

Current Opinion in Neurobiology
Rhythms of Behavior: Are the times changin'?
--Manuscript Draft--

Manuscript Number:	CONEUR-D-19-00014R1
Full Title:	Rhythms of Behavior: Are the times changin'?
Article Type:	60 Neurobiology of Behavior (2020)

1 Rhythms of Behavior: Are the times changin’?

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6

7 Abstract

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

17

18 Introduction

19 While few have put it into words just as poetically as Bob Dylan, it is clear that life is full of changes,
20 many of which are rhythmic. Environmental cycles impact humans in various ways, but are also central
21 in shaping the biology and interactions of countless other species. In fact, the list of rhythmic behaviors
22 is seemingly endless ([1–4], Table 1). Abiotic cycles are driven by the celestial movements of earth and
23 moon, as well as the inclination of the earth axis relative to the sun. The earth’s rotation creates the
24 day/night cycle, while its revolution around the sun, together with the inclination of the earth’s axis,
25 results in annual cycles. Our planet’s rotation and inclination also shape the global wind and water
26 current system – both with their own rhythms – partially also depending on local environmental and
27 global physical interactions. Not all climate rhythms (e.g. El Niño) are fully understood. The revolution
28 of the moon around earth and its relative position to the sun further create light, gravitational and

29 magnetic cycles of 27.3 days (sidereal period), 29.5 days (synodic period) and subsets thereof, as well
30 as lunidian and tidal cycles of 24.8 and 12.4 hours, respectively [2,3]. Other rhythms, such as the about
31 eleven-year cycle of solar activity exist and others, less prominent to humans, might not have even been
32 uncovered.

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

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

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

56 physical forcing (e.g. due to waves) are mostly irrelevant on land, but can be highly cyclic in aquatic
57 habitats like the intertidal zone.

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

60 **The control by environmental cues**

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

66 The environmental cues evoking rhythmicity and entraining clock systems are diverse (Table 2) and can
67 send conflicting information (e.g. light vs. temperature). The same type of cue informs about multiple
68 rhythms (e.g. light provides diel, monthly & seasonal information), while also itself being subject to
69 short-term non-cyclic perturbances (e.g. cloud cover). How do animals sense these stimuli, prioritize the
70 input, filter for signal/noise and adjust their behaviors accordingly? Below we somewhat artificially split
71 the sensory cues by types of rhythm for better readability, but it should be clear that sensory input for
72 different rhythms occurs at the same time.

73 **Daily cycles**

74 With a focus on land animals as experimental models, light and temperature are typically considered the
75 most important cues for the entrainment of diel behavioral rhythms and circadian clocks. Light is a
76 complex cue, as different wavelengths can have different effects on animal rhythms [11,12]. Blue light
77 is most prominently referred to for circadian clock entrainment, likely due to the large proportion of
78 research focusing on mammalian entrainment mechanisms. In mammals, light information is transmitted
79 via melanopsin-positive retinal ganglion cells to the central brain circadian pacemaker (i.e. the mammal
80 suprachiasmatic nucleus, SCN) [13–15], but also directly modulates behavior [16]. However, it has
81 become increasingly clear that light information provided by rods and cones is also channeled to the
82 SCN for circadian clock entrainment [13,17], and possibly other brain areas. In insects blue light leads
83 to the activation of a light-responsive cryptochrome (cry1, also known as L-cry or *Drosophila*-type cry),
84 which affects the stability of Timeless and by this re-sets the phase of the circadian clock [18–20]. In

85 addition to cry1, light also impacts via several Opsins expressed in the fly's eyes and ocelli, likely
86 improving the adjustment of daily circadian rhythms to different seasons [21,22].
87 In *Drosophila* light and temperature jointly affect the activity rhythm. *ionotropic receptor 25a* is
88 required for temperature entrainment of the fly's circadian clock, independent of light [23], while *nocte*
89 integrates both cues [24]. In mice diel changes in tissue oxygen levels can further alter the expression
90 rhythms of circadian clock genes via *hypoxia-inducible factor 1a* [25]. Interestingly, oxygen is also used
91 as an entrainment cue in a sea-anemone-symbiont relationship, where the endosymbiotic algae
92 *Symbiodinium* sets the 24hrs behavioral rhythm of its host *Aiptasia diaphana*. Without symbionts, the
93 sea-anemone exhibits a circatidal rhythm [26]. Such effects on rhythmicity caused by symbionts (or
94 parasites) even extend to humans. The circadian rhythms of human gut bacteria and their metabolites
95 can entrain the liver circadian oscillator and in extend affect human health. In turn, the gut microbiome
96 shows direct responses to the host's eating habits and circadian rhythms, as well as disruption thereof
97 (reviewed in [27]). These examples provide evidence that rhythmic cues are not limited to the external
98 environment, but also extend to the internal, physiological level. Thus, the principles of ecological
99 interactions may also help to better understand rhythmic aspects of human physiology and health.

