



Rhythms of behavior: are the times changin'?

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Animal life is rhythmic. Here we provide an overview of various rhythmic behaviors, connected environmental factors and endogenous mechanisms. We not only cover terrestrial species, but also highlight aquatic environments with typically complex interconnected rhythms. We further address diel, seasonal and potential lunar rhythms of humans. While we cannot be complete, we aim to emphasize three aspects: First, to raise awareness for the all-encompassing presence of behavioral rhythms and their importance in ecology and evolution. Second, to raise awareness how limited our mechanistic understanding is, besides analyses in a small set of model species. Finally, we discuss how anthropogenic effects can affect behavioral rhythmicity and how this might affect ecosystems in the future, as 'For the times they are a-changin'.

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Introduction

While few have put it into words just as poetically as Bob Dylan, it is clear that life is full of changes, many of which are rhythmic. Environmental cycles impact humans in various ways, but are also central in shaping the biology and interactions of countless other species. In fact, the list of rhythmic behaviors is seemingly endless ([1–4], [Table 1](#)). Abiotic cycles are driven by the celestial movements of earth and moon, as well as the inclination of the earth axis relative to the sun. The earth's rotation creates the day/night cycle, while its revolution around the sun, together with the inclination of the earth's axis, results in annual cycles. Our planet's rotation and inclination also shape the global wind and water current system — both with their own rhythms — partially also depending on

local environmental and global physical interactions. Not all climate rhythms (e.g. El Niño) are fully understood. The revolution of the moon around earth and its relative position to the sun further create light, gravitational and magnetic cycles of 27.3 days (sidereal period), 29.5 days (synodic period) and subsets thereof, as well as lunidian and tidal cycles of 24.8 and 12.4 hours, respectively [2,3]. Other rhythms, such as the about eleven-year cycle of solar activity exist and others, less prominent to humans, might not have even been uncovered.

Organisms can either respond directly to these cyclic changes of their environment or they can anticipate them with endogenous oscillators ('clocks'), providing advantage for animal fitness. The endogenous period of these oscillators corresponds closely to the respective environmental cycle (e.g. a ~24 hours circadian oscillator for the solar day/night cycle, a ~29.5 day circalunar oscillator for the monthly lunar cycle) and can also synchronize physiology and behavior across a population. For most of the mentioned abiotic cycles reports of corresponding endogenous oscillator systems exist [2,5,6,7*].

However, while endogenous oscillator systems improve species fitness as long as the ecological conditions remain stable, a too rigid coupling of behavior and physiology to oscillators limits species adaptation, and hence expansion potential. This aspect is particularly interesting in the context of large-scale environmental changes in the earth's past and future. In order to predict, how animals might respond to such changes, the mechanisms and their possible modulators controlling the different rhythms and endogenous oscillators need to be understood. Yet, while the molecular and cellular manifestation of circadian clocks in animals have been unraveled in great detail [5], much less is known about the mechanistic nature of rhythms and clocks with different period lengths, for example, circatidal, circalunar [8,9] or circannual rhythms (reviewed in Ref. [7*]), and about the pathways by which these clocks affect animal behavior.

While molecular model species are typically analyzed under highly artificial laboratory conditions, the environmental cycles animals experience and that govern their behavioral rhythms strongly depend on their natural habitats. The tropics are mostly dominated by diel light cycles that are constant throughout the year, while high latitude habitats experience strong seasonal cycles which include phases of polar night and midnight sun [10]. Temperature is a rather reliable time cue in most terrestrial habitats [10], but in large aquatic habitats the heat capacity of water, currents and vertical mixing often results in constant or unpredictable temperature

Table 1

Selection of behavioral rhythms. We present a (far from complete) list of different behavioral rhythms, the factors controlling them and their relevance for the organisms as well as other species. In cases where examples are mentioned for different rhythmicities, this is because behavioral rhythms can cycle over multiple periods, usually in an interactive manner. Question marks (?) indicate that the respective points are still under debate or completely unknown

