Chapter 10
Lunar and Tidal Rhythms and Clocks

Jule Neumann and Tobias S. Kaiser

Abstract The presence of the moon results in tidal and lunar cycles that particularly affect life in the intertidal zone through tidal motion. A few insect species managed to colonize this dynamic interface between marine and terrestrial habitats, displaying tidal and lunar rhythms. These rhythms are caused by endogenous time-keeping mechanisms, namely, circatidal and circalunar clocks, but to date, the molecular mechanisms of lunar and tidal time-keeping remain largely unknown. Extensive chronobiological behavioral experiments conducted in a few insect species have identified the basic properties of circatidal and circalunar clocks, such as the free-running period, zeitgebers for entrainment, phase response curves, and temperature compensation. First molecular insights have been obtained for the circatidal clock of the mangrove cricket. Further development of molecular manipulation methods, as well as of genetic screens and omics experiments, will pave the way to unravel the mechanisms of both circatidal and circalunar clocks.

Keywords *Apteronemobius asahinai* · Circalunar clock · Circatidal clock · *Clunio*

10.1 Introduction

The moon has been our planet's most loyal companion. Its presence inevitably shaped the appearance of Earth, most evidently through tidal motion – the greatest synchronized movement of matter on our planet (Bowers and Roberts 2019). Both the 29.5-day lunar cycle and the 12.4-h tidal cycle are induced by the moon and influence life in the oceans. Consequently, lunar and tidal rhythms are found in the life cycles and synchronized reproduction of many marine species. This is especially true for coastal habitats, where the intertidal zone alternates between marine and terrestrial conditions.

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Historically, causal relationships between lunar and tidal cycles and their related biological rhythms have been difficult to demonstrate by experimental verification. At the same time, a plethora of pseudoscientific publications debase the authenticity of such phenomena. Today, not only the existence but also the endogenous nature of circalunar and circatidal clocks have been experimentally confirmed in organisms across eukaryotes. Such prevalence underlines the ecological and evolutionary significance of moon-related biological rhythms. Even though only a few insect species have adapted to the marine environment, they provide us with the unique opportunity to study the acquisition of circalunar and circatidal clocks in organisms which colonized the ocean secondarily. Today, we are only at the beginning of an exciting journey to unravel the molecular mechanisms of lunar and tidal time-keeping, their operating principles, and their underlying genes.

10.1.1 The Moon Causes Environmental Cycles with Different Periods

The combined gravitational pull of the moon and sun on large water bodies, along with the rotation of the Earth, results in the phenomenon of tides, i.e., the periodic rise and fall of the water surface at a particular place (Fig. 10.1a, b). Along most coasts, tides rise and fall twice a day (every 12.4 h) and are called semidiurnal tides (Fig. 10.1b). In a few locations, tides occur only once a day (every 24.8 h) and are therefore referred to as diurnal tides. When sun, moon, and Earth align every 14.77 days during full and new moon, their gravitational pull interferes constructively, and the tidal amplitude is highest, resulting in so-called spring tides (Fig. 10.1a). The synodic lunar cycle is completed when all visible phases of the moon in relation to the Earth and sun have passed after 29.53 days (Fig. 10.1c). There are two spring tide events in a full synodic lunar cycle, i.e., spring tides occur in a semilunar rhythm (Fig. 10.1c). Tidal (12.4 h), semilunar (14.77 days), and lunar (29.53 days) rhythms are to be found in many marine organisms inhabiting the intertidal zone, including insects.

10.1.2 Organisms Anticipate Moon-Related Cycles by Endogenous Circasemilunar, Circalunar, and Circatidal Clocks

Lunar and tidal rhythms could either be merely induced by external stimuli or could result from an endogenous biological clock. This is a fundamental difference, and hence, the first question with respect to an observed biological rhythm is always: Is there an endogenous (molecular) time-keeping mechanism that can tell time even in the absence of environmental cycles? The matter has been a long-standing debate in

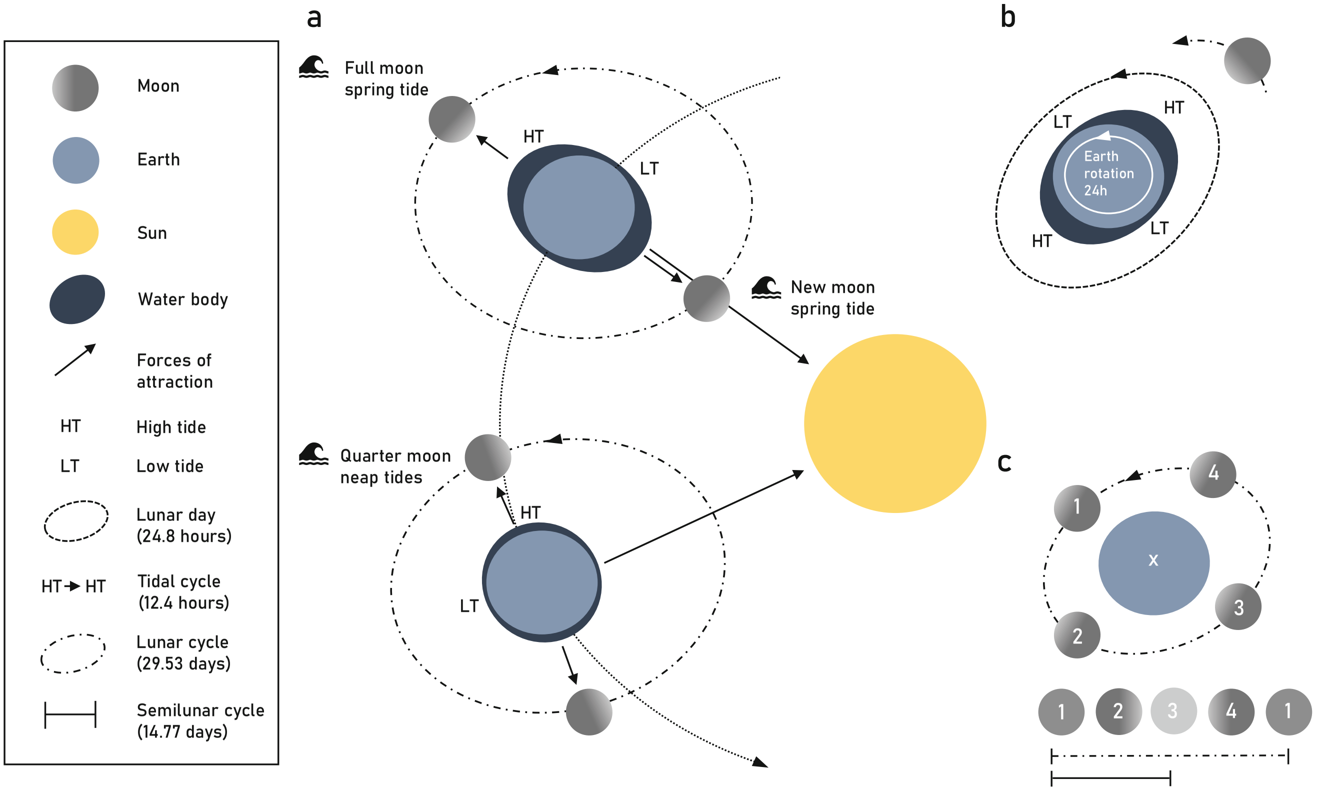

Fig. 10.1 The interaction of the sun, moon, and Earth results in tidal and lunar cycles. (**a**) Forces of attraction between the sun, moon, and Earth on Earth's water body result in the occurrence of tides. When all celestial bodies align during the full and new moon, the forces add up, and the tidal amplitude is highest (spring tides), while when the sun and moon pull on Earth's water body at a 90° angle, forces cancel each other out, and the tidal amplitude is lowest (neap tides). (**b**) The moon orbits Earth in the same direction as Earth rotates around its own axis. To regain its exact position in relation to the moon, every location on Earth has to