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

106 Seasonal cycles

107 For seasonal behaviors and life cycles like hibernations/diapause, migrations or reproduction (Table 1),
108 the most relevant environmental terrestrial cues are likely light, temperature and food availability (Table
109 2). Photoperiod (daylength) can be measured by the co-incidence timing of light signals relative to
110 circadian time, resulting in long-day or short-day responses [32]. For sheep and mice melatonin, whose
111 expression is regulated by circadian time and directly by light, serves as a molecular readout for
112 daylength. Melatonin controls peak levels of the transcription factor *eya3* by two means. It synchronizes
113 its height phase to about 12hrs after night onset, causing a peak in the late night/early morning,

114 depending on daylength. In addition, melatonin also suppresses *eya3* expression. Under long
115 photoperiods melatonin is absent at the time *eya3* peaks. The resulting increased EYA3 levels together
116 with the circadian transcription factor TEF result in an upregulation of TSH and subsequently
117 hypothalamic Deiodinase 2. This enzyme converts the inactive form of thyroid hormone (T4) to the
118 active version (T3), which finally stimulates gonadotropins and the downstream physiological and
119 behavioral responses (reviewed in [7,33]). This switch between responses seems to be rather binary
120 causing a sharp switch in behavior [34] at the critical photoperiod [35]. The critical photoperiod itself
121 can change depending on the environmental temperature [36,37], via an unknown mechanism. Many
122 species show a latitudinal gradient in their critical photoperiods corresponding to the latitudinal changes
123 in day length [10,38]. In insects and birds this is possibly connected to differences in allele frequencies
124 of circadian clock and neuropeptide genes [39–41].

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

132 While diel and seasonal behavioral rhythms are just as common in aquatic habitats as they are on land
133 [50], they are less studied. Medakafish has started to emerge as functionally well-amenable model to
134 study the role of seasons. Animals kept under different seasonal conditions exhibit multifold changes in
135 their retinal opsins and phototransduction repertoire, modulating visual perception and subsequent
136 behavior [51]. Interestingly, also humans exhibit such seasonal changes in color perception, albeit the
137 underlying mechanisms are still unclear [52].

138 An ecologically crucially relevant emerging marine model is the copepod *Calanus finmarchicus* (Figure
139 1, Table 1), which reproduces and feeds in surface waters in spring/summer and overwinters in deeper
140 water layers. The initiation and termination of the overwintering phase (referred to as diapause) have
141 been studied intensively, but the controlling factors are still unclear [53]. Seasonal copepod gene

142 expression, physiology and circadian clock rhythmicity suggest that initiation could be controlled by
143 internal lipid levels and a critical photoperiod potentially affected by temperature and food availability.
144 In contrast, a circannual clock could trigger the copepod's emergence from diapause [54].

145 Lunar, lunidian and tidal cycles

146 Moon-related behavioral cycles with a circatidal period (~12.4 hours), circalunidian (~24.8h) or a
147 circa(semi)lunar period (~14.8/~29.5 days) are especially well-documented in the marine environment,
148 but have also been observed in terrestrial and limnic habitats [55–57]. Most intertidal species display
149 tidal rhythms in activity and foraging and for several species these rhythms also persist under constant
150 conditions, implying an endogenous oscillator [2,3,58,59]. So far, the mechanisms entraining and
151 maintaining circatidal rhythmicity are mostly unclear. In the horseshoe crab *Limulus polyphemus* water
152 pressure is the major circatidal entrainment cue, while light and temperature are of minor importance
153 (Table 2) [60]. The circatidal activity rhythm of the isopod *Eurydice pulchra* can be entrained by
154 mechanical stimulation, and a knock-down of *period* and circadian clock disruptions by LL did not
155 abolish it, while a CK1d/e inhibitor led to period lengthening of both circadian and circatidal periods
156 (Table 1) [9]. This result and other behavioral studies suggest that while circadian and circatidal clocks
157 can be separated, common molecular denominators exists [2,3,9,61–63].