Behavioral process	Rhythmicity	Example	Controlling factor(s)	Fitness benefits	Ecological relevance	Possible anthropogenic threats
Reproduction	Seasonal	Spawning once per year (e.g. coral <i>Acropora millepora</i>) [75,76]	Temperature, circannual clock?, photoperiod?	Mating coordination	Massive food burst, timing of predator reproduction	Temperature increase, ocean acidification?
		winter mating (e.g. sheep <i>Ovis aries</i>) [7]	Circannual clock, photoperiod	Food for offspring	Timing of predator reproduction?	Light pollution
		Spawning in spring/summer (e.g. polychaete <i>Platynereis dumerilii</i>) [8]	Temperature?	Food for offspring	?	Temperature increase
	Lunar	Spawning after full moon (e.g. coral <i>Acropora millepora</i>) [75,76]	Moonlight, circalunar clock	Mating coordination, reduced predation risk	Massive food burst, timing of predator reproduction	Light pollution, ocean acidification?
		Spawning after full moon (e.g. polychaete <i>Platynereis dumerilii</i>) [8]	Moonlight, circalunar clock	Mating coordination, reduced predation risk	?	Light pollution
		Emergence & nuptial dance at lowest low tide (e.g. midge <i>Clunio marinus</i>) [67]	Moonlight, circalunar clock	Mating coordination, offspring protection	?	Light pollution
		Mating behavior around new moon (e.g. badger <i>Meles meles</i>) [55]	Moonlight?	Predator avoidance?	?	Light pollution
	Diel	Norcturnal spawning (e.g. coral <i>Acropora millepora</i>) [75,76]	Light, circadian clock	Mating coordination, reduced predation risk	Massive food burst, timing of predator reproduction	Light pollution, ocean acidification?
		Nocturnal spawning (e.g. polychaete <i>Platynereis dumerilii</i>) [8]	Light, circadian clock	Mating coordination, reduced predation risk	?	Light pollution
		Emergence & nuptial dance at lowest low tide (e.g. midge <i>Clunio marinus</i>) [67]	Light, circadian clock	Mating coordination, offspring protection	?	Light pollution
		Larvae release at sunset (e.g. crab <i>Rhithropanopeus harrisi</i>) [116]	Light, circadian clock	Reduced predation risk	?	Light pollution
		Nocturnal egg laying & emergence (e.g. sea turtles) [117,118]	Light, circadian clock?	Reduced predation risk	?	Light pollution, poaching
	Tidal	Larvae release at high-tide transition (e.g. crab <i>Rhithropanopeus harrisi</i>) [116]	Water pressure, circatidal clock	Larvae dispersal	?	?

Table 1 (Continued)

Behavioral process	Rhythmicity	Example	Controlling factor(s)	Fitness benefits	Ecological relevance	Possible anthropogenic threats
Migration	Seasonal	Latitudinal migration (e.g. various bird species, butterfly <i>Danaus plexippus</i> , hoverflies Syrphinae) [41,115,119-121]	Photoperiod, circadian clock, magnetic compass, sun compass, temperature	Cold temperature evasion, increased genetic exchange, food availability	Dispersal of plants & small invertebrates, pollination, parasite consumption, food	Light pollution, magnetic fields, pesticides
		Shoreward migration (e.g. Christmas Island red crab <i>Gecarcoidea natalis</i>) [122,123]	Monsoon rain, others?	Terrestrial lifestyle, mating coordination	?	Human infrastructure creates obstacles
	Lunar	Migration & foraging intensity in nocturnal birds (<i>Caprimulgus europeus</i>) [57*]	Moonlight, circalunar clock?	Increased overall migration speed & coordination	Rhythmic predation pressure on bird prey	Light pollution
		Shoreward migrations peak at new moon (e.g. Christmas Island red crab <i>Gecarcoidea natalis</i>) [122,123]	Moonlight?, circalunar clock?	Avoidance of desiccation and high temperatures	?	?
	Diel	Vertical migration (e.g. zooplankton <i>Calanus finmarchicus</i>) [72]	Light, circadian clock	Optimized feeding vs. predator risk	Shapes pelagic ecosystems, global carbon cycle	?
Activity & Inactivity	Seasonal	Diapause in deep waters (e.g. copepods <i>Calanus spec.</i>) [53**,54]	Lipid content?, photoperiod?, circannual clock?	Winter survival, additional energy for reproduction	Global carbon cycle, trophic energy transfer	Temperature increase, shifts in phytoplankton timing
		sleep/wake cycle (e.g. <i>Homo sapiens</i>) [85]	Light, circadian clock	Regeneration, predator avoidance	Temporal niche creation	Light pollution
	Diel	Locomotion (e.g. horseshoe crab <i>Limulus polyphemus</i>) [60]	Light, circadian clock	Mating coordination	Food chain	Light pollution
		Locomotion/foraging (e.g. <i>Drosophila melanogaster</i>) [28,29]	Light, circadian clock	Predator avoidance	?	?
	Tidal	Locomotion (e.g. horseshoe crab <i>Limulus polyphemus</i> , acoel <i>Symsagittifera roscoffensis</i> , isopod <i>Eurydice pulchra</i>) [9,60,124]	Water pressure, vibration, light, circatidal clock	Mating coordination, avoidance of displacement, optimization of feeding/ photosynthesis of symbionts	Food chain	Light pollution, chemical pollution
		Others	Activity of deep sea vent/seep fauna (several taxa) [125,126]	Water pressure?, currents?, chemical food cues?	Increased food consumption?	?

