apteronemobius asahinai* • Intertidal insects • Mangrove cricket

2.1 Introduction

The tides flood and ebb twice each day in most coastal regions. This tidal cycle shows a period of approximately 12.4 h. The tidal cycle is an important factor for animals living in the intertidal and sublittoral zones to determine the timing of activity. For many aquatic animals, high tides are the most suitable time of activity. The activity of terrestrial animals in intertidal zones should, however, be strictly limited to the time of low tides, when their living space emerges from the sea.

Then, how do animals determine the "correct" timing of activity? There are two solutions to this problem: by using external environmental cues related to the tidal cycle or by using endogenous biological clocks. For example, fiddler crabs, *Uca uruguayensis*, open their burrows during the periods of simultaneous light and low

---

A. Satoh (✉)
School of Advanced Sciences, The Graduate University for Advanced Studies,
Hayama, Japan
e-mail: ayasatohjp@gmail.com

H. Numata
Graduate School of Science, Kyoto University, Kyoto, Japan

H. Numata, B. Helm (eds.), *Annual, Lunar, and Tidal Clocks*,
DOI 10.1007/978-4-431-55261-1_2

tide and close them at the times of high tide or darkness (De la Iglesia et al. 1994). De la Iglesia et al. (1994) showed that the rhythm of burrow plugging did not show clear endogenous tidal components under experimental conditions, but that crabs plugged their burrows in response to the entrance of water into them. Direct responses to environmental stimuli, however, may lead the organism to be active at the "wrong" time by responding to nontidal events such as rainfall or storm surge. Alternatively, many marine organisms show tidal activity rhythms that persist under constant conditions, that is, circatidal rhythms (Gibson 1965; Barnwell 1966; Enright 1972; Akiyama 1995). Thus, these organisms determine suitable timing for activity using one or more endogenous biological clock(s).

Biological clocks usually show a periodicity that is not exactly the same as the periodicity of the environmental cycle. In the field, the endogenous rhythm is entrained to the environmental cycle; as a result, the period of the rhythm equals the period of the environmental cycle. An environmental stimulus that can act to entrain biological clocks is called a "zeitgeber" (Johnson et al. 2003). Many environmental cues related to tidal cycles have been reported as the zeitgeber for the entrainment of circatidal activity rhythms, such as periodic changes in water turbulence (Enright 1965; Klapow 1972; Ehlinger and Tankersley 2006), hydrostatic pressure (Reid and Naylor 1990; Morgan 1965; Northcott et al. 1991; Akiyama 2004), salinity (Taylor and Naylor 1977), and water temperature (Naylor 1963; Holmström and Morgan 1983).

In this chapter, we review studies of the circatidal activity rhythms of intertidal insects and the entrainment of the circatidal rhythm to the tidal cycle.

2.2 Life of Insects in Marine Environment

Not many but some insects spend at least part of their life cycle in the marine environment, which includes many habitats from the upper intertidal to the open ocean (Cheng 2003). Usually people do not even think that they can meet insects in marine environments. However, actually we can find many taxonomic groups of insects at the seaside, such as springtails (Collembola), crickets (Orthoptera), true bugs (Heteroptera), beetles (Coleoptera), moths (Lepidoptera), flies (Diptera), and ants (Hymenoptera) (Cheng 2003).

Here we introduce some unique lifestyles of marine insects. Larvae of moths are generally herbivorous, but some moth species at the seaside use unique feeding habitats. For example, larvae of *Tatobotys aurantialis* (Crambidae) can be found at the high-water line of spring tide on rocky shores and eat the intertidal red alga *Bostrychia tenella* at night (A. Satoh, personal observation). Another example is the mangrove moth *Hymenoptychis sordida* (Crambidae), the larvae of which feed indiscriminately on decaying wood, leaves, and green algae on mangrove forest floors (Murphy 1990).

Some marine insects live in burrows on tidally inundated ground. These insects have to solve the important problem of how to prevent water from intruding into the burrow and to maintain airspace within the burrow during submergence. The mangrove ant *Polyrhachis sokolova* (Formicidae) nests in the muddy soil of the mangrove forest. For this species, when the tide reaches the nest entrance, loose soil particles at the nest entrances collapse and function as a stopper, which prevents water from intruding into the nest (Nielsen 1997). When the water withdraws, the ants reopen the entrances as soon as they are above the water level, and resume foraging before the soil dries (Nielsen 1997). Similarly, the subsocial beetle *Bledius spectabilis* (Staphylinidae) also has a burrow in the mud in the intertidal zone, which it leaves to eat algae on the surface of mud during low tides. For this beetle, a critical minimum diameter of the burrow entrance (2–3 mm) prevents sudden flooding by exploiting a surface entrance effect, giving beetles time to block the entrance hole with mud (Wyatt 1986). Females of this species lay eggs around the burrow from inside of it, and take care of their young until approximately 1 week old, which is why this beetle is categorized as a ‘subsocial’ insect. The importance of maternal care is indicated by the fact that orphaned first instars did not block or reopen the burrow in accordance with the state of the tide (Wyatt 1986).

Although all insects in the marine environment, except those in a pelagic habitat, must be influenced by the tidal cycle to some greater or lesser degree, only a few studies have demonstrated circatidal activity rhythms and their entrainment to the tidal cycle for insects. Circatidal activity rhythms have been reported only in the following three taxonomic groups: springtails (Collembola), beetles (Coleoptera), and crickets (Orthoptera).

2.3 Circatidal Rhythms

2.3.1 Springtails

Many species of springtails can be found in the soil of the forest, but they are also found in the marine environment. The salt-marsh collembolan *Anurida maritima* (Neanuridae) is distributed in various types of intertidal habitats, such as tidal marshes and rocky shores, throughout the Holarctic. Foster and Moreton (1981) found that this species becomes active or inactive in accordance with the tidal cycle: a large proportion of the individuals emerge from their underground refuges shortly after the retreat of the tide, forage there for a few hours, and retire underground at least 1 h before the return of the tide. This tidal activity rhythm persisted in the laboratory under constant light for at least 7 days (McMeechan et al. 2000).