chronobiology. Today, the criteria characterizing an endogenous biological clock are well defined: The clock must be free-running, be temperature-compensated, and be subject to entrainment by specific stimuli (Pittendrigh 1993). The following section will explain these basic features.

Biological clocks are described in the terminology of physics and mathematics. They are viewed as oscillatory systems (limit-cycle oscillators) with a natural, endogenous period τ which is slightly different from the period T of the corresponding exogenous environmental cycle. To test for the existence of an internal oscillator with period τ, the organism displaying the rhythm of interest is transferred into constant conditions (e.g., for a tidal rhythm, none of the environmental conditions should have a 12.4-h period). If the organism still displays rhythmicity with τ close to T over several cycles in this constant environment, the rhythm is free-running. Furthermore, the free-running period of the rhythm must be temperature-compensated, meaning that within a given range of temperatures, the period τ does not change. This is in stark contrast to most other chemical and metabolic processes, which increase at a rate of 2 to 3 times with every 10 °C increase in temperature (Q_{10} temperature coefficient = 2–3). Temperature compensation is important for reliably keeping track of time independent of the naturally fluctuating temperature of the environment. Finally, it must be possible to synchronize the endogenous biological clock to the exogenous environmental cycle via specific environmental cues, which are called zeitgebers. The process of synchronization is called entrainment, during which the observed biological rhythm assumes a specific phase relationship to the environmental cycle. Zeitgebers therefore set the phase of the displayed rhythm. For lunar and tidal rhythms, tidal vibration, tidal temperature cycles, and moonlight have all been identified as zeitgebers for entraining the circatidal, circasemilunar, and circalunar clocks in insects (Table 10.1).

10.1.3 Evolutionary Significance of Circatidal, Circasemilunar, and Circalunar Clocks: Why Should We Study Lunar and Tidal Rhythms in Insects?

Studying the evolutionary causes and history of circatidal and circalunar clocks will be valuable to understand biological temporal organization. In this section, we will explore three evolutionary concepts:

Fig. 10.1 (continued) catch up with the 50-min discrepancy between both trajectories. Therefore, a lunar day from Earth's perspective is 24 h and 50 min. Hence, a location experiences two low and high tides per day, resulting in a tidal cycle of 12.4 h. (**c**) From Earth's perspective (x), the moon passes through all lunar phases every 29.53 days (synodic lunar cycle). A synodic semilunar cycle corresponds to half a synodic lunar cycle (14.77 days)

Table 10.1 Insects displaying lunar and tidal rhythms for which endogenous biological clock criteria have been experimentally examined

Species	Behavioral rhythm	(1) Free-run demonstrated in the laboratory	(2) Entrainment		(3) Temperature compensation
			Identified cue (zeitgeber)	Phase response curve	
Circatidal rhythms in hexapods					
Anurida maritima (Collembola)	Locomotor activity, aggregation behavior, phototaxis	[1] LL [2] LL, [2] LL, [3]	– – –	– – –	– – –
Thalassotrechus barbarae (Coleoptera)	Locomotor activity	[4] LL	–	–	–
Callytron inspecularis (Coleoptera)	Burrow plugging	[5] LL	[5] TSu	–	–
Apteronemobius asahinai (Orthoptera)	Locomotor activity	[6] DD [9] LL	[7] TSu [8] Wa	[7] [8]	–
Circalunar rhythms in insects					
Clunio marinus (Diptera)	Semilunar or lunar adult emergence	[10] LD [11] LL	[10] ML [12] TVi [13] TTe	–	–
Clunio tsushimensis (Diptera)	Semilunar adult emergence	[14] DD	[14] ML	[15]	[14]
Pontomyia oceana (Diptera)	Semilunar adult emergence	[16] LD, LL, and DD	[16] ML	–	[16]

ML moonlight, *TVi* tidal vibration, *TTe* tidal temperature, *TSu* tidal submergence, *DD* constant darkness, *LL* constant light, *LD* light-dark cycle, *Wa* water stimulus

[1] Foster and Moreton 1981, [2] Mcmeechan et al. 2000, [3] Manica et al. 2000, [4] Evans 1976, [5] Satoh et al. 2006, [6] Satoh et al. 2008, [7] Satoh et al. 2009, [8] Sakura and Numata 2017, [9] Satoh 2017, [10] Neumann 1966, [11] Neumann 1976, [12] Neumann 1978, [13] Neumann and Heimbach 1984, [14] Neumann 1988, [15] Kaiser and Neumann 2021, [16] Soong et al. 2011

(a) The adaptive benefits of circalunar and circatidal clocks: Why did circatidal and circasemilunar clocks evolve? In other words, what is the ultimate or evolutionary advantage for keeping track of the tides and the lunar cycle?
(b) The diversity of time-keeping mechanisms: Do organisms find different solutions for circalunar and circatidal time-keeping mechanisms? This will help to understand how tidal and lunar biological rhythms evolved or how plastic time-keeping can be organized.
(c) The temporal organization within an organism: How do organisms track different geophysical cycles simultaneously?

10.1.3.1 The Adaptive Benefits of Circalunar and Circatidal Clocks

The intertidal zone is defined as the area lying within the tidal range. This means that during low tides, the seafloor is exposed, while at high tides, it is submerged. Changes in the water level are accompanied by considerable differences in temperature, salinity, UV exposure, nutrient availability, or predator abundance. While the adaptive value of the circadian clock has been demonstrated (Abhilash and Sharma 2016), such evidence is entirely lacking for circatidal or circa(semi)lunar clocks. However, there are two main hypotheses for the adaptive benefits of these moon-related rhythms. The first is that they may synchronize important life cycle events, such as reproduction or hatching, as well as locomotor and feeding behavior, with favorable tidal conditions. This is known as the extrinsic advantage hypothesis (Naylor 2010). Second, they may serve to synchronize these same life cycle events within a population (Naylor 1976). In particular, lunar rhythms may serve to synchronize reproduction within a population, especially in marine or tropical habitats where seasonality is often not very pronounced (Hartland-Rowe 1958). In a sparse population, it will be harder to find a suitable mate, and therefore, reproductive success decreases, which is known as the Allee effect (Courchamp et al. 1999). Precise synchronization of reproduction reduces the Allee effect. Despite the lack of experimental evidence, the omnipresence of (semi)lunar and tidal rhythms across the tree of life suggests that moon-related rhythms are adaptive for many organisms, particularly in marine environments.