conditions. In contrast, parameters like oxygen concentration or physical forcing (e.g. due to waves) are mostly irrelevant on land, but can be highly cyclic in aquatic habitats like the intertidal zone.

Here we aim to provide an overview on recent findings how environmental cues and endogenous clocks evoke rhythms of behavior.

The control by environmental cues

All regularly occurring major behavioral processes have their time niche(s) during which they preferably occur (Table 1). The detection of endogenous oscillators relies on laboratory experiments. Of note, when observing populations in the absence of entrainment cues, a lack of synchronized behaviors can also reflect the desynchronization of the individual oscillators instead of their absence. For these reasons it is often still unclear if a specific naturally occurring behavior is oscillator controlled (Table 1).

The environmental cues evoking rhythmicity and entraining clock systems are diverse (Table 2) and can send conflicting information (e.g. light versus temperature). The same type of cue informs about multiple rhythms (e.g. light provides diel, monthly & seasonal information),

while also itself being subject to short-term non-cyclic perturbances (e.g. cloud cover). How do animals sense these stimuli, prioritize the input, filter for signal/noise and adjust their behaviors accordingly? Below we somewhat artificially split the sensory cues by types of rhythm for better readability, but it should be clear that sensory input for different rhythms occurs at the same time.

Daily cycles

With a focus on land animals as experimental models, light and temperature are typically considered the most important cues for the entrainment of diel behavioral rhythms and circadian clocks. Light is a complex cue, as different wavelengths can have different effects on animal rhythms [11^{••},12]. Blue light is most prominently referred to for circadian clock entrainment, likely due to the large proportion of research focusing on mammalian entrainment mechanisms. In mammals, light information is transmitted via melanopsin-positive retinal ganglion cells to the central brain circadian pacemaker (i.e. the mammal suprachiasmatic nucleus, SCN) [13–15], but also directly modulates behavior [16[•]]. However, it has become increasingly clear that light information provided by rods and cones is also channeled to the SCN for circadian clock entrainment [13,17[•]], and possibly other brain areas. In insects blue

Table 2

Overview of rhythmic environmental cues. The mentioned mechanisms mediating the cues to endogenous timing systems and behavioral rhythms were identified in individual species, but can not be assumed to apply generally