2.3.2 Beetles

Beetles are observed rather often in marine environments. The nocturnal beetle *Thalassotrechus barbarae* (Carabidae) inhabits the rocky intertidal zone on the western coastline of the United States (USA) and Mexico (Evans 1976). Adults of this species show circadian rhythms in their locomotor activity under constant conditions; however, they are more active during the period corresponding to low tide than at other times of night. It appears that the circatidal rhythm modifies the predominant circadian rhythm by inhibiting activities during high tides (Evans 1976).

Larvae of the intertidal tiger beetle *Callytron inspecularis* (Cicindelidae) live in well-formed ground burrows at the high-water line of spring tide on muddy estuary riverbanks in East Asia. Usually, larvae wait patiently at their burrow opening for prey to approach within striking distance throughout the day and night. In spring tides of the lunar cycle, however, larval activity is interrupted during high tides because the larval burrows become submerged. In this period, they show a unique rhythmic behavior: They plug their burrow opening with soil before submergence at high tide and open it again soon after the water recedes. Satoh et al. (2006) observed that a larva plugged its burrow periodically under constant conditions in the laboratory for 3 days after being subjected to the artificial tidal cycle (Fig. 2.1). The mean interval between consecutive burrow plugging was 12.45 h (Satoh et al. 2006), suggesting that this burrow-plugging behavior is governed by an endogenous circatidal rhythm. A similar rhythmic plugging behavior was also observed in larvae of the tiger beetle *Callytron yuasai okinawense* on the mangrove forest floor (Satoh and Hayaishi 2007), although it was not confirmed whether this behavior was endogenous. On the other hand, the activity rhythm in adults of these tiger beetle species, which walk over the intertidal flats for foraging and mating, has not yet been studied.

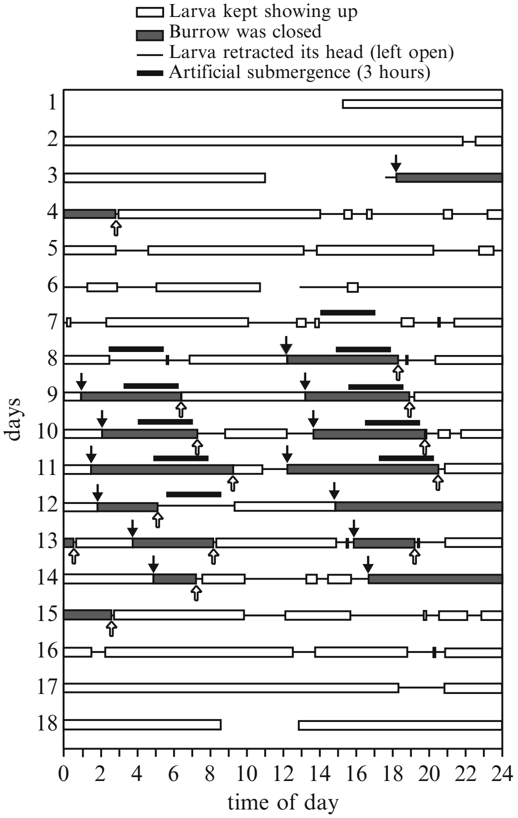

Fig. 2.1 Example of a larval activity record of the tiger beetle *Callytron inspecularis* under constant light at 25 °C. Larval behavior was recorded using time-lapse photography for 18 days. An artificial submergence (3 h) was provided ten times, at intervals of 12.4 h from day 7. *Black arrows* indicate times of burrow plugging; *white arrows* indicate times of burrow opening. (From Satoh et al. 2006)

2.3.3 Crickets

The mangrove cricket *Apteronemobius asahinai* (Trigonidiidae) is known as the only insect species that shows a clear circatidal rhythm persisting for a long period under constant conditions (Satoh et al. 2008). *A. asahinai* is distributed only on the floors of mangrove forests in East Asia. In the field, this species is found to be active during low tide and to rest on mangrove stems or mounds built by the mud lobster *Thalassina anomala* during high tide, regardless of whether it was day or night.

Under constant conditions, crickets showed clear circatidal activity rhythms that persisted for at least 24 days (Satoh et al. 2008). The activity rhythm consisted of active phases of about 10 h alternating with inactive phases of about 2 h (Fig. 2.2). The mean free-running period was 12.56 h. After the light condition switched from constant darkness to a light–dark cycle, the amount of activity was suppressed in the photophase, but the endogenous rhythmicity itself was not influenced by the light–dark cycle (Fig. 2.3a).