158 Circa(semi)lunar rhythms occur in various species from corals to vertebrates and typically time
159 reproductive behavior and physiology. The moon determines the days when gametes are ready for
160 release and particular mating behaviors will be exerted [64]. Often, this timing is interlinked with
161 circalunidian or circadian timing, i.e. the exact mating and spawning happens only at specific hours
162 that themselves shift with the moon phase [65,66]. For example, in the intertidal midge *Clunio marinus*
163 both circalunar and circadian clocks, genetically adapted to match the local tidal regime, determine the
164 exact timing of eclosion and subsequent mating [67]. In the bristle worm *Platynereis dumerilii* the
165 circalunar clock and light modulate circadian clock gene expression and locomotor activity, while a
166 chemical disruption of *P. dumerilii*'s circadian clock did not disrupt the circalunar spawning rhythm.
167 This implies that circadian clock oscillations are not required for circalunar core clock functions
168 [8,68,69].

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

176 Probably the so far best-studied example for the interaction of different rhythms are the annual mass
177 spawning events of corals [73–75]. Multiple detailed transcriptomic studies have started to identify
178 potential molecular players in the coral *Acropora millepora* [75–77]. However, functional studies will
179 be required to disentangle the roles of individual genes in the interacting rhythms. In the jellyfish *Clytia*
180 *hemisphaerica* disruption of *Opsin9* implicates this photoreceptor as trigger for gamete release [78] and
181 a similar mechanism may help to coordinate coral spawning.

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

185 Human rhythms of behavior

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

191 The roles of other rhythms and possible oscillators are less clear. Strong evidence for human behavioral
192 seasonality comes from mood disorders, e.g. seasonal affective disorder (SAD) [86] and the increase of
193 suicides during spring times [87,88]. However, the extent of human seasonality and the mechanisms
194 behind it are unclear. Lunar-related behavioral rhythms in humans are still subject to intensive
195 discussions. This is likely because reported instances are sporadic and sometimes contradictory, such as
196 in sleep studies where smaller studies showed statistically significant lunar-phase differences whereas a

197 study that pooled data over a large geographic range did not [89–91]. The sleep studies were performed
198 under laboratory conditions, i.e. in the absence of moonlight. This implies that any effect should be
199 caused by an endogenous oscillator with a circalunar period, ~29.5 days. The menstrual cycle of human
200 females fits this description and it is clear that it is connected to a range of hormonal changes, influencing
201 mood and behavior. Evidence for monthly hormonal changes have also been described for men, albeit
202 the results should be treated with caution due to the small study group size [92]. If such endogenous
203 monthly hormonal (i.e. circalunar) cycles can be locally synchronized across a population by
204 environmental cues, then its effects – including behavioral alterations – will be phase-synchronized with
205 the natural moon phases. This could explain synchronizations across smaller groups. Alternatively, the
206 moon can still function as a non-photic weak zeitgeber and depending on the signal/noise ratio this might
207 be picked up in some studied cohorts.

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

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

214 Finally, bipolar mood cycles were found to oscillate in synchrony with three types of lunar cycles: the
215 14.8-day spring–neap cycle, the 13.7-day declination cycle and the 206-day cycle of perigee-syzygies.

216 Additional analyses of body temperature cycles suggest that this could be explained by a periodic
217 entrainment of the circadian pacemaker to the slightly longer circalunidian (24.8hr) cycle of the moon
218 and by this resulting in pacemaker's phase-relationship to sleep that triggers switches from depression
219 to mania [94]. Overall, the possibility of lunar rhythms impacting on human behavior should not be too
220 readily dismissed. Humans are just another species of animals after all. Future work on animal models
221 with clear circalunar rhythmicity will allow to uncover molecular mechanisms which can subsequently
222 be tested in humans.