Rhythmic cue	Period	Terrestrial/aquatic relevance	Known mediating mechanism(s)
Sunlight	intensity	Daily, Annual	Both (aquatic → change with depth)
	spectral composition	Daily, Annual	Both (aquatic → change with depth)
	photoperiod	Annual	Both (aquatic → change with depth)
Moonlight	Monthly	Both (aquatic → change with depth)	Opsins [22], cryptochromes [19]
	Daily (circalunidian)	Both (aquatic → change with depth)	Opsins [78], cryptochromes [127] External coincidence via melatonin & <i>eya3</i> (pituitary) [7 [*]], opsins [128]
Temperature	Annual	Both	Cryptochromes [129], post-transcriptional? [130], GnRH-like pathways? (Andreatta <i>et al.</i> , in revision)
	Daily	Mostly terrestrial	Cryptochromes?, opsins?
Food availability	Annual	Both	?
	Monthly	Aquatic	<i>ionotropic receptor 25a</i> [23], <i>nocte</i> [131]
Food availability	Daily	Both	Starvation response?
Oxygen concentration	Annual	Aquatic	?
	Daily	Both (physiological oxygen levels)	Insulin-triggered cascade [132]
Pressure/mechanical forces/vibration (tides)	Tidal	Aquatic	?
	(Semi)monthly	Aquatic	HIF1 α [25]
Salinity	Tidal	Aquatic	?
	Tidal	Aquatic	?
Magnetic field	Daily, tidal, monthly	Likely both	Cryptochromes [133,134], others?

light leads to the activation of a light-responsive cryptochrome (cry1, also known as L-cry or *Drosophila*-type cry), which affects the stability of Timeless and by this re-sets the phase of the circadian clock [18–20]. In addition to cry1, light also impacts via several Opsins expressed in the fly's eyes and ocelli, likely improving the adjustment of daily circadian rhythms to different seasons [21,22].

In *Drosophila* light and temperature jointly affect the activity rhythm. *ionotropic receptor 25a* is required for temperature entrainment of the fly's circadian clock, independent of light [23], while *nocte* integrates both cues [24^{*}]. In mice diel changes in tissue oxygen levels can further alter the expression rhythms of circadian clock genes via *hypoxia-inducible factor 1 α* [25]. Interestingly, oxygen is also used as an entrainment cue in a sea-anemone-symbiont relationship, where the endosymbiotic algae *Symbiodinium* sets the 24 hours behavioral rhythm of its host *Aiptasia diaphana*. Without symbionts, the sea-anemone exhibits a circatidal rhythm [26^{*}]. Such effects on rhythmicity caused by symbionts (or parasites) even extend to humans. The circadian rhythms of human gut bacteria and their metabolites can entrain the liver circadian oscillator and in extend affect human health. In turn, the gut microbiome shows direct responses to the host's eating habits and circadian rhythms, as well as disruption thereof (reviewed in Ref. [27]). These examples provide evidence that rhythmic cues are not limited to the external environment, but also extend to the internal, physiological level. Thus, the principles of ecological interactions may also help to better understand rhythmic aspects of human physiology and health.

All these different biotic and abiotic environmental cues act together in the natural habitat, and it is hence not too surprising that artificial experimental conditions can cause different behavioral rhythms than the environmental cycles in the natural habitat. For example, while *Drosophila melanogaster* has a crepuscular activity pattern in laboratory recordings, experiments under natural light conditions revealed an additional activity peak in the afternoon [28,29^{**}]. Similar observations exist for mice and hamsters [30,31], highlighting the importance of more naturalistic studies.

Seasonal cycles

For seasonal behaviors and life cycles like hibernations/diapause, migrations or reproduction (Table 1), the most relevant environmental terrestrial cues are likely light, temperature and food availability (Table 2). Photoperiod (daylength) can be measured by the co-occurrence timing of light signals relative to circadian time, resulting in long-day or short-day responses [32]. For sheep and mice melatonin, whose expression is regulated by circadian time and directly by light, serves as a molecular readout for daylength. Melatonin controls peak levels of the transcription