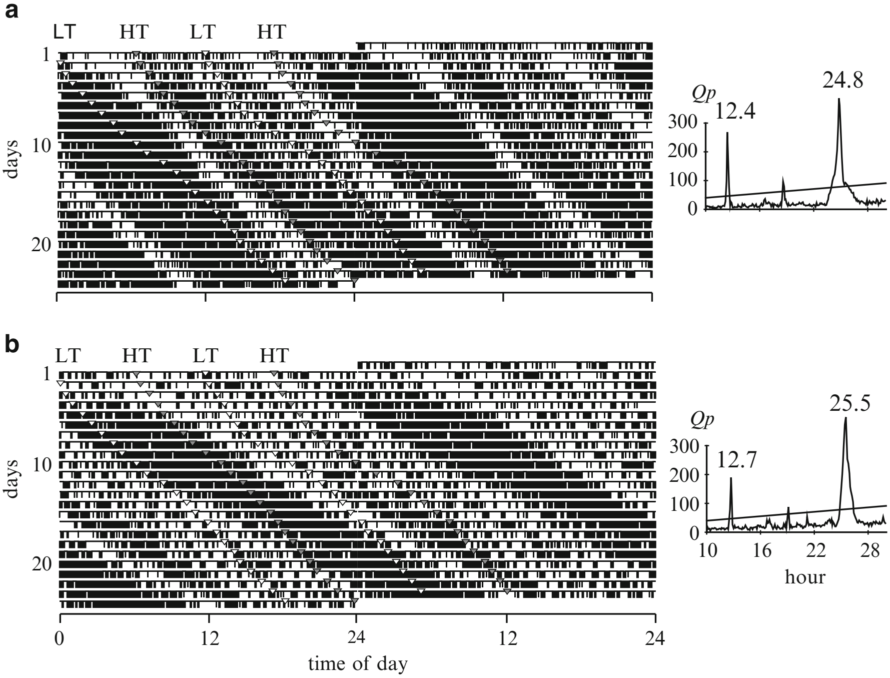

Fig. 2.2 Two examples (**a**, **b**) of the locomotor activity of *Apteronemobius asahinai* under constant darkness at 25 °C. The locomotor activity rhythm is represented by a *double plotted actogram* over a 48-h time period. *Triangles* indicate times of expected low (LT; *white*) and high (HT; *gray*) tides in the field. Rhythmicity was determined by chi-square periodogram analysis (*line graphs at the right side*). An oblique line in the periodogram indicates significance level of $P = 0.05$; a peak value above the line is designated as significant. *Qp* is statistic value (ratio of variances) of chi-square periodogram (Sokolove and Bushell 1978). (From Satoh et al. 2008)

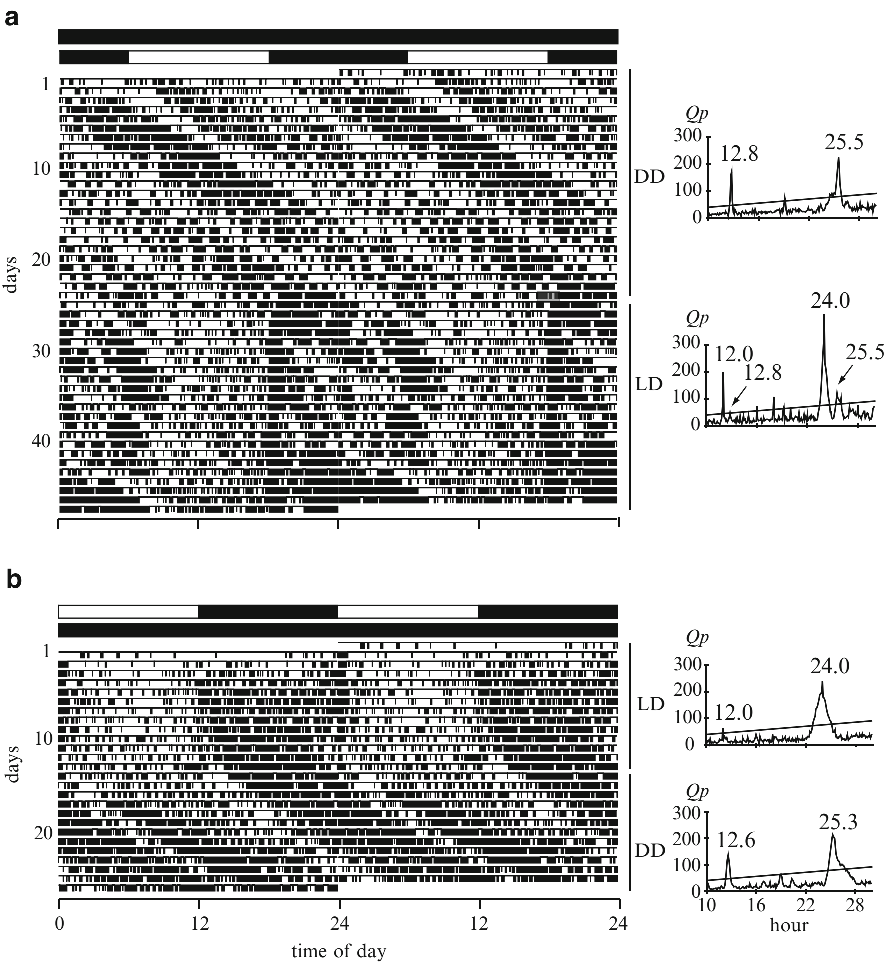

Fig. 2.3 Two examples (**a**, **b**) of the locomotor activity of *Apteronemobius asahinai* under constant darkness (*DD*) and a light–dark cycle (*LD*) at 25 °C. In (**a**), the constant darkness was interrupted by turning on a fluorescent lamp for about 2 h on the 25th day (within the period shown by *shaded region* on the last day of DD) for mechanical maintenance. *Black* and *white bars above the actograms* indicate light and dark phases, respectively, during LD. Displays of actograms and rhythmic analysis are same as in Fig. 2.2. *Qp* is statistic value (ratio of variances) of chi-square periodogram (Sokolove and Bushell 1978). (From Satoh et al. 2008)

On the other hand, intense activity alternating with weak activity was observed in some crickets under constant darkness (Fig. 2.2b). The intense activity phase was observed during expected nighttime during the first few days in captivity. In addition, when the locomotor activity was first recorded under a light–dark cycle, and then under constant darkness, the endogenous rhythm under constant darkness was more intense in the active phase continuing from the dark phase than from the light phase of the preceding light–dark cycle (Fig. 2.3b). These tendencies demonstrated the presence of circadian modulation, that is, the circadian rhythm superimposed on the circatidal rhythm (Satoh et al. 2008).

2.4 Entrainment of Circatidal Rhythms

The zeitgebers for circatidal rhythms in insects have rarely been identified. Satoh et al. (2006) demonstrated that cyclic submergence acted as the zeitgeber for the circatidal burrow-plugging rhythm of larvae of *C. inspecularis*. However, the conclusion of this study was based on observations of only one specimen (see Fig. 2.1). Exceptionally, the entrainment of the circatidal activity rhythm was well demonstrated quantitatively for *A. asahinai*. The inundation acted as the zeitgeber for the circatidal rhythm of this species (Satoh et al. 2009). When an inundation pulse (30 min) was provided four times at intervals of 12.4 h (Fig. 2.4), the circatidal rhythm of *A. asahinai* responded differently to the zeitgeber at different phases of its cycle (Fig. 2.5). When periodic inundations were initiated during the first half of the active phase, the activity onset was considerably delayed (Fig. 2.5a), whereas when periodic inundations were initiated during the latter half of the active phase, the activity onset was considerably advanced (Fig. 2.5b). After treatment, the specimen became inactive around the times when inundation was expected (Fig. 2.5a, b). On the other hand, when periodic inundations were initiated during the middle of the active phase or during the inactive phase, the treatment had little effect (Fig. 2.5c, d).