223 Times of environmental change

224 Rhythms and their underlying clocks likely allow animals to be optimally prepared for the environmental
225 conditions of their ecological niches. However, changing environmental conditions will force species to
226 shift their habitats and temporal niches. Already in the past, adaptation to global climate change and
227 radiation required the adaptation to new ecological niches. A prominent example for this is the radiation
228 of nocturnal mammals to all timing niches after the dinosaur extinction, suggesting that a certain level
229 of flexibility in the underlying clock systems is advantageous [95]. Nevertheless, the adaptive capacities
230 of behavioral rhythmicity and the corresponding oscillator systems have so far received little attention.
231 In the future, behavioral rhythms of animals will be affected by several major developments:
232 Environmental changes due to anthropogenic CO₂ emissions affect ecosystems on a global scale. Human
233 infrastructure and the associated light pollution disrupt behavior and physiology of animals and humans.
234 Another biologically highly relevant effect is the increase of environmental temperatures. Species try to
235 stay within their optimal temperature range to avoid heat/cold stress, meaning that increasing
236 temperatures cause shifts to higher (colder) latitudes, as observed in various terrestrial and marine
237 species [96–99]. These shifts to higher latitudes are accompanied by more pronounced seasonal changes
238 in photoperiod and ultimately phases of permanent darkness or sunlight in polar regions. Photoperiod is
239 unaffected by climate change and these extreme light conditions could inhibit latitudinal distribution
240 shifts leading to fitness loss due to suboptimal temperatures [100]. Alternatively, the circadian clock
241 systems, while itself less affected by temperature changes due to its intrinsic temperature compensation
242 mechanisms, may have to work under photoperiods that exceed their entrainment range, resulting in
243 circadian arrhythmicity. While the originally tropic, strongly rhythmic *Drosophila melanogaster* loses
244 its rhythmicity under extreme photoperiods, high latitude *Drosophila* species already exhibit weaker
245 overall circadian rhythmicity and higher plasticity [101].
246 Especially for aquatic habitats in high latitudes, ecological timing mismatches in food-chains are being
247 reported, e.g. while seasonal phytoplankton blooms tend to occur earlier, the behavioral and
248 physiological rhythms of higher trophic levels like zooplankton or predatory fish change less (Figure 1)
249 [102–105].

250 However, disruptive effects by increasing temperature are likely not be restricted to animals in higher
251 latitudes. Possibly connected to higher temperatures, behavioral timing alteration have been reported for
252 large populations of red sea corals, which start to exhibit a loss of spawning synchrony [106].
253 Nowadays, natural darkness is virtually absent in areas inhabited by humans. Artificial light at night
254 (ALAN) delays the human circadian cycle and shortens rest times [107], likely contributing to
255 psychological disorders [108], while also a variety of animal rhythms are affected [109,110]. Bird
256 melatonin levels are reduced by ALAN, affecting diel activity patterns and seasonal reproduction times
257 [111]. A recent study provides compelling reasoning that the dramatic decline of the European hamster
258 is largely due to timing problems of its circannual reproductive cycle, part of this problem might be
259 caused by light pollution [112]. In aquatic habitats nocturnal light reduced the magnitude of DVM in
260 the model crustacean *Daphnia* [113], while similar effects were observed in an Arctic zooplankton
261 community during polar night [114].
262 Further and largely unexplored impacts on animal behavioral rhythms can arise from chemicals (e.g.
263 pesticides, sewage or pharmaceutical drugs). For example, the ingestion of insecticide-treated seeds
264 delays bird migrations. This likely reduces their fitness due to a delayed arrival at their destination [115].
265 As human impact on earth will likely not decrease in the future, a detailed understanding of mechanisms
266 controlling behavioral rhythms will be essential to make predictions about future ecosystem changes, as
267 well as to propose measures to minimize anthropogenic effects.

268 **Conclusions**

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

278 the chronobiological mechanisms underlying behavior in animals from diverse habitats, including land
279 and sea.

280 Acknowledgement

281 We thank the members of the Tessmar-Raible and Raible groups for discussions.

282 K.T-R. received funding for this research from the European Research Council under the European
283 Community's Seventh Framework Programme (FP7/2007–2013) ERC Grant Agreement 337011, the
284 research platform 'Rhythms of Life' of the University of Vienna, the Austrian Science Fund (FWF,
285 <http://www.fwf.ac.at/en/>) research grant #P28970.