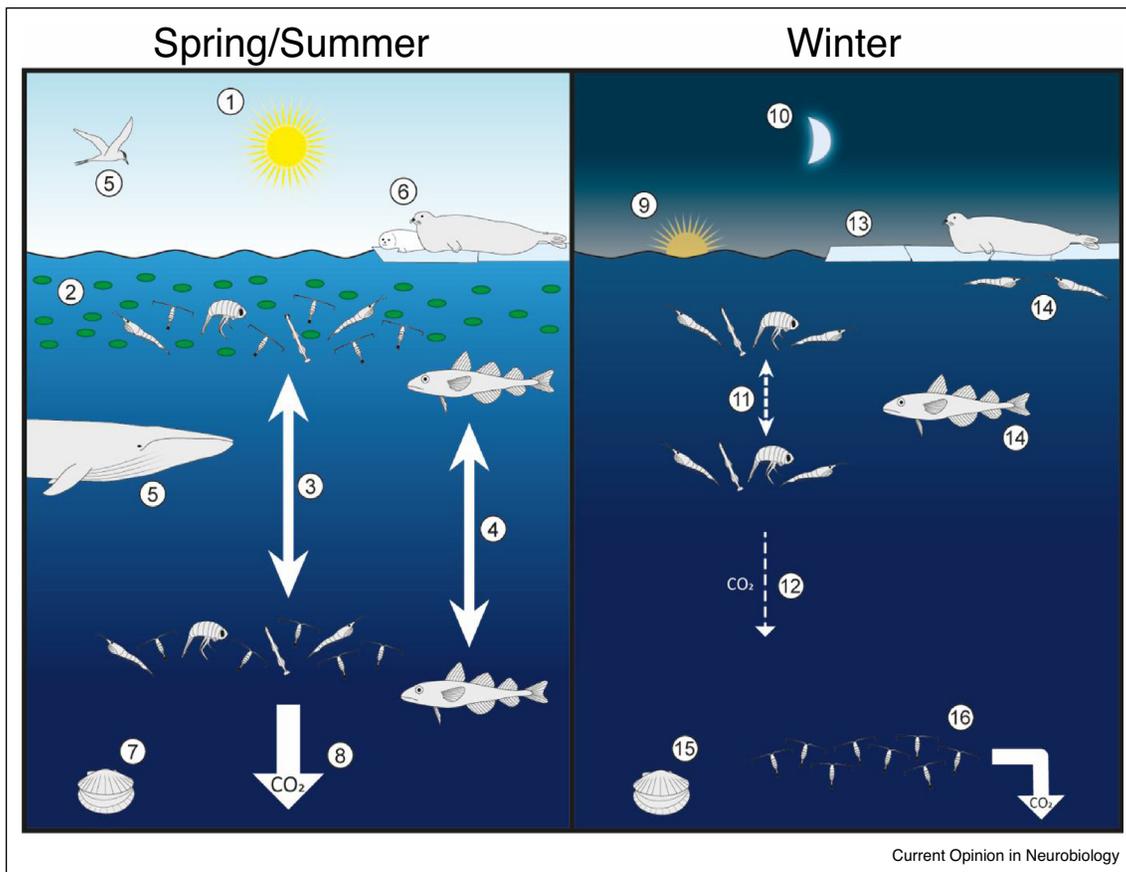
factor *eya3* by two means. It synchronizes its height phase to about 12 hours after night onset, causing a peak in the late night/early morning, depending on daylength. In addition, melatonin also suppresses *eya3* expression. Under long photoperiods melatonin is absent at the time *eya3* peaks. The resulting increased EYA3 levels together with the circadian transcription factor TEF result in an upregulation of TSH and subsequently hypothalamic Deiodinase 2. This enzyme converts the inactive form of thyroid hormone (T4) to the active version (T3), which finally stimulates gonadotropins and the downstream physiological and behavioral responses (reviewed in Refs. [7^{*},33]). This switch between responses seems to be rather binary causing a sharp switch in behavior [34] at the critical photoperiod [35]. The critical photoperiod itself can change depending on the environmental temperature [36,37], via an unknown mechanism. Many species show a latitudinal gradient in their critical photoperiods corresponding to the latitudinal changes in day length [10,38^{*}]. In insects and birds this is possibly connected to differences in allele frequencies of circadian clock and neuropeptide genes [39–41].

Again, natural light conditions are important. *D. melanogaster* displays more pronounced photoperiodic responses under natural lights with gradual changes compared to a rectangular lights on/off regime [42]. These external cues can either act directly or by entraining an endogenous circannual oscillator [1,7^{*},43–48], the latter being particularly important if the physiological and behavioral responses need preparation time and/or sensory stimuli might not be perceived (e.g. awakening from diapause). The mechanisms of circannual clocks are still poorly understood, but cyclic changes in chromatin condensation [7^{*}], as well as histogenesis [49] are being discussed.

