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Rhythms and Clocks in Marine Organisms

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Abstract

The regular movements of waves and tides are obvious representations of the oceans' rhythmicity. But the rhythms of marine life span across ecological niches and timescales, including short (in the range of hours) and long (in the range of days and months) periods. These rhythms regulate the physiology and behavior of individuals, as well as their interactions with each other and with the environment. This review highlights examples of rhythmicity in marine animals and algae that represent important groups of marine life across different habitats. The examples cover ecologically highly relevant species and a growing number of laboratory model systems that are used to disentangle key mechanistic principles. The review introduces fundamental concepts of chronobiology, such as the distinction between rhythmic and endogenous oscillator–driven processes. It also addresses the relevance of studying diverse rhythms and oscillators, as well as their interconnection, for making better predictions of how species will respond to environmental perturbations, including climate change. As the review aims to address

scientists from the diverse fields of marine biology, ecology, and molecular chronobiology, all of which have their own scientific terms, we provide definitions of key terms throughout the article.

Biological rhythm: cyclic changes in an organism's biology, ranging from behavior to rhythms in physiology and gene expression; these changes may be evoked by external cues or controlled by an endogenous oscillator

Environmental cycle: cyclic and predictable changes in the environmental conditions affecting an organism; cycles can be abiotic (e.g., light and temperature) or related to biological rhythms (e.g., predation risk and food availability)

Endogenous oscillator: an internal timing mechanism that is self-sustained but can be entrained by environmental cues

Entrainment: phase adjustment (synchronization) of an endogenous oscillator through environmental cues

Transcriptional/translational feedback loop (TTFL): autoregulation of genes via interactions of the translated proteins with other genes or proteins

1. CYCLES OF THE SUN AND MOON CAUSE A MULTITUDE OF BIOLOGICAL RHYTHMS

"The Blue Marble" is the title of a series of images produced during various NASA missions, starting with the Apollo 17 mission in 1972. The view of Earth from space (**Figure 1*a***) not only prominently shows that marine environments dominate Earth but also provides a reminder that, as part of the solar system, our planet is exposed to regular astronomical and geophysical cycles. The most relevant of these are the rhythmic impacts of the sun and moon, which shape physicochemical cycles that organisms have been exposed to since the dawn of life. Adaptations to these cycles have therefore likely been a fundamental aspect of survival. The relative positions of the sun, the moon, and Earth result in cycles with a complexity of different period lengths, ranging from tidal periods in the range of 12 h to diel and monthly periods and annual/seasonal cycles (**Figure 1*g*,*h***). Furthermore, these cycles differ depending on geographic location (**Figure 1*b*–*f***).

Life is commonly assumed to have originated in the marine environment, which is dominated by periodicity on these different timescales. A large number of species indeed make use of distinct cycles generated by the sun and moon to adjust their behavior and physiology, as detailed below. In chronobiology, the regular reoccurrence of a distinct physiological, behavioral, or cellular event is referred to as a biological rhythm. The periodicities of these rhythms approximate those of the underlying natural cycles (**Figure 1*g*,*h***). An important conceptual distinction concerns the question of how biological rhythms are elicited: On the one hand, biological rhythms can result from direct organismal responses to environmental cycles, but on the other hand, they are often caused by endogenously driven cellular/molecular oscillators, also referred to as inner clocks or calendars. Such endogenous oscillators, in turn, are synchronized to the respective environmental cycles by a process called entrainment. Endogenous oscillators allow organisms to anticipate predictable changes in their environment and therefore adjust their behavior and physiology before the actual changes occur. In many scenarios, this ability is likely advantageous for the fitness of an organism (Dodd et al. 2005, Johnson & Golden 1999, Krittika & Yadav 2020, Sanchez et al. 2011). The general mechanistic principle of such oscillators is positive–negative feedback loops, using different cell-biological processes.