286 None of the funding bodies was involved in the design or writing of the manuscript.

287 Both authors declare no conflict of interest.

288

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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	?	?	
	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 europaeus</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
	Diel	sleep/wake cycle (e.g. <i>Homo sapiens</i>) ^[85]	Light, circadian clock	Regeneration, predator avoidance	Temporal niche creation	Light pollution
		Locomotion (e.g. horseshoe crab <i>Limulus polyphemus</i>) ^[60]	Light, circadian clock	Mating coordination	Food chain	Light pollution
	Diel, bimodal?	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?	?	?	

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

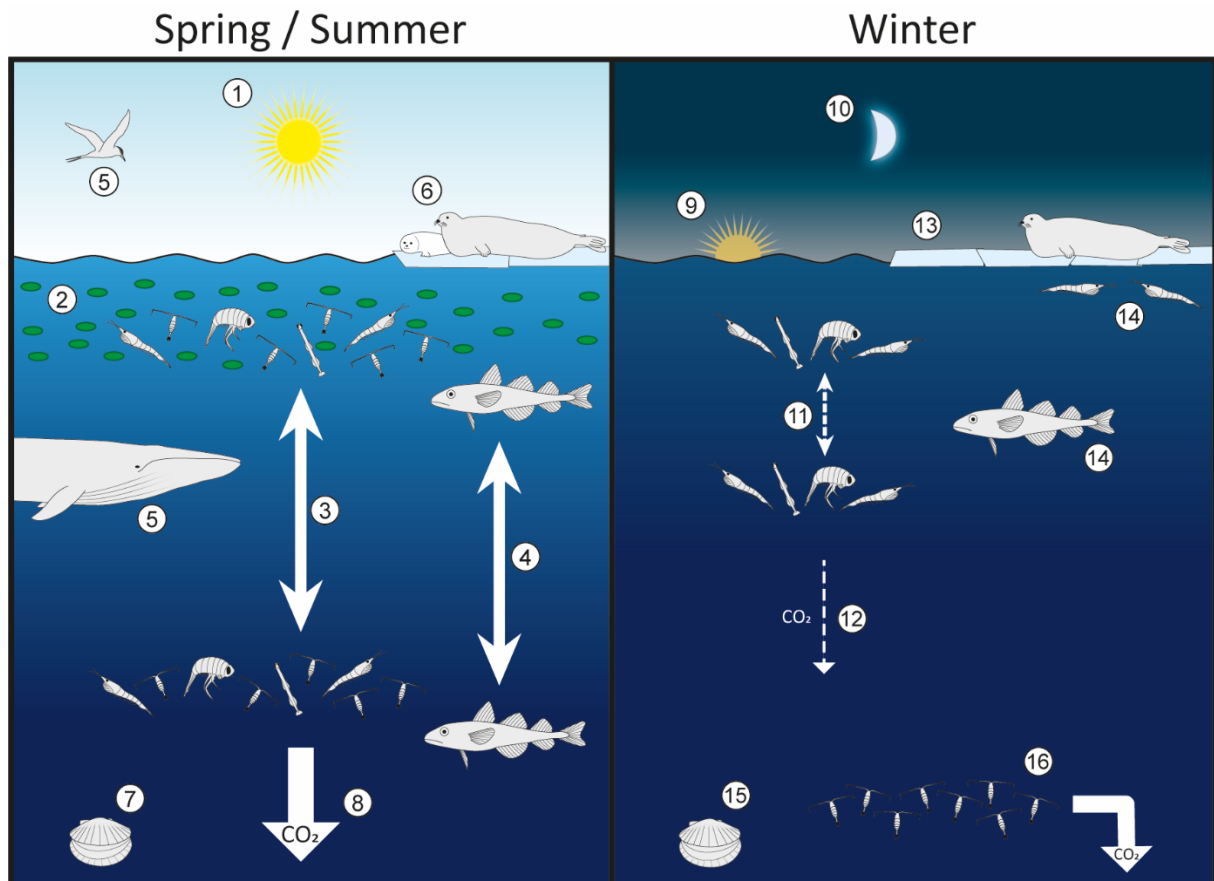


Figure 1: Environmental and biological rhythms. The figure illustrates different diel and seasonal rhythms on the example of a polar pelagic ecosystem. Spring/Summer: (1) Clear day/night cycle and midnight sun in summer, (2) Phytoplankton bloom triggered by light after ice breakup. (3) Pronounced zooplankton 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: [54,70,71,135–140]

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