While diel and seasonal behavioral rhythms are just as common in aquatic habitats as they are on land [50], they are less studied. Medakafish has started to emerge as functionally well-amenable model to study the role of seasons. Animals kept under different seasonal conditions exhibit multifold changes in their retinal opsins and phototransduction repertoire, modulating visual perception and subsequent behavior [51]. Interestingly, also humans exhibit such seasonal changes in color perception, albeit the underlying mechanisms are still unclear [52].

An ecologically crucially relevant emerging marine model is the copepod *Calanus finmarchicus* (Figure 1, Table 1), which reproduces and feeds in surface waters in spring/summer and overwinters in deeper water layers. The initiation and termination of the overwintering phase (referred to as diapause) have been studied intensively, but the controlling factors are still unclear [53^{**}]. Seasonal copepod gene expression, physiology and circadian clock rhythmicity suggest that initiation could be controlled by internal lipid levels and a critical photoperiod potentially affected by temperature and food availability. In contrast,

Figure 1



Environmental and biological rhythms. The figure illustrates different diel and seasonal rhythms on the example of a polar pelagic ecosystem. Spring/Summer: (1) Clear day/night cycle and midnight sun in summer, (2) Phytoplankton bloom triggered by light after ice breakup. (3) Pronounced zooplankton diel vertical migration (DVM) → desynchronized during midnight sun. (4) Larger predators follow zooplankton migration. (5) Seasonal migrators benefit from food availability. (6) Seal reproduction anticipates ice breakup and productive season. (7) Diel activity rhythms of benthic species. (8) High productivity and vertical migrations contribute to carbon export. Winter: (9) Weak day/night cycle or permanent night. (10) Moonlight can directly affect DVM. (11) DVM weaker but still existent. (12) Minimal carbon export. (13) Seasonal sea ice cover → delayed relative to photoperiod. (14) Seasonal changes in habitat usage. (15) Benthic diel rhythms can persist in polar night. (16) Seasonal copepod diapause at depth → metabolization of energy storages contributes to carbon export. References: [54,70*,71*,135–141].

a circannual clock could trigger the copepod's emergence from diapause [54].

Lunar, lunidian and tidal cycles

Moon-related behavioral cycles with a circatidal period (~12.4 hours), circalunidian (~24.8 hours) or a circa(semi) lunar period (~14.8/~29.5 days) are especially well-documented in the marine environment, but have also been observed in terrestrial and limnic habitats [55,56,57*]. Most intertidal species display tidal rhythms in activity and foraging and for several species these rhythms also persist under constant conditions, implying an endogenous oscillator [2,3,58,59]. So far, the mechanisms entraining and maintaining circatidal rhythmicity are mostly unclear. In the horseshoe crab *Limulus polyphemus* water pressure is the major circatidal entrainment cue,

while light and temperature are of minor importance (Table 2) [60]. The circatidal activity rhythm of the isopod *Eurydice pulchra* can be entrained by mechanical stimulation, and a knock-down of *period* and circadian clock disruptions by LL did not abolish it, while a CK1d/e inhibitor led to period lengthening of both circadian and circatidal periods (Table 1) [9]. This result and other behavioral studies suggest that while circadian and circatidal clocks can be separated, common molecular denominators exists [2,3,9,61–63].

Circa(semi)lunar rhythms occur in various species from corals to vertebrates and typically time reproductive behavior and physiology. The moon determines the days when gametes are ready for release and particular mating behaviors will be exerted [64]. Often, this timing is interlinked with circalunidian or circadian timing, that is, the exact

mating and spawning happens only at specific hours that themselves shift with the moon phase [65,66]. For example, in the intertidal midge *Clunio marinus* both circalunar and circadian clocks, genetically adapted to match the local tidal regime, determine the exact timing of eclosion and subsequent mating [67]. In the bristle worm *Platynereis dumerilii* the circalunar clock and light modulate circadian clock gene expression and locomotor activity, while a chemical disruption of *P. dumerilii*'s circadian clock did not disrupt the circalunar spawning rhythm. This implies that circadian clock oscillations are not required for circalunar core clock functions [8,68,69].