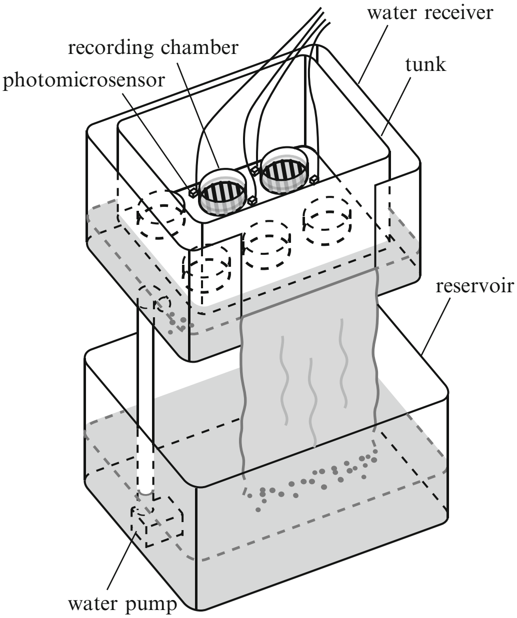

Fig. 2.4 Simplified diagram of the recording apparatus that provides an inundation stimulus to *Apteronemobius asahinai*. Crickets were housed individually in recording chambers with several slits in the bottom. When the receiver was filled by pumping tap water from a reservoir, the water flowed into the chambers through the bottom slits, thereby providing an inundation stimulus. Crickets could escape from drowning by climbing the chamber wall. When the water pump was stopped, the water immediately drained back into the reservoir. A photomicrosensor was used to record locomotor activity. (Modified from Satoh et al. 2009)

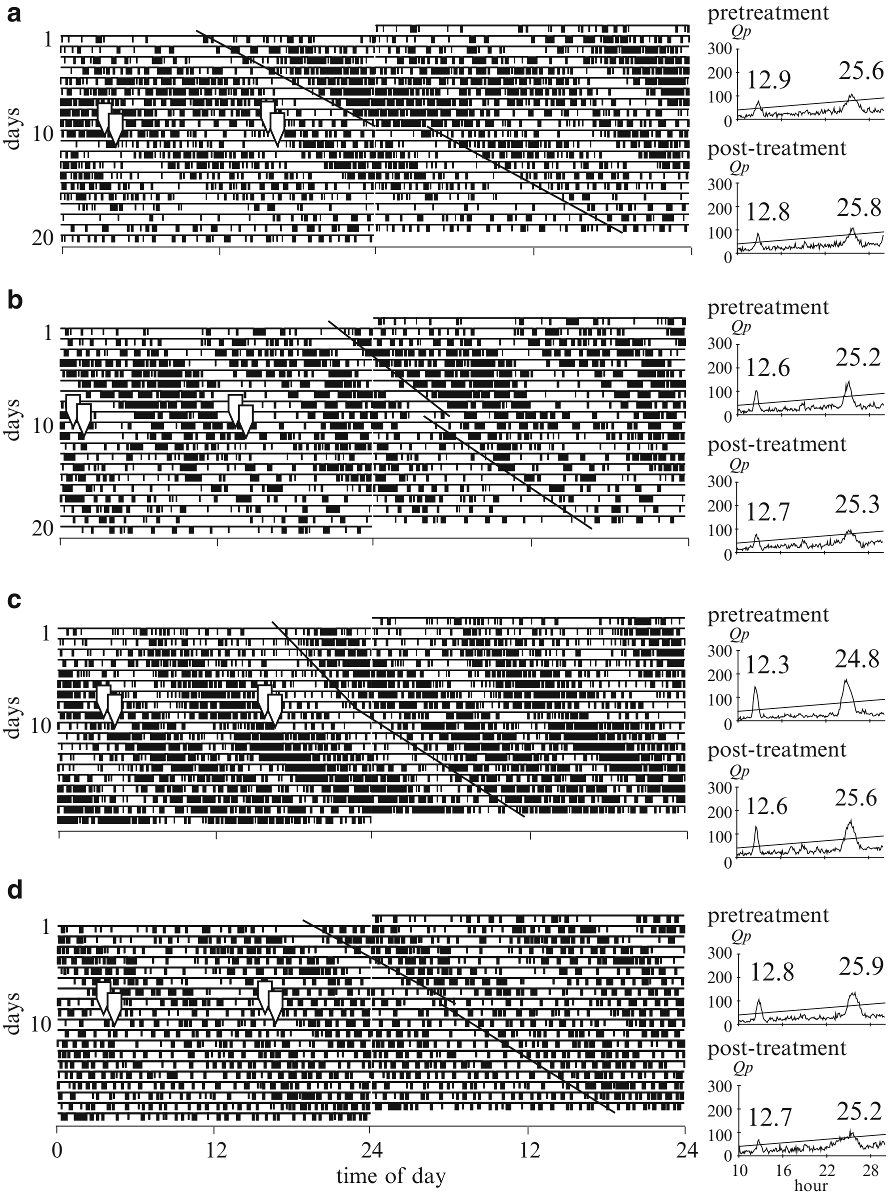

Fig. 2.5 Four typical examples (**a**–**d**) of the phase responsiveness of the circatidal rhythm in *Apteronemobius asahinai* to periodic inundations under constant darkness at 25 °C. Periodic inundations (*arrows*) were initiated during the first half of the active phase (i.e., subjective low tide) (**a**), during the second half of the active phase (**b**), during the middle of the active phase (**c**), and during the inactive phase (i.e., subjective high tide) (**d**). The phase shifts are visualized by *regression lines*, separated for the time before versus time after inundations. The regression lines were fitted by eye through the sequential points of activity onset. Displays of actograms and rhythmic analysis are the same as in Fig. 2.2. *Qp* is statistic value (ratio of variances) of chi-square periodogram (Sokolove and Bushell 1978). (From Satoh et al. 2009)