10.1.3.2 Diversity of Circatidal and Circalunar Clocks

As insects first evolved in terrestrial habitats, all marine insect species must have colonized the ocean secondarily (Andersen 1999; Misof et al. 2014). These insects provide us with an excellent opportunity to study recently acquired endogenous timing systems as adaptations to the tidal environment. The principles of these timing mechanisms can then be compared to those that have evolved in primordial marine organisms, like those of marine annelids. First evidence suggests that the circa(semi)lunar clocks of annelids, insects, and algae may follow different functional principles (Kaiser and Neumann 2021). Unraveling these principles and the molecular clockwork of circatidal and circa(semi)lunar clocks across the tree of life will help to fully understand their divergent mechanisms and multiple evolutionary origins (Rock et al. 2022).

10.1.3.3 Temporal Organization on Different Time Scales

Organisms are simultaneously exposed to a variety of environmental cycles of different periods. The circadian clock might time the feeding behavior of an organism, while a circalunar clock times reproduction, and a photoperiodic response regulates overwinter dormancy. The interplay of time-keeping mechanisms, their interrelations, coordination, and dependencies are ultimately what ensures survival of an organism and is subject to selection. It remains an exciting challenge to unravel the complex interplay of time-keeping mechanisms. Only organisms that show robust phenotypes on all different time scales will allow us to understand their overall temporal organization. Insects displaying tidal and (semi)lunar rhythms are a starting point for addressing such complex questions.

10.2 Circatidal Clocks in Hexapods

Tides and lunar cycles predominantly impact life in the ocean where insects are rare. Approximately 50% of all insect orders contain marine species, most notably the orders Collembola (springtails), Hemiptera (true bugs), Coleoptera (beetles), and Diptera (true flies) (Cheng 2009). The vast majority of marine insects inhabit the intertidal zone, and some of them display behavioral rhythms related to tides. For example, hemipteran bugs of the genus *Halovelia* and members of the family Hermatobatidae leave their refuge of the upper tidal zone to forage during low tide (Cheng 2009). The common tiger beetle *Cicindela* inhabits sandy shores and populates the intertidal zone when the tide recedes. Larvae of the beetles plug their burrow entrances shortly before the tide returns to avoid flooding of their refuge (Cheng 2009). Similar burrow-plugging behavior was also observed in the mangrove forests of Japan for the tiger beetle *Callytron yuasai* (Satoh and Hayaishi 2007). Interestingly, a circaseptan activity rhythm was recorded in the laboratory for the beach beetle *Chaerodes trachyscelides* (Meyer-Rochow and Brown 1998). The authors speculate that such weekly rhythms could be an adaptation to the position of the wrack line, which is altered by weekly alternation of spring and neap tides and may serve as shelter and foraging grounds.

Despite these observations, experimental confirmation of circatidal clocks in insects is scarce (Table 10.1). The criteria for endogenous circatidal rhythms have been investigated in only four hexapod species: the springtail *Anurida maritima* (Collembola) (Foster and Moreton 1981), the beetles *Callytron inspecularis* and *Thalassotrechus barbarae* (Coleoptera) (Evans 1976; Satoh et al. 2006), and the mangrove cricket *Apteronemobius asahinai* (Orthoptera) (Satoh et al. 2008). It appears that tidal rhythms generally dampen rapidly under constant conditions, which complicates their study in the laboratory. With respect to zeitgebers, artificial submergence given in a tidal pattern has been identified to entrain *C. inspecularis* and *A. asahinai* (Satoh et al. 2006; Satoh et al. 2009). Temperature compensation of the tidal rhythm has never been experimentally verified in any of the examined insect species (see Table 10.1). This may be due to the quick dampening, as well as a lack of efficient culturing procedures for most intertidal species.

10.2.1 Collembola: Anurida maritima

The small Collembola *Anurida maritima* inhabits rocky intertidal zones and salt marshes (Cheng 2009). During high tide, *A. maritima* can be found hiding among rocks, while during low tide, they come out to forage. This circatidal locomotor rhythm has been demonstrated to be free-running under constant light (LL) in the laboratory for at least 7 days (Mcmeechan et al. 2000; Foster and Moreton 1981). Early anticipation of the approaching tide is essential for survival of the Collembola because it physically cannot outrun the water (Foster and Moreton 1981). Some individuals inhabit the higher intertidal zone, which is not exposed to high tides every day. Interestingly, *A. maritima* there still displays a tidal activity rhythm, providing a rare opportunity to investigate an apparently free-running rhythm under field conditions (Foster and Moreton 1981). When *A. maritima* moves toward the upper shore around high tide, they often aggregate with hundreds of individuals (Joosse 1966). This aggregation behavior also persists rhythmically under LL, matching the phase of lowest locomotor activity (Mcmeechan et al. 2000). Additionally, it has been reported that in the field, the peak of activity occurring during the night low tide in *A. maritima* can be suppressed (Foster and Moreton 1981). This raises the question as to whether the circadian clock modulates the tidal activity pattern or whether darkness or temperature instantly suppresses the behavior (Foster and Moreton 1981; Mcmeechan et al. 2000). Interestingly, *A. maritima* is usually negatively phototactic, meaning they move away from light, consistent with the shelter searching behavior in the field observed during high tide. However, for 2–7 h after high tide, most of the population becomes positively phototactic, coinciding with *A. maritima* leaving their refuge to feed (Manica et al. 2000). This change in phototactic behavior has been shown to follow a circatidal rhythm, potentially using the horizon brightness as a guidepost (Manica et al. 2000). Water reflects light better than soil, and thus, the horizon toward the water is brighter, attracting *A. maritima* during their foraging excursions (Manica et al. 2000).

10.2.2 Coleoptera: **Thalassotrechus barbarae** *and* **Callytron inspecularis**

The carabid beetle *Thalassotrechus barbarae* was the first insect for which a circatidal locomotor rhythm had been investigated in the laboratory. The beetles inhabit the rocky tidal shore along the American continent. Adults forage during the night, but just at low tide. Hence, they display a lunidian (lunar-day) locomotor activity rhythm (24.8 h) during night tides. Consistently, under LD (light:dark) 15:9 in the laboratory, beetles were active only during the dark phase, suggesting either a circadian or circalunidian rhythm, which could not be distinguished statistically (Evans 1976). However, under LL, a significant correlation between the amplitude of the corresponding field night tide and the amount of activity was demonstrated for the first 3 days after beetles were brought to the laboratory (Evans 1976). Accordingly, it has been proposed that a circatidal oscillator might suppress the beetle's activity during high tide (Evans 1976). It should be noted, however, that there was never a follow-up publication investigating the endogenous nature of the tidal rhythm in *T. barbarae.*

Larvae of the tiger beetle *Callytron inspecularis* reside in sand burrows, which they plug shortly before high tide. It was found that this burrow-plugging behavior continues under LL in the laboratory (Satoh et al. 2006). When one larva was subjected to an artificial tidal cycle of submergence, the burrow-plugging rhythm was entrained and, after cessation of the cue, was free-running with a period of 12.45 ± 0.51 h (Satoh et al. 2006). Interestingly, larvae only start the plugging behavior after their burrows have been submerged by one to three high tides (Satoh et al. 2006). When approaching neap tide, the tides, and therefore tidal submergence, cannot reach the beetle's habitat, and the burrow-plugging behavior eventually ceases (Satoh et al. 2006). It has been hypothesized that the circatidal oscillator is entrained by tidal submergence but dampened with subsiding tides, in accordance with the observation that burrow plugging in the field has not been observed during neap tides.