There are several examples for circalunar behavioral rhythms (Table 1) that are so impressive that they even serve as touristic advertisement. The mass migrations of the red crabs on the Christmas islands, the Palolo worms' nuptial dances close to Samoa, the ostracods' bioluminescent mating signals close to Belize and the mass spawning events of corals at the Great Barrier Reef unequivocally demonstrate the influence of lunar (and connected solar) timing on biology and ecology (Table 1). Moonlight can further directly modulate zooplankton diel vertical migrations (DVM) in polar habitats (Figure 1) [70*], while DVM itself is at least partially controlled by a circadian clock (Table 1) [71*,72].

Probably the so far best-studied example for the interaction of different rhythms are the annual mass spawning events of corals [73–75]. Multiple detailed transcriptomic studies have started to identify potential molecular players in the coral *Acropora millepora* [75–77]. However, functional studies will be required to disentangle the roles of individual genes in the interacting rhythms. In the jellyfish *Clytia hemisphaerica* disruption of *Opn9* implicates this photoreceptor as trigger for gamete release [78] and a similar mechanism may help to coordinate coral spawning.

Especially the latter examples illustrate the complexity of timing systems in the marine environment, the environment, in which animal life with its rhythms originally evolved [79,80]. It is hence likely that their better understanding will also help to unravel the foundations on which human rhythmicity is built.

Human rhythms of behavior

The fact that circadian timing is very important for human behavior and physiology and that its disruptions results in severe health consequences is well-established and covered in detail elsewhere, including clinically relevant recommendations [81–83], impacts on fear behavior, food consumption, cognition, sleep and the interconnection to hormonal control and possible genetically anchored inter-individual variables [84,85].

The roles of other rhythms and possible oscillators are less clear. Strong evidence for human behavioral seasonality

comes from mood disorders, for example, seasonal affective disorder (SAD) [86] and the increase of suicides during spring times [87,88]. However, the extent of human seasonality and the mechanisms behind it are unclear. Lunar-related behavioral rhythms in humans are still subject to intensive discussions. This is likely because reported instances are sporadic and sometimes contradictory, such as in sleep studies where smaller studies showed statistically significant lunar-phase differences whereas a study that pooled data over a large geographic range did not [89–91]. The sleep studies were performed under laboratory conditions, that is, in the absence of moonlight. This implies that any effect should be caused by an endogenous oscillator with a circalunar period, ~29.5 days. The menstrual cycle of human females fits this description and it is clear that it is connected to a range of hormonal changes, influencing mood and behavior. Evidence for monthly hormonal changes have also been described for men, albeit the results should be treated with caution due to the small study group size [92]. If such endogenous monthly hormonal (i.e. circalunar) cycles can be locally synchronized across a population by environmental cues, then its effects — including behavioral alterations — will be phase-synchronized with the natural moon phases. This could explain synchronizations across smaller groups. Alternatively, the moon can still function as a non-photic weak zeitgeber and depending on the signal/noise ratio this might be picked up in some studied cohorts.

Interestingly, recent work on two small-scale African populations in their local environments showed that sleep/activity differences correlated with the lunar cycle in hunter-gatherers, but not in rural agriculturists [93].

Another heavily debated field is the connection between birth rate and lunar cycle. Studies performed during the 1940ies–1960ies repeatedly observed statistically significant correlations, while they vanished from the studies performed later on and the reasons are debated (reviewed in Ref. [64]).

Finally, bipolar mood cycles were found to oscillate in synchrony with three types of lunar cycles: the 14.8-day spring–neap cycle, the 13.7-day declination cycle and the 206-day cycle of perigee-syzygies. Additional analyses of body temperature cycles suggest that this could be explained by a periodic entrainment of the circadian pacemaker to the slightly longer circalunidian (24.8 hours) cycle of the moon and by this resulting in pacemaker's phase-relationship to sleep that triggers switches from depression to mania [94**]. Overall, the possibility of lunar rhythms impacting on human behavior should not be too readily dismissed. Humans are just another species of animals after all. Future work on animal models with clear circalunar rhythmicity will allow to uncover molecular mechanisms which can subsequently be tested in humans.