A phase-response curve (PRC) is the description of the phase-dependent response of the endogenous rhythm to the zeitgeber. The circadian PRCs are generally constructed on the bases of phase responsiveness to a single light pulse under constant darkness (Johnson 1999). In our study, on the basis of the phase-response data of *A. asahinai*, a PRC was constructed by plotting the phase shift of a circatidal rhythm as a function of the phase at which the first inundation pulse was initiated (Fig. 2.6). The comparison of the shape of this circatidal PRC to those of circadian PRCs gives useful information about the nature of the underlying oscillator of the circatidal rhythm. Periodic inundations started during the first half of the subjective low tide caused a phase delay of the circatidal rhythm of *A. asahinai*, whereas those during the second half of the subjective low tide caused a phase advance (Fig. 2.6). This response is similar to the effective action of light pulses against the circadian rhythm; light pulses given during the first half of the subjective night caused a phase delay, whereas those during the second half of the subjective night caused a phase advance. In addition, periodic inundations had less phase-resetting efficacy during the subjective high tide, which is similar to light pulses during the subjective day. The crossover point between the delays and advances existed near the middle of the subjective low tide in the PRC of *A. asahinai*. This characteristic is common with type 1 PRC of circadian rhythms, which show a continuous transition between delays and advances in the middle of the subjective night. The similarity between the PRC on a

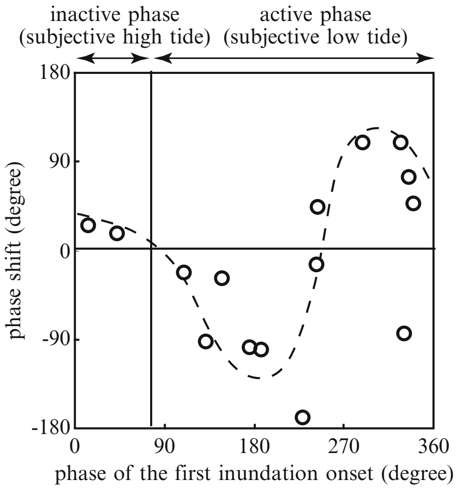

Fig. 2.6 Phase-response curve (PRC) of the circatidal rhythm of *Apteronemobius asahinai* treated with periodic inundations. The period under constant conditions before the treatment is shown in terms of phase angle (0–360°). The phase shift of activity (*vertical axis*) and the phase of first inundation onset (*horizontal axis*) are expressed as angular proportions of the free-running period of each individual. The phase shift of activity was determined from each actogram (see Fig 2.5) by measuring the distance between the two regression lines extrapolated to the day the first inundation was provided. *Dotted line* indicates the form of the PRC as determined by eye. *Arrows* indicate periods of subjective high and low tides, respectively. (From Satoh et al. 2009)

tidal (12.4 h) time base and circadian PRCs indicates that an underlying oscillator of the circatidal rhythm of *A. asahinai* is similar to a circadian oscillator but that its period is approximately 12.4 h, that is, a circatidal clock.

2.5 Molecular and Physiological Basis of Circatidal Rhythms in Insects

The molecular and physiological basis of circatidal rhythms had not been examined in insects until Takekata et al. (2012) studied the circatidal rhythm in *A. asahinai*. As mentioned earlier, this species shows two kinds of rhythms simultaneously in its locomotor activity: a circatidal rhythm producing active and inactive phases and a circadian rhythm modifying the activity intensity of circatidal active phases. Takekata et al. (2012) examined the role of the circadian clock gene *period* (*per*) in these two rhythms by RNA interference (RNAi) of the gene. RNAi is a method to suppress expression of a target gene product by introducing double-stranded RNA that is complementary in sequence to the target gene and is effective in many insect species (Mito et al. 2011). The *per* gene is one of the key components of the circadian clock in insects (Tomioka and Matsumoto 2010), and *per* RNAi completely disrupts the circadian rhythm in the two-spotted cricket *Gryllus bimaculatus* (Gryllidae) (Moriyama et al. 2008).

Adult male crickets collected from the field were used for the RNAi experiment. Their locomotor activities were recorded under a light–dark cycle, and they were anaesthetized (control), injected with double-stranded RNA for the control gene (*β-lactamase*), or injected with double-stranded RNA for *per* on the 6th day. Then, to analyze the effect of RNAi on the circatidal rhythm and circadian modulation, the locomotor activity was recorded under constant darkness from the 11th day (Fig. 2.7). The circatidal rhythm and circadian modulation under constant darkness were detected by the following method. The circatidal rhythm was detected by the presence of a single peak between 10 and 15 h in the periodogram above the 0.05 confidence level. Because the peak of the circadian rhythm was not clear in the periodogram, the presence of the circadian modulation was explored by the following method: The activity level was counted for every circatidal period, and the differences between the activity level of even- and odd-number cycles was examined by analysis of covariance (ANCOVA; Fig. 2.8). Activity was judged to be influenced by the circadian rhythm when the slope or the elevation was significantly different between even- and odd-number cycles ($p \leq 0.05$).

Most of the control crickets, that is, intact and injected with double-stranded RNA for *β-lactamase*, still showed a circatidal rhythm and a circadian modulation of activity under constant darkness after the treatment (Fig. 2.7a, b). After *per* RNAi, however, most crickets did not show circadian modulation of activity, but the circatidal rhythm persisted without a significant difference in the period from controls (Fig. 2.7c). There were significant differences in the proportion of crickets with a circadian rhythm between the *per* RNAi group and the control groups (Takekata et al. 2012), which means that *per* is involved in the circadian rhythm but has no role or a less important role in the circatidal rhythm.