10.2.3 Orthoptera: Apteronemobius asahinai

10.2.3.1 The Circatidal Activity Rhythm in the Mangrove Cricket Free-Runs Under LL and DD

By far, the best studied circatidal rhythm of an insect is found in the mangrove cricket *Apteronemobius asahinai*. These crickets are active during low tide but remain inactive around high tide, residing on mangrove roots. The locomotor rhythm of field-caught crickets has a free-running period of approximately 12.6 h under constant darkness (DD) (Satoh et al. 2008) as well as under LL (Satoh 2017). Notably, the recorded activity levels differed in amplitude under DD, alternating between strong and weak activity peaks (Fig. 10.2a, a'). This can be interpreted as a diel modulation of the activity, with the crickets being less active during the night. Such diel modulation might be controlled by a circadian clock. Indeed, the difference in activity levels was absent in LL, and it has been hypothesized that under LL, the circadian modulation diminishes because of the suspension of the circadian clock (Satoh 2017). Under DD, the circadian oscillations can persist, and hence, the circadian modulation of the circatidal rhythm is reflected in an unequal activity rhythm.

To further disentangle circatidal and circadian rhythms, locomotor activity of crickets that never experienced a natural tidal cue (raised from eggs in the laboratory) was monitored under dim red light (Sakura and Numata 2021). Some crickets showed significant circatidal rhythmicity for more than 20 days, while others showed circatidal rhythmicity only within the first 10 days but switched to diurnal rhythmicity afterward. Additionally, some crickets displayed a circatidal rhythm in the first 10 days but became arrhythmic thereafter. To investigate whether the diel rhythm was controlled by a circadian clock, the crickets were subjected to LL, as well as light-dark cycles (LD) with phase advances and delays. However, no consistent responses could be obtained, and more experiments are required to investigate whether the diel activity rhythm is controlled by a circadian clock.

10.2.3.2 Inundation Stimuli Entrain the Circatidal Rhythm in the Mangrove Cricket

Artificial inundation was found to be a zeitgeber for the circatidal clock of *Apteronemobius asahinai* and served to obtain the only circatidal phase response curve for insects (Satoh et al. 2009). Field-caught crickets were exposed to DD for approximately 10 days, and free-running circatidal locomotor rhythm was recorded. When a 30-min inundation stimulus was given at different times of the tidal cycle, the onset of activity was shifted depending on when the cue was given. If the stimulus was given during subjective high tide, only a small phase advance could be invoked, while a stimulus given during the subjective low tide resulted in noticeable phase delays (first half) and advances (second half).

Although inundation was shown to entrain the circatidal clock in the mangrove crickets, the particular sensory stimulus could not be clarified from the experiment. As a follow-up, it was tested whether contact with water was the cue (Sakura and Numata 2017). In cold-anesthetized and immobilized crickets, a water stimulus given during the middle phase of the subjective low tide resulted in a delay of locomotor rhythm, while a stimulus given during the later phase of the subjective low tide advanced the rhythm (Sakura and Numata 2017). Only a slight phase shift was observed when the water stimulus was given during the subjective high tide. The authors proposed that water receptors could perceive the water stimulus, as they have been described in the legs of another cricket, *Gryllus bimaculatus* (Kanou et al. 2007).

10.2.4 Involvement of the Circadian Clock in Circatidal Time-Keeping

It has been a long-standing debate whether the circatidal clock in one way or the other involves the circadian clock's molecular machinery. There are three main hypotheses. Enright suggested that a single clock could govern both circatidal and circadian rhythms and be entrained by both tidal and circadian zeitgebers (Enright 1976). Palmer proposed the presence of two 24.8-h oscillators that run in antiphase and produce a rhythm that appears to be only 12.4 h apart, known as the circalunidian clock hypothesis (Palmer 1995; Palmer and Williams 1986).

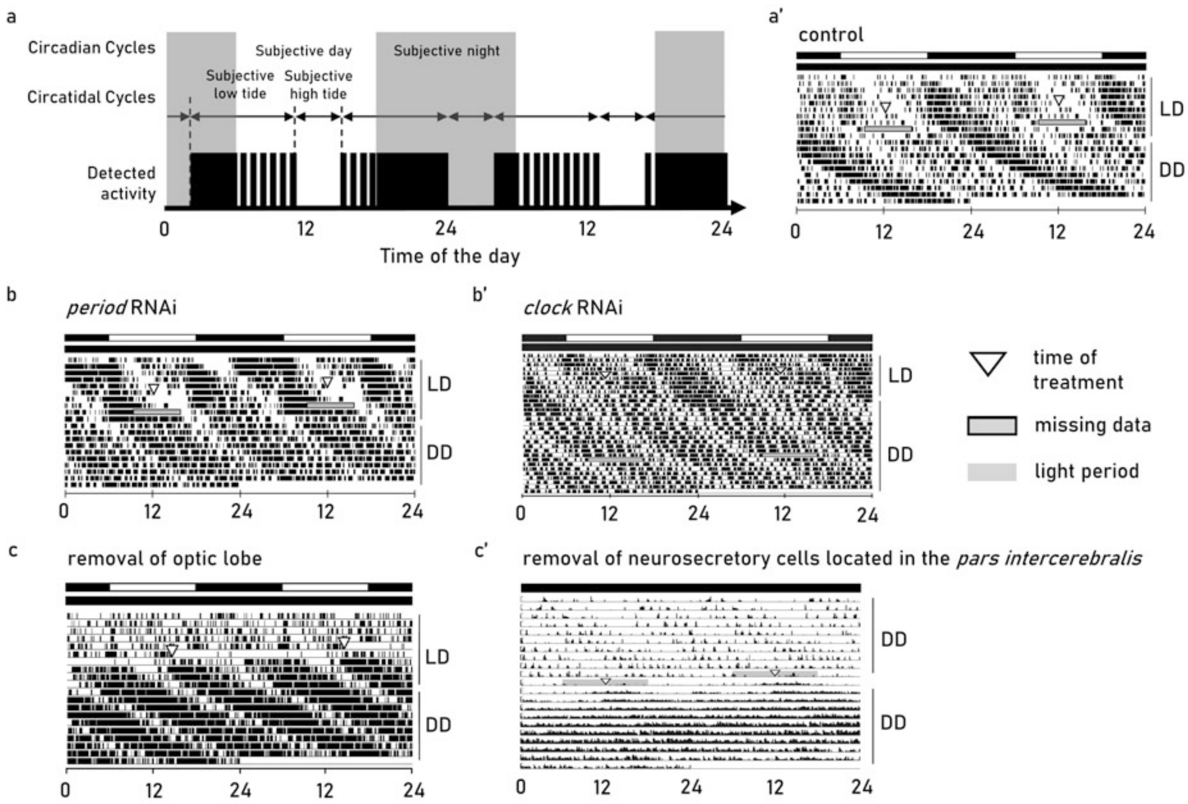

Fig. 10.2 (**a**, **a'**) The circadian clock modulates the circatidal activity rhythm of the mangrove cricket *Apteronemobius asahinai*. Crickets are active during subjective low tide, but this activity remains suppressed by the circadian clock during the subjective day. Schematic figure **a** modified from Goto and Takekata (2015), Copyright (2015), with permission from Elsevier. Experimental figure **a'** used with permission of The Royal Society from Takekata et al. (2012),