Times of environmental change

Rhythms and their underlying clocks likely allow animals to be optimally prepared for the environmental conditions of their ecological niches. However, changing environmental conditions will force species to shift their habitats and temporal niches. Already in the past, adaptation to global climate change and radiation required the adaptation to new ecological niches. A prominent example for this is the radiation of nocturnal mammals to all timing niches after the dinosaur extinction, suggesting that a certain level of flexibility in the underlying clock systems is advantageous [95]. Nevertheless, the adaptive capacities of behavioral rhythmicity and the corresponding oscillator systems have so far received little attention.

In the future, behavioral rhythms of animals will be affected by several major developments: Environmental changes due to anthropogenic CO₂ emissions affect ecosystems on a global scale. Human infrastructure and the associated light pollution disrupt behavior and physiology of animals and humans. Another biologically highly relevant effect is the increase of environmental temperatures. Species try to stay within their optimal temperature range to avoid heat/cold stress, meaning that increasing temperatures cause shifts to higher (colder) latitudes, as observed in various terrestrial and marine species [96–99]. These shifts to higher latitudes are accompanied by more pronounced seasonal changes in photoperiod and ultimately phases of permanent darkness or sunlight in polar regions. Photoperiod is unaffected by climate change and these extreme light conditions could inhibit latitudinal distribution shifts leading to fitness loss due to suboptimal temperatures [100]. Alternatively, the circadian clock systems, while itself less affected by temperature changes due to its intrinsic temperature compensation mechanisms, may have to work under photoperiods that exceed their entrainment range, resulting in circadian arrhythmicity. While the originally tropic, strongly rhythmic *D. melanogaster* loses its rhythmicity under extreme photoperiods, high latitude *Drosophila* species already exhibit weaker overall circadian rhythmicity and higher plasticity [101**].

Especially for aquatic habitats in high latitudes, ecological timing mismatches in food-chains are being reported, for example, while seasonal phytoplankton blooms tend to occur earlier, the behavioral and physiological rhythms of higher tropic levels like zooplankton or predatory fish change less (Figure 1) [102–105].

However, disruptive effects by increasing temperature are likely not be restricted to animals in higher latitudes. Possibly connected to higher temperatures, behavioral timing alteration have been reported for large populations of red sea corals, which start to exhibit a loss of spawning synchrony [106].

Nowadays, natural darkness is virtually absent in areas inhabited by humans. Artificial light at night (ALAN)

delays the human circadian cycle and shortens rest times [107], likely contributing to psychological disorders [108], while also a variety of animal rhythms are affected [109,110]. Bird melatonin levels are reduced by ALAN, affecting diel activity patterns and seasonal reproduction times [111]. A recent study provides compelling reasoning that the dramatic decline of the European hamster is largely due to timing problems of its circannual reproductive cycle, part of this problem might be caused by light pollution [112**]. In aquatic habitats nocturnal light reduced the magnitude of DVM in the model crustacean *Daphnia* [113], while similar effects were observed in an Arctic zooplankton community during polar night [114].

Further and largely unexplored impacts on animal behavioral rhythms can arise from chemicals (e.g. pesticides, sewage or pharmaceutical drugs). For example, the ingestion of insecticide-treated seeds delays bird migrations. This likely reduces their fitness due to a delayed arrival at their destination [115].

As human impact on earth will likely not decrease in the future, a detailed understanding of mechanisms controlling behavioral rhythms will be essential to make predictions about future ecosystem changes, as well as to propose measures to minimize anthropogenic effects.

Conclusions

Here we aim to emphasize the omnipresence of rhythms in animal behaviors and how little we know about them, beyond daily timing mechanisms in mouse and *Drosophila*. Yet, understanding different clocks and rhythms other than circadian, the integration of different timing regimes in one individual and in different species adapted to different ecological niches is crucial to understand how networks of species might respond to changes in their current ecological niches due to climate change and artificial light at night. Understanding the interplay of different rhythms is likely also important for a better understanding of human behavior and behavioral disorders, for example, sleep and mood. We also put a specific focus on the aquatic habitats due to the complexity of this environment and the interacting behavioral rhythms and clock system resulting from it. In summary, this is a strong pledge for dedicated studies on the chronobiological mechanisms underlying behavior in animals from diverse habitats, including land and sea.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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