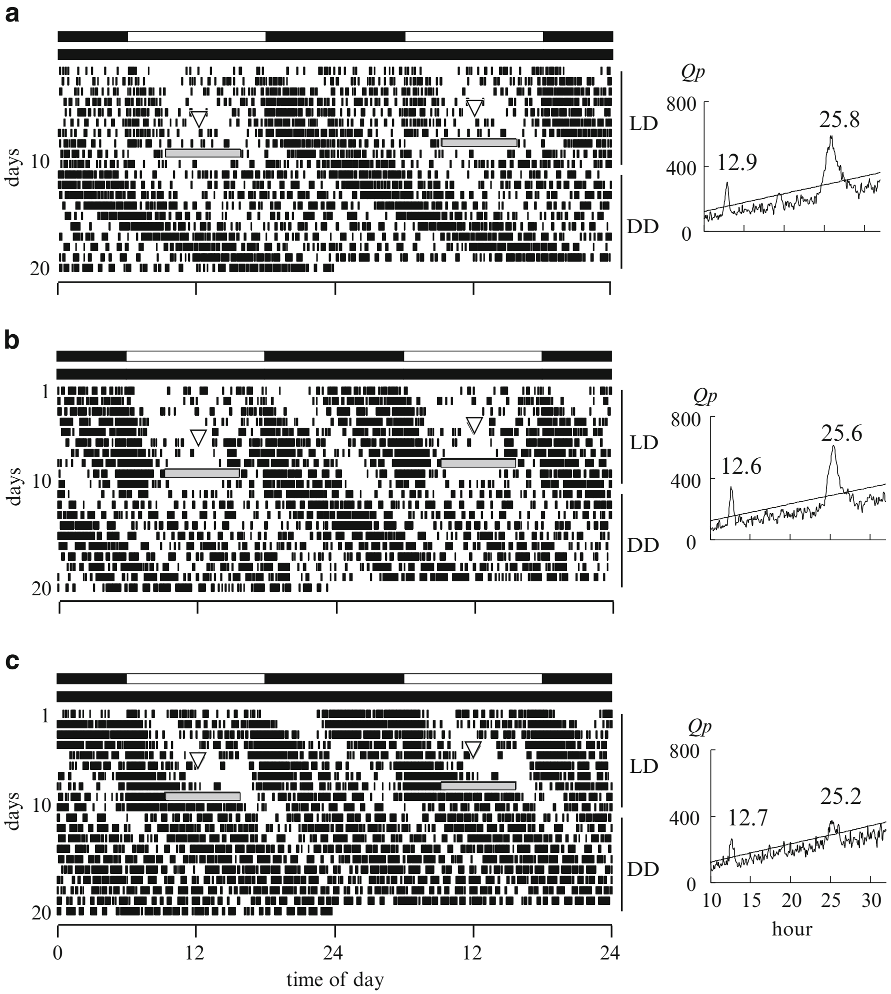

Fig. 2.7 Examples of the locomotor activity of *Apteronemobius asahinai* anaesthetized (control) (**a**), injected with double-stranded RNA for the control gene (*ß-lactamase*) (**b**), and injected with double-stranded RNA for *per* (**c**). Injection was performed on the 6th day (*triangles*). Rhythmicity under DD was determined by chi-square periodogram analysis (*line graphs at the right side*). *Black* and *white bars above the actograms* indicate light and dark phases, respectively, during LD. *Gray boxes in actograms* indicate no data. Circadian modulation under DD was significantly detected for the free-running rhythm of (**a**) and (**b**) but not for (**c**) by using the method described in Fig. 2.8. *Qp* is statistic value (ratio of variances) of chi-square periodogram (Sokolove and Bushell 1978). (From Takekata et al. 2012)

Furthermore, Takekata et al. (2014) examined the role of the optic lobe in the circatidal rhythm. The optic lobe in the brain is the circadian clock locus in crickets (Tomioka and Abdelsalam 2004). The surgical removal of the optic lobes of *A. asahinai* disrupted the circadian modulation but did not affect the circatidal rhythm,