Circadian clocks in land organisms are the only clocks currently understood in molecular mechanistic detail. Whereas animals, plants, and fungi all rely on transcriptional/translational feedback loops (TTFLs) for their central clock machinery, and phosphorylation/dephosphorylation cycles play critical roles, the exact molecular factors in these three groups are not homologous or show sequence similarities only to a limited extent (Brenna & Albrecht 2020, Narasimamurthy & Virshup 2021, Saini et al. 2019, Yan et al. 2021, Yildirim et al. 2022). Furthermore, non-TTFL-based ∼24-h oscillatory systems also exist. Even though these were originally uncovered in the marine alga *Acetabularia* (Sweeney et al. 1967), they are investigated mainly in terrestrial systems (Edgar et al. 2012), and knowledge of their molecular mechanisms remains scarce. The understanding of other oscillatory systems (e.g., circatidal, circalunar, and circannual) is less advanced, and particularly for the interplay between solar and lunar timing systems, marine systems have been helping significantly to advance our understanding (see below).

Whether a rhythm is endogenous needs to be experimentally determined. A hallmark of inner oscillators is a free-running biological rhythm that is maintained even under environmental

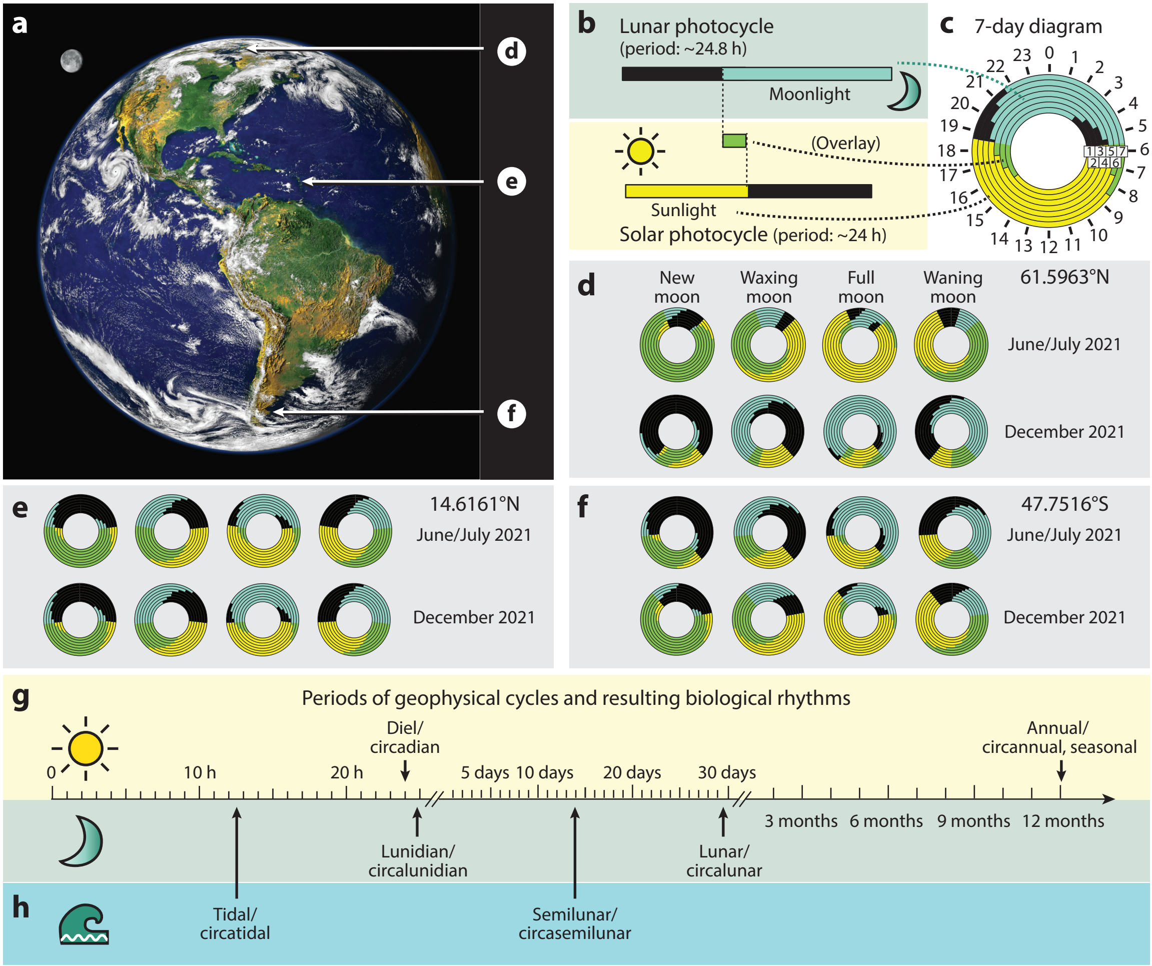

Figure 1

The emergence of complex rhythms from solar and lunar cycles in marine ecosystems. (*a*) Earth and the moon as seen from space. Arrows highlight coordinates used in panels *d–f*. (*b*,*c*) Summary of weekly solar and lunar photocycles, with the perimeter indicating hours of the day and concentric circles representing