Circalunidian refers to the period between consecutive moonrises, equaling 24.8 h (Fig. 10.1b). Given the period close to 24 h, such circalunidian oscillators could be based on the circadian clock machinery. Finally, Naylor proposed an independent circatidal clock mechanism with its own molecular machinery (Naylor 1996; Naylor 1958).

Given the inability of the circadian clockwork to adopt periods that deviate significantly from 24 h, Enright's idea of a single clock would only work if the overt 12.4-h tidal rhythm is generated as a submultiple of a 24.8-h circalunidian oscillator (Enright 1976; Goto and Takekata 2015). Additionally, the circalunidian instance of such a single multipurpose clockwork must not respond to light entrainment, as then night and day should force it to a 24-h period (Palmer 1995). There are no observations in insects that would support such a single clockwork mechanism, but it was demonstrated for fish (Gibson 1973) and crustaceans (Akiyama 1997).

Interestingly, it is well documented that in *Drosophila* the morning (M) and evening (E) activity peaks are generated by two oscillators in antiphase (Helfrich-Förster 2009; Yoshii et al. 2012). Considering that marine insects evolved from terrestrial ancestors, it might be that by extending the M-E interval, an adaptation to the tides (a 12.4-h rhythm) could have been achieved (Zhang et al. 2013). The burrow-plugging behavior of the tiger beetle *Callytron inspecularis* has been hypothesized to be explained by the circalunidian hypothesis because the time intervals between two consecutive burrow-plugging events vary in the field (Satoh et al. 2006). This suggests that the two oscillators are slightly out of phase. In line with that, in free-run experiments with crabs, the two daily activity peaks sometimes seem to run with different free-running periods (Palmer 2000; Palmer and Williams 1986). However, based on experiments in *Carcinus maenas* (Naylor 1996; Naylor 1958), Naylor argued that the observed patterns under free-run conditions can rather be explained by the interplay of independent circatidal and circadian oscillators. Indeed, for the mangrove cricket, an independent circatidal clock has been proposed based on molecular knockdown of core circadian clock genes (see next paragraph). Additionally, recent molecular findings in the crustacean *Eurydice pulchra* suggest that the circatidal oscillator may use some molecules of the circadian clock, but not

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Fig. 10.2 (continued) Copyright (2012), permission conveyed through Copyright Clearance Center, Inc. (**b**, **b'**) RNAi of the circadian clock gene *period* (**b**) and *clock* (**b'**) abolishes the circadian modulation of the circatidal activity rhythm, indicating that both genes are essential for the circadian but not the circatidal clock. (**b**) used with permission of The Royal Society from Takekata et al. (2012), Copyright (2012), permission conveyed through Copyright Clearance Center, Inc. (**b'**) Reprinted from Takekata et al. (2014b), Copyright (2014), with permission from Elsevier. (**c**) Removal of the optic lobe results in a circatidal activity rhythm without circadian modulation. Reprinted from Takekata et al. (2014a), Copyright (2014), with permission from SAGE. (**c'**) More than half of the crickets display an arrhythmic activity pattern after removal of the neurosecretory cells in the pars intercerebralis (PI), indicating that this region is important for both circadian and circatidal time-keeping. Adapted from Takekata et al. (2018), with permission from Springer Nature: Copyright (2018) all of them (Zhang et al. 2013). This finding might support an independent circatidal oscillator with some circadian clock components reused.

10.2.4.1 Molecular and Neurophysiological Data Support an Independent Circatidal Pacemaker in the Mangrove Cricket

The circadian clock is by far the best studied biological clock at the molecular level. As a consequence, involvement of the circadian clock in other biological timekeeping systems – including photoperiodism, circatidal, circalunar, and circannual clocks – has been the focus of research for a long time. Knocking down known core circadian clock genes using RNA interference (RNAi) is one approach for investigating the role of the circadian clock. If the circadian phenotype is disrupted but the tidal, lunar, or photoperiodic rhythm persists, the underlying clock is assumed to run independently of the circadian system. Knockdown methods are often the only available tool for non-model species displaying circatidal, circalunar, or circannual rhythms. In the long run, not only knockdown but also knockout and gain of function studies need to be established and conducted to clarify the involvement of the circadian clock.

In the mangrove cricket *Apteronemobius asahinai*, knockdown experiments using RNAi against the core clock gene *period* and *clock* support the independence of the circatidal and circadian clocks (Takekata et al. 2012; Takekata et al. 2014b). The circadian modulation of the tidal locomotor rhythm was disrupted, while the tidal rhythm persisted (Fig. 10.2b, b’). Neurophysiological ablation experiments were also conducted in the mangrove cricket to identify the pacemaker center of the circatidal clock. It is known that the optic lobe is the location of the circadian clock pacemaker in crickets (Shiga et al. 1999; Tomioka and Chiba 1992). Removal of the optic lobe in the mangrove cricket disrupted circadian but not circatidal rhythmicity, indicating that this region is not important for circatidal time-keeping (Fig. 10.2c) (Takekata et al. 2014a). When the pars intercerebralis (PI, another region relevant to the circadian clock (Sokolove and Loher 1975)) and/or surrounding regions were removed, the tidal rhythm was perturbed, i.e., more than half of the crickets became tidally arrhythmic. This suggests that the PI is important not only for the circadian clock but also for the circatidal clock (Fig. 10.2c’) (Takekata et al. 2018).

The possibility of global genomic and transcriptomic screens offered by next-generation sequencing methods can be key for getting hold of yet unknown components of circatidal and circalunar clocks. Unfortunately, such screens are still scarce for organisms with robust tidal rhythms. A pilot study (only one replicate per time point) analyzed RNA-sequencing (RNA-Seq) data over two tidal cycles sampled every 3 h under DD of the mangrove cricket’s head (Satoh and Terai 2019). A total of 206 genes were found cycling with a circadian period. Arrhythmic expression of *clock* is in accordance with Takekata et al. (2012), in which mRNA of *clock* was found not cycling under LD in crickets with β-lactamase RNAi. However, the RNA-Seq data could not recapture the cycling pattern of *period* mRNA, probably because one replicate did not give enough power to detect all cycling transcripts. Nevertheless, more than 284 genes were found to cycle tidally in the cricket brain, with most of them peaking around either subjective high or low tide, indicating that their transcript abundance might be correlated with the tidal cycle. Moreover, genes involved in metabolic processes and molecular chaperons were upregulated at low tide (Satoh and Terai 2019). Because only half of all tidally cycling genes could be annotated, the authors speculated that some of them could potentially be noncoding RNAs. More sophisticated RNA-Seq experiments are required to understand tidal gene regulation in insects. As an important step on the way, an annotated genome has been recently published for the mangrove cricket (Satoh et al. 2021).