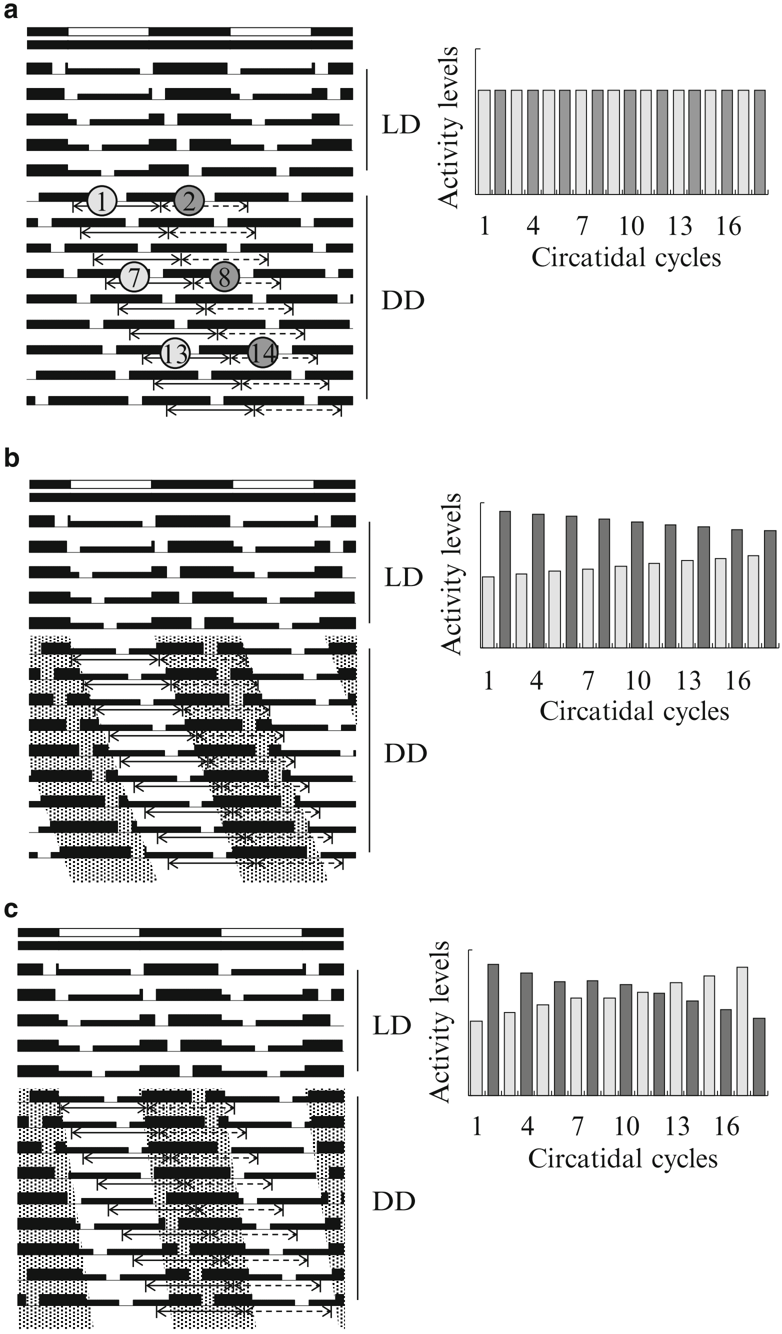

Fig. 2.8 Method for detecting circadian modulation of activity in *Apteronemobius asahinai* that show a circatidal rhythm. It is assumed that crickets under light–dark cycles (LD) were transferred to constant darkness (DD) just after the injection of double-stranded RNA. Double-plotted actograms (*left*) and histograms of activity levels counted for each circatidal period in DD (*right*) are shown.

which was maintained with no remarkable changes in its free-running period (Takekata et al. 2014). Although the circatidal rhythm in *A. asahinai* is controlled by a circatidal clock of which the phase responses are similar to those of the circadian one (Satoh et al. 2009), the molecular and neural bases of the circatidal clock appear to be different from the circadian clock.

2.6 Conclusions

There are not enough studies to discuss the general characteristics of circatidal rhythm in insects. Collecting outputs of endogenous activity rhythms for many species is primarily needed. Many intriguing insects in the marine environment are yet to be studied. By analyzing many outputs of endogenous activity rhythms, we can also know whether the circatidal rhythm is widely observed among intertidal insects. The zeitgeber and the physiological and molecular basis also need to be studied as the next step.

Finally, we refer briefly to the origin of the circatidal rhythm in insects. Intertidal insects are essentially terrestrial and have been derived from the inland ancestor by penetrating secondarily to marine environment. It is, therefore, easy to accept that the circatidal rhythm in intertidal insects is controlled by a clock originating from the circadian clock widely distributed in insects. At present, one negative answer to this implication is, however, obtained by the study of *A. asahinai*. As already mentioned, Takekata et al. (2012, 2014) indicated that the circatidal rhythm in *A. asahinai* is controlled by a circatidal clock of which the molecular and neural mechanism is different from that of the circadian clock. This observation might suggest that the tidal clock has evolved from the genetic background unrelated to the circadian clock. Nevertheless, circadian clock genes other than *per* may possibly be involved in the clock. Only after we determine the circatidal clock genes and the genes related to those could we answer clearly the question about the origin of the circatidal clock. Advances in studies of *A. asahinai* as a model organism will lead to better understanding about the circatidal rhythm in insects and, possibly, its evolutionary basis.

◄

Fig. 2.8 (continued) *Black and white bars above the actograms* indicate light and dark phases, respectively, under LD. The *shaded areas* show subjective nights under DD in crickets with the circadian rhythm. The difference in the activity levels counted for each circatidal period of odd (*light gray*) and even (*dark gray*) number cycles was examined by analysis of covariance (ANCOVA) on the assumption that the activity levels regress linearly. In a cricket without the circadian rhythm, the activity levels are the same between adjacent circatidal rhythm, and there is no difference in the elevations and the slope (**a**). In a cricket with the circadian rhythm of which the free-running period almost coincides with twice of the circatidal rhythm, the elevations of activity levels are different between circatidal even- and odd-number cycles because the subjective day corresponds to odd or even circatidal cycles throughout the experimental period (**b**). When the circadian free-running period slightly deviates from twice of the circatidal rhythm, the slopes of the activity levels are different because the subjective day moves from odd to even circatidal cycles or vice versa during the experimental period (**c**). Thus, the activity was judged to be influenced by a circadian rhythm when the slope or the elevation was significantly different between odd and even number cycles ($p \leq 0.05$)

References

Akiyama T (1995) Circatidal swimming activity rhythm in a subtidal cumacean *Dimorphostylis asiatica* (Crustacea). Mar Biol 123:251–255. doi:10.1007/BF00353616

Akiyama T (2004) Entrainment of the circatidal swimming activity rhythm in the cumacean *Dimorphostylis asiatica* (Crustacea) to 12.5-hour hydrostatic pressure cycles. Zool Sci 21: 29–38. doi:10.2108/zsj.21.29

Barnwell FH (1966) Daily and tidal patterns of activity in individual fiddler crab (genus *Uca*) from the Woods Hole region. Biol Bull 130:1–17. doi:10.2307/1539948

Cheng L (2003) Marine insects. In: Resh VH, Carde RT (eds) Encyclopedia of insects. Academic, San Diego

De la Iglesia HO, Rodríguez EM, Dezi RE (1994) Burrow plugging in the crab *Uca uruguayensis* and its synchronization with photoperiod and tides. Physiol Behav 55:913–919. doi:10.1016/0031-9384(94)90079-5

Ehlinger GS, Tankersley RA (2006) Endogenous rhythms and entrainment cues of larval activity in the horseshoe crab *Limulus polyphemus*. J Exp Mar Biol Ecol 337:205–214. doi:10.1016/j.jembe.2006.06.035

Enright JT (1965) Entrainment of a tidal rhythm. Science 147:864–867. doi:10.1126/science.147.3660.864