consecutive days (1–7). The daily cycles of solar light cause the well-known diel light cycle of ~24 h. The gradual shifts of moonrise and moonset cause an independent lunidian photocycle, with an average period of ~24.8 h. Twilight is not included. (*d–f*) Exemplary 7-day diagrams covering one month (new moon, waxing moon, full moon, and waning moon) around the summer (*top*) and winter (*bottom*) solstices at three distinct coastal locations at different latitudes, illustrating the complexity of superimposed solar and lunar light cycles. Twilight is not included. (*g*) Overview of the period lengths of major natural cycles and the associated (endogenous) biological rhythms generated by the solar (*top*) and lunar (*bottom*) photocycles. (*h*) Period lengths of major natural cycles and associated biological rhythms generated by the lunar gravitational cycles. Tidal cycles have a basic period length of half a lunar day (~12.4 h), while the mutual constellation of the sun, the moon, and Earth also causes a longer cycle (semilunar, ~14.8 days, spring tides). Image in panel *a* created by Reto Stockli with the help of Alan Nelson, under the leadership of Fritz Hasler, and reproduced from NASA's Visible Earth catalog (**https://visibleearth.nasa.gov/images/54388/earth-the-blue-marble**).

conditions that do not provide regular cues for the entrainment of that rhythm. The individual cases highlighted in the following sections suggest that molecular oscillators are likely present across a diverse array of marine species and period lengths. By contrast, most of our molecular and cellular knowledge about the molecular sensors and timing systems still stems