10.2.5 Tidal Non-oscillatory Timing Mechanisms

Although a biological clock has been traditionally defined as an oscillatory system, it is worth noting that other ways of tidal time-keeping exist. Adults of an Arctic population of the marine midge *Clunio marinus* emerge every low tide during midsummer. The temperature increase associated with exposure of the substrate during low tide causes the start of an 11- to 13-h hourglass timer, which allows the midges to emerge during the subsequent low tide (Pflüger 1973). In the laboratory, no free-running emergence rhythm was observed, consistent with the idea that a non-oscillatory or highly dampened oscillatory system times emergence of the midge (Pflüger 1973).

10.3 Circalunar Clocks in Insects

10.3.1 Lunar Rhythms of Insects in Terrestrial Habitats

Lunar periodicity of abundance in insects has been observed for various insect orders, including Ephemeroptera, Trichoptera, and Diptera (Hartland-Rowe 1955; Corbet 1958), as well as Lepidoptera and Coleoptera (Nowinszky et al. 2010). Lunar periodicity in flight behavior has also been observed for a few species of Hymenoptera, Heteroptera, Isoptera, and Orthoptera (Danthanarayana 1986). It should be noted, however, that some controversy among authors exists. Lunar phase and rhythmicity have been inconsistently reported for the same insect species (Danthanarayana 1986; Nowinszky 2004). Danthanarayana (1986) provides an extensive list of insect species for which flight activity has been correlated to lunar phases, noting that not only aquatic but also entirely terrestrial species show clear lunar rhythmicity in abundance. It is accepted that changes in insect abundance in relation to the lunar phase can be attributed to a reduction in the effectiveness of the trap (light of the trap essentially competes with moonlight) (Williams et al. 1956).

However, some species truly vary in abundance due to changes in the lunar phase (Bowden and Church 1973). It has been hypothesized that such lunar periodicity in emergence may be an adaptation to wind-assisted dispersal (migration) (Danthanarayana 1976).

However, to date, there is no fully convincing evidence for an endogenous lunar time-keeping mechanism in a terrestrial insect. Ito et al. (1993) found that the catch size of adult Malayan black rice bugs *Scotinophara coarctata* was highest around full moon. However, when second instar nymphs were isolated and monitored in the laboratory, adult emergence was not synchronized with the lunar cycle. The mayfly *Povilla adusta* shows a lunar rhythm in emergence, peaking around full moon (Hartland-Rowe 1955). Although it was shown that this emergence peak persists in DD and artificial LD (Hartland-Rowe 1955; Hartland-Rowe 1958), the very small number of individuals examined (< 10) in a short time frame (< 1 month) disqualifies the use of these experiments as evidence for an endogenous lunar free-run in the mayfly. The pit volume of the ant lion *Myrmeleon obscurus* is highest around full moon and was observed for two peaks subjected to daylight conditions as well as in DD in the laboratory (Youthed and Moran 1969). An interesting example of a semilunar rhythm comes from the cockroach *Periplaneta americana*, for which neurotransmitter-like substances in the central nervous system reach their highest levels around full and new moon (Rounds 1981).

10.3.2 Lunar Rhythms of Insects in Marine Habitats

Lunar rhythms are prevalent in the marine environment across the tree of life, and free-run criterion has been experimentally validated in many species, including algae (Bünning and Müller 1961), annelids (Hauenschild 1960; Franke 1985), mollusks (Yoshioka 1989), crustaceans (Saigusa 1980; Enright 1972), and fish (Hsiao and Meier 1992). Interesting cases of lunar rhythms can be found in marine midges of the genera *Clunio* and *Pontomyia* (Diptera, Chironomidae), which have extremely short adult life spans of only 1–2 h. Adult emergence is precisely timed to the lowest low tides around full and new moon by a circalunar clock. For both *Pontomyia* and *Clunio*, free-run, entrainment, and temperature compensation are well documented, making them attractive systems to study the circalunar clock (Table 10.1).

10.3.2.1 The Case of *Clunio*

In marine nonbiting midges of the genus *Clunio*, development is tightly coupled with the lunar cycle (Neumann and Spindler 1991; Krüger and Neumann 1983). Chevrel (1894) was the first to notice that adults of *Clunio marinus* only swarm around full and new moon for mating. Enduring most of their life as larvae, adult emergence is restricted to only a few days around full and new moon, precisely matching the spring tides. *Clunio marinus* can be found along the entire rocky Atlantic coast of

Europe from Portugal to Norway, wherever spring tides expose the seafloor and larval substrate becomes available to oviposition of the sticky egg clutches. To achieve this precise synchronization to the lunar cycle and the tides, a developmental waiting stage (CDA, circalunar developmental arrest) occurs during the early fourth instar in *Clunio* (Neumann and Spindler 1991). This developmental stage experiences a brief increase in ecdysone titer followed by temperature-compensated development (Neumann and Spindler 1991). It is the circa(semi)lunar clock that controls the developmental switching point in the fourth instar and ultimately synchronizes development of the marine midge with the lunar cycle. During the 1960s, Dietrich Neumann established a culturing protocol for *Clunio* which allowed to systematically study endogenous clock criteria in the laboratory (Neumann 1966).

The Semilunar Emergence Rhythm of *Clunio* Is Free-Running and Temperature-Compensated

The (semi)lunar adult emergence rhythm of *Clunio* persists under constant conditions (LD, but no lunar time cues), verifying the endogenous nature of the rhythm (Neumann 1966; Neumann 1976). Free-running lunar and semilunar emergence rhythms also persist in DD (Neumann 1988) as well as in LL (Neumann 1976). Additionally, the free-running semilunar period has been found to be temperature-compensated between 14 °C and 24 °C in the Japanese midge *Clunio tsushimensis* (Fig. 10.3) (Neumann 1988).

Moonlight, Tidal Turbulence, and Temperature Cycles Can Entrain the Circalunar Clock of *Clunio*

When artificial moonlight (0.3 lux) was given for four consecutive nights every 30 days, a semilunar or lunar emergence rhythm can be evoked in southern populations of *Clunio marinus* (Neumann 1966) and in *Clunio tsushimensis* (Neumann 1988). Importantly, only light perceived during the subjective night synchronizes the phase of the lunar rhythm (Neumann 1995). It was shown that the circadian clock is important to set such a nocturnal light sensitivity window (Neumann 1995). As the rising and setting of the moon changes with the lunar cycle, moonlight is only available throughout the night around full moon. Moonlight is detected when the presence of moonlight during the night-time low tide and the nocturnal light sensitivity window coincide (Kaiser et al. 2011); hence, this is an instance of coincidence detection.