Enright JT (1972) A virtuoso isopod. Circa-lunar rhythms and their tidal fine structure. J Comp Physiol 77:141–162. doi:10.1007/BF00693603

Evans WC (1976) Circadian and circatidal locomotor rhythms in the intertidal beetle *Thalassotrechus barbarae* (Horn): Carabidae. J Exp Mar Biol Ecol 22:79–90. doi:10.1016/0022-0981(76)90110-6

Foster WA, Moreton RB (1981) Synchronization of activity rhythms with the tide in a saltmarsh collembolan *Anurida maritima*. Oecologia (Berl) 50:265–270. doi:10.1007/BF00348049

Gibson RN (1965) Rhythmic activity in littoral fish. Nature (Lond) 207:544–545. doi:10.1038/207544a0

Holmström WF, Morgan E (1983) Laboratory entrainment of the rhythmic swimming activity of *Corophium volutator* (Pallas) to cycles of temperature and periodic inundation. J Mar Biol Assoc UK 63:861–870. doi:10.1017/S0025315400071277

Johnson CH (1999) Forty years of PRC: What have we learned? Chronobiol Int 16:711–743. doi:10.3109/07420529909016940

Johnson CH, Elliott JA, Foster R (2003) Entrainment of circadian programs. Chronobiol Int 20:741–774. doi:10.1081/CBI-120024211

Klapow LA (1972) Natural and artificial rephrasing of a tidal rhythm. J Comp Physiol 79:233–258. doi:10.1007/BF00694219

McMeechan FK, Manica A, Foster WA (2000) Rhythms of activity and foraging in the intertidal insect *Anurida maritima*: coping with the tide. J Mar Biol Assoc UK 80:189–190. doi:10.1017/S0025315499001770

Mito T, Nakamura T, Bando T, Ohuchi H, Noji S (2011) The advent of RNA interference in entomology. Entomol Sci 14:1–8. doi:10.1111/j.1479-8298.2010.00408.x

Morgan E (1965) The activity rhythm of the amphipod *Corophium volutator* (Pallas) and its possible relationship to changes in hydrostatic pressure associated with the tides. J Anim Ecol 34:731–746. doi:10.2307/2459

Moriyama Y, Sakamoto T, Karpova SG, Matsumoto A, Noji S, Tomioka K (2008) RNA interference of the clock gene *period* disrupts circadian rhythms in the cricket *Gryllus bimaculatus*. J Biol Rhythms 23:308–318. doi:10.1177/0748730408320486

Murphy DH (1990) The natural history of insect herbivory on mangrove trees in and near Singapore. Raffles Bull Zool 38:119–203

Naylor E (1963) Temperature relationships of the locomotor rhythm of *Carcinus*. J Exp Biol 40:669–679

Nielsen MG (1997) Nesting biology of the mangrove mud-nesting ant *Polyrhachis sokolova* Forel (Hymenoptera, Formicidae) in northern Australia. Insectes Soc 44:15–21. doi:10.1007/s000400050026

Northcott SJ, Gibson RN, Morgan E (1991) Phase responsiveness of the activity rhythm of *Lipophrys polis* (L.) (Teleostei) to a hydrostatic pressure pulse. J Exp Mar Biol Ecol 148: 47–57. doi:10.1016/0022-0981(91)90146-N

Reid DG, Naylor E (1990) Entrainment of bimodal circatidal rhythms in the shore crab *Carcinus maenas*. J Biol Rhythms 5:333–347. doi:10.1177/074873049000500405

Satoh A, Hayaishi S (2007) Microhabitat and rhythmic behavior of tiger beetle *Callytron yuasai okinawense* larvae in a mangrove forest in Japan. Entomol Sci 10:231–235. doi:10.1111/j.1479-8298.2007.00218.x

Satoh A, Momoshita H, Hori M (2006) Circatidal rhythmic behaviour in the coastal tiger beetle *Callytron inspecularis* in Japan. Biol Rhythm Res 37:147–155. doi:10.1080/09291010500429939

Satoh A, Yoshioka E, Numata H (2008) Circatidal activity rhythm in the mangrove cricket *Apteronemobius asahinai*. Biol Lett 4:233–236. doi:10.1098/rsbl.2008.0036

Satoh A, Yoshioka E, Numata H (2009) Entrainment of the circatidal activity rhythm of the mangrove cricket, *Apteronemobius asahinai*, to periodic inundations. Anim Behav 78:189–194. doi:10.1016/j.anbehav.2009.04.018

Sokolove PG, Bushell WN (1978) The chi square periodogram: its utility for analysis of circadian rhythms. J Theor Biol 72:131–160. doi:10.1016/0022-5193(78)90022-X

Takekata H, Matsuura Y, Goto SG, Satoh A, Numata H (2012) RNAi of the circadian clock gene *period* disrupts the circadian rhythm but not the circatidal rhythm in the mangrove cricket. Biol Lett 8:488–491. doi:10.1098/rsbl.2012.0079

Takekata H, Numata H, Shiga S (2014) The circatidal rhythm persists without the optic lobe in the mangrove cricket *Apteronemobius asahinai*. J Biol Rhythms 29:28–37. doi:10.1177/0748730413516309

Taylor AC, Naylor E (1977) Entrainment of the locomotor rhythm of *Carcinus* by cycles of salinity change. J Mar Biol Assoc UK 57:273–277. doi:10.1017/S002531540002141X

Tomioka K, Abdelsalam S (2004) Circadian organization in hemimetabolous insects. Zool Sci 21:1153–1162. doi:10.2108/zsj.21.1153

Tomioka K, Matsumoto A (2010) A comparative view of insect circadian clock systems. Cell Mol Life Sci 67:1397–1406. doi:10.1007/s00018-009-0232-y

Wyatt TD (1986) How a subsocial intertidal beetle, *Bledius spectabilis*, prevents flooding and anoxia in tis burrow. Behav Ecol Sociobiol 19:323–331. doi:10.1007/BF00295705