At higher latitudes, the moon stays close to the horizon, and days become very long during summer, making it difficult to perceive “light at night” as a distinct cue (Neumann 1995). Correspondingly, the (semi)lunar rhythm of northern populations of *Clunio marinus* is often more precisely entrained by vibration (Neumann and Heimbach 1979) or temperature (Neumann and Heimbach 1984) given in a tidal pattern (Neumann 1968; Neumann 1978). Such tidal cycles of vibration or

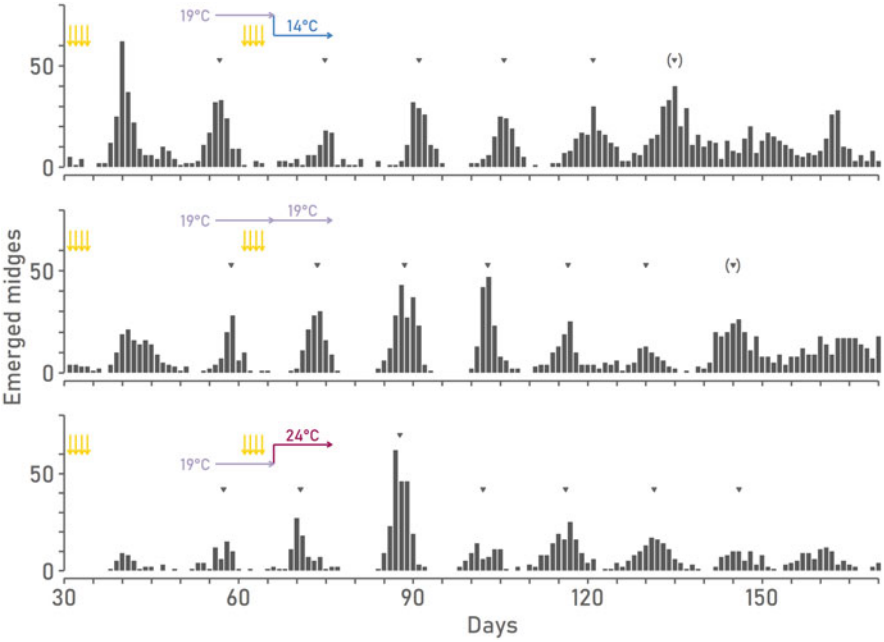

Fig. 10.3 The free-running semilunar emergence rhythm of the marine midge *Clunio tsushimensis* is temperature-compensated. After entrainment by moonlight (four nights every 30 days; yellow arrows), the semilunar rhythm free-runs for several months with a period of approximately 15 days. From Kaiser and Neumann (2021) licensed under CC BY 4.0

temperature can be used as a semilunar time cue because – just as the rising and setting of the moon – the 12.4-h tidal cycle advances every day by approximately 50 min relative to the 24-h LD. This unique phase relationship between LD and the tidal cycle recurring every 15 days serves as a semilunar cue. It is assumed that the detection of these tidal cues is also based on a coincidence detection mechanism, very similar to the detection of moonlight (Neumann 1995; Neumann and Heimbach 1985).

A lunar phase response curve has been recently published for *Clunio tsushimensis* (Kaiser and Neumann 2021). Interestingly, there is a linear phase response without transient cycles, suggesting an immediate resetting of the circalunar clock. This implies a tight coupling of the overt rhythm to the pacemaker. *Clunio's* lunar PRC is different from that of the marine annelid *Syllis prolifera*, which has a nonlinear phase response and characteristic transient cycles, suggesting that the two species may rely on different circalunar clock mechanisms (Franke 1986).

10.3.2.2 The Case of *Pontomyia*

Midges of the genus *Pontomyia* inhabit tidal pools and shallow waters of the Western Pacific (Huang and Cheng 2011). The Taiwanese midge *Pontomyia oceana* has a well-studied semilunar rhythm of adult emergence (Soong et al. 1999). Midges emerge around full and new moon in the field. The semilunar rhythm has been shown to persist under LD as well as in DD in the laboratory for at least two peaks. Hence, it is free-running (Soong et al. 2011). The semilunar emergence rhythm is also temperature-compensated between 24 °C and 30 °C, although the Q_{10} value of 0.86 is lower than the expected value of 1 (Soong et al. 2011).

10.3.3 The Role of the Circadian Clock in Circalunar Time-Keeping

Bünning and Müller proposed three hypotheses on how a lunar or semilunar period could be evoked by the circalunar clock (Bünning and Müller 1961). First, an independent semilunar or lunar oscillator of yet unknown molecular nature could run with a period of 15 or 30 days, respectively. Second, the beat hypothesis assumes superposition of a circadian rhythm (24 h) with either a circalunidian (24.8 h) or a circatidal rhythm (12.4 h). This would result in a beat wave with an amplitude changing in a lunar or semilunar rhythm. Third, there could be a counter mechanism based on either counting endogenous circadian oscillations or LD. Importantly, a circadian system is indispensable for the beat hypothesis as well as the counter hypothesis. In contrast, a circa(semi)lunar oscillator could hypothetically run independently of the circadian system.

When exposing *Pontomyia* midges to different T-cycles between LD 11:11 and LD 14:14, the period of the semilunar emergence rhythm was found to change linearly with the change in LD, i.e., the free-running semilunar emergence rhythm has a shorter period under short T-cycles and a longer period under longer T-cycles (Soong and Chang 2012). However, the semilunar emergence rhythm was unchanged under multiples of 24 h (LD 3:3, LD 6:6, and LD 12:36). These experiments suggest that *Pontomyia* uses a mechanism based on counting endogenous circadian oscillations.

Persistence of rhythmic emergence of *Clunio* in experiments conducted in DD (Neumann 1988) and LD (Neumann 1976) has been taken as evidence that *Clunio's* circalunar clock is an independent self-sustained oscillator. However, the existence of a counter mechanism based on endogenous circadian oscillations cannot be excluded. When reanalyzing the circadian phenotype under DD (Neumann 1988), a significant circadian period of approximately 25 h persisted for up to 17 days. This is long enough to explain the observed persistence of the lunar rhythm in DD, and thus, a counting mechanism might also exist in *C. marinus*. The fact that the marine midge *Pontomyia oceana* was already found to count circadian cycles for lunar time-keeping (Soong and Chang 2012) allows one to speculate that marine midges in general could use a counter mechanism for lunar time-keeping. In an evolutionary context, this makes sense: Diptera evolved on land (Misof et al. 2014) and marine midges secondarily colonized the ocean. Many terrestrial insects possess a photoperiodic counting mechanism. It seems possible that marine insects coopted the photoperiodic counter for circalunar time-keeping, i.e., as a circalunar counter.

10.3.4 Molecular and Genetic Data on Circalunar Time-Keeping in Insects

To understand the mechanisms of lunar time-keeping, a combination of molecular and genetic methods is indispensable. Considering that *Clunio* and *Pontomyia* – the only insects with described robust lunar rhythms – are still non-model organisms, molecular methods often need to be established from scratch. Even annotated reference genomes cannot be taken for granted. Generating these resources will be necessary to unravel the pathways and genes underlying lunar rhythmicity.

As a major asset, *Clunio marinus* has a highly complete and well-annotated reference genome on chromosomal scale (Kaiser et al. 2016). Additionally, there are many laboratory strains of *C. marinus* that differ in various timing phenotypes and can hence serve for comparative molecular analysis and genetic dissection of the circa(semi)lunar clockworks (Fig. 10.4a). First, populations of *Clunio marinus* differ in whether they emerge only around full moon, only around new moon, or during both full and new moon (Fig. 10.4b). The phase of emergence within the lunar cycle is genetically determined (Kaiser et al. 2011) (Fig. 10.4c). Through crossing experiments and quantitative trait locus (QTL) mapping, it was found that the lunar emergence phase is determined by two major QTLs (Kaiser et al. 2016; Kaiser and Heckel 2012). Second, populations of *Clunio marinus* differ in whether they respond to moonlight or tidal cycles of vibration. These phenotypes offer a starting point to understand the entrainment pathways. The shielding pigment transparency changes over the lunar cycle in larval ocelli of *Clunio* (Fleissner et al. 2008; Falkenberg et al. 2013). Therefore, the ocelli might play a crucial role in the perception of moonlight. Finally, Arctic and Baltic populations of *C. marinus* have lost the lunar rhythm altogether, as the lunar rhythm has no adaptive value in the absence of tides in the Baltic Sea and detection of the lunar time cues is not possible during the polar day in the Arctic. Recent genome screens that compared the lunar-arrhythmic Baltic ecotype to the lunar-rhythmic Atlantic ecotype suggest that lunar arrhythmicity is primarily dependent on circadian clock genes as well as genes involved in nervous system development (Fuhrmann et al. 2023). These findings are in line with the involvement of the circadian clock in the perception of lunar zeitgebers (Neumann 1995; Neumann and Heimbach 1985; Neumann 1989), as well as a possible counting mechanism based on circadian clock cycles.

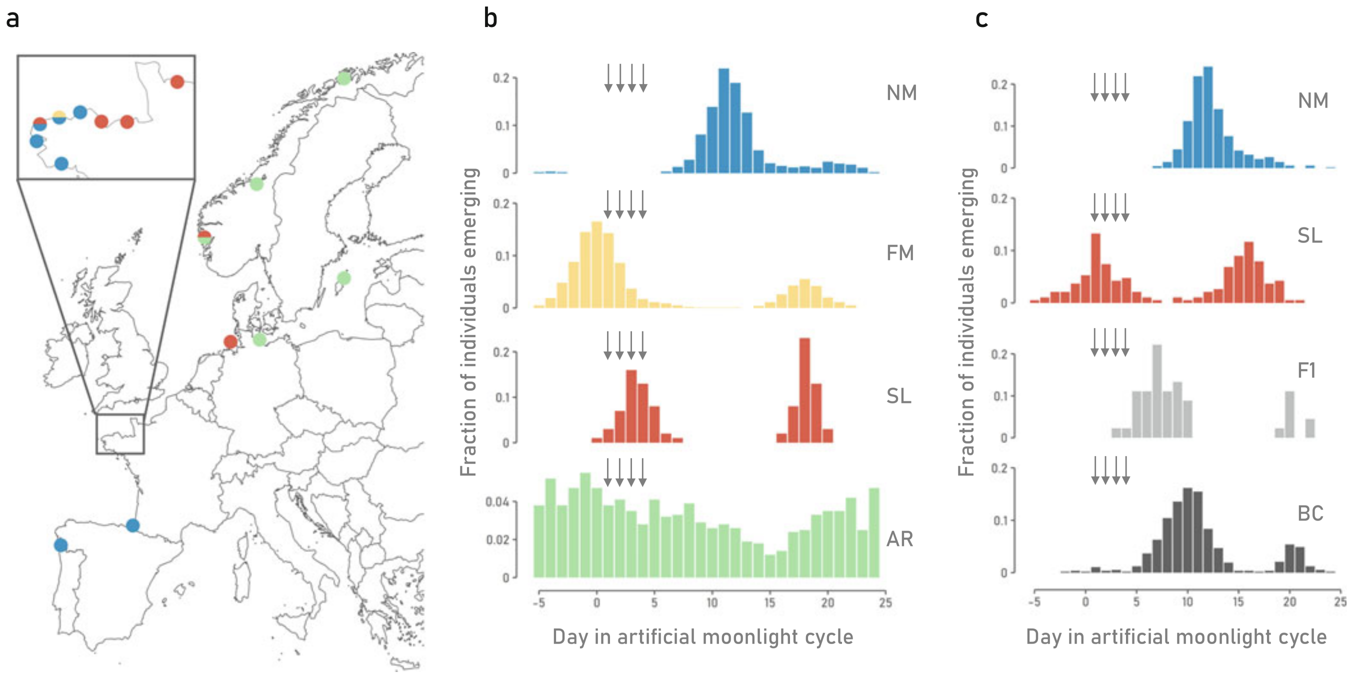

Fig. 10.4 Lunar rhythmicity, as well as phase and period are genetically determined in the marine midge *Clunio marinus* and differ between populations. *Clunio marinus* is therefore an attractive model to study the genetic architecture of lunar time-keeping using quantitative trait locus (QTL) mapping and genome-wide association screens (GWAS). (**a**) *Clunio marinus* inhabits the intertidal zone along the rocky Atlantic coast of Europe. Dots mark sampling locations from which lab strains were derived. Color coding denotes the emergence phenotype. (**b**) Under artificial moonlight (arrows, four nights of dim night light), populations emerge either around the new moon (NM) or the full moon (FM), both at the full and new moon (semilunar, SL) or arrhythmically (AR). **c** The phase of the lunar rhythm is genetically determined. When crossing a semilunar strain (Por) and a new moon strain (Jean), the F1 generation emerges in an intermediate phase and a semilunar period with unequal peaks. Based on Kaiser et al. (2011) licensed under CC BY 2.0

10.4 Conclusions

Despite their importance for numerous organisms, circalunar and circatidal clocks are still scarcely addressed in the field of chronobiology. Studying lunar and tidal rhythms provides us with the unique opportunity to understand time-keeping on multiple time scales as well as its evolution under multiple geophysical cycles. Tidal and lunar rhythms remain hard to study because they are displayed by marine non-model organisms which are often difficult to culture in the laboratory and for which molecular methods usually still need to be established. However, insects might be the key to addressing such a task. They have adapted multiple times to the marine environment and are a very diverse group providing us with the opportunity to study potentially different tidal and lunar clock mechanisms. Knowledge about lunar and tidal rhythms is as old as the field of chronobiology, but advances in understanding them at the molecular level lag far behind those of the circadian clock. Thus, the fascinating world of lunar and tidal rhythms still offers ample opportunities for discovery.

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