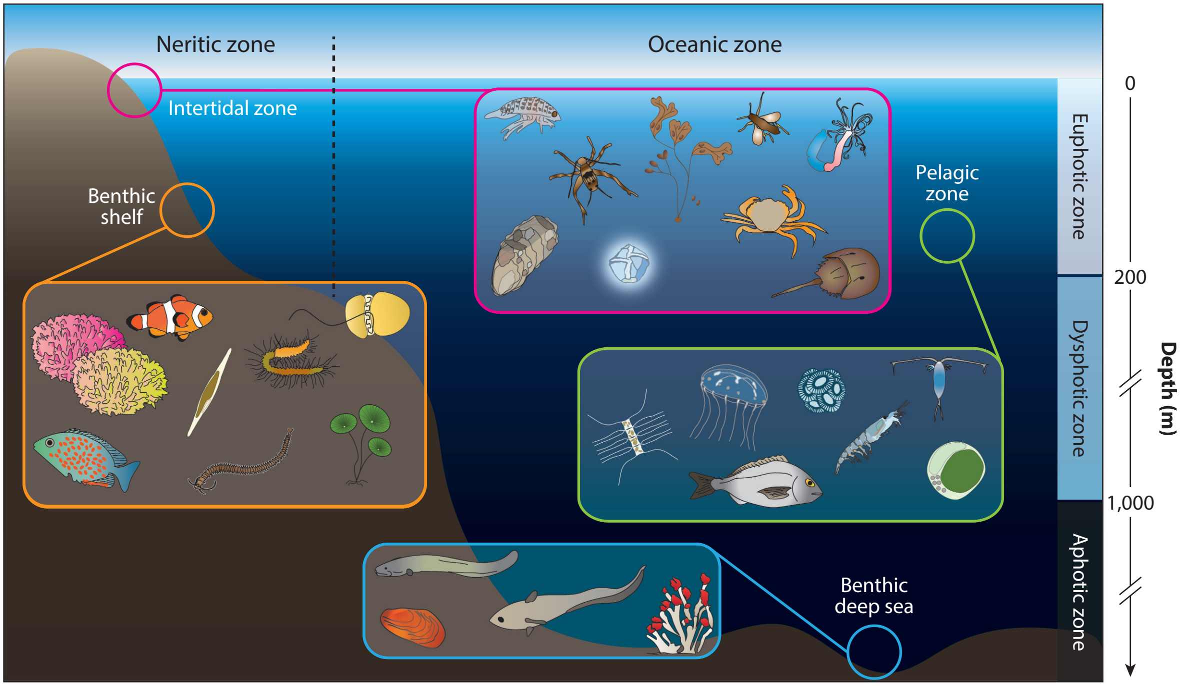

Figure 2

Overview of the diverse marine habitats and exemplary organisms discussed in this review. Important subdivisions of marine habitats include open waters (pelagic) versus the seafloor (benthic), as well as nearshore shelf seas (neritic) versus the open ocean (oceanic). Temporary air exposure defines the intertidal zone. Differences in light penetrance further separate euphotic (typically 0–200-m depth), dysphotic (200–1,000-m depth; light from the sun or moon is detectable but insufficient for photosynthesis), and aphotic (>1,000-m depth; light from the sun or moon is completely absent) zones. Each zone exhibits a different combination of rhythmic factors relevant to its inhabitants.

from terrestrial model systems. We outline below that such models have natural limitations for marine chronobiology; in turn, chronobiological research in marine organisms can help us to understand phenomena that are present in nonmarine species. To cover at least a part of the marine species diversity, this review focuses on animals and the polyphyletic group of eukaryotic algae. Chronobiological research on these groups has particularly advanced during recent years; they represent different types of marine environments (**Figure 2**) and different levels of the food web, such that the comparative overview of the chronobiology of these groups begins to address the biodiversity and evolution of timekeepers in eukaryotic organisms.

2. OTHER PLACES, OTHER RHYTHMS: THE OCEANS HARBOR MULTIPLE AND DIVERSE HABITATS WITH VERY DIFFERENT PROPERTIES FROM LAND

Free-running biological rhythm: a biological rhythm that is maintained in environments without time cues relevant to the tested oscillator

The regular cycles of the sun and moon produce the principal physical framework that generates regular environmental cycles, but the exact nature of these cycles depends on the habitat and its physicochemical properties. This aspect is particularly relevant when considering the rhythmic biological processes present in terrestrial versus marine environments and across the diversity of marine habitats (**Figure 2**).

Temperature is a prominent cyclic cue for terrestrial organisms, for both diel and annual cycles (Buhr et al. 2010, Chen et al. 2015, Yocum et al. 2016). In marine environments, however, temperature rhythms (on daily and yearly scales) are restricted mainly to tidal habitats and uppermost surface layers (d'Alcalà et al. 2004). The exact depth at which temperature changes rhythmically differs among locations and depends on water currents and mixing, which can even vary between days (Moum 2021). Moreover, temperature can be quite strongly offset from photoperiod (Häfker et al. 2018b); for instance, Mediterranean seawater in the Gulf of Naples at 50–70-m depths is warmest from October to December and cooler throughout the rest of the year (d'Alcalà et al. 2004). Furthermore, seasonal temperature cycles and the timing of sea ice breakup and formation in polar regions are typically delayed relative to the photoperiod cycle (Kahru et al. 2010, Wallace et al. 2010). As discussed in Section 5, the fact that temperature is a less predictable cue in marine environments, but at the same time strongly influences biomass production, has significant consequences for the effects of climate change on marine ecosystems.

Phytoplankton: a large and highly diverse group of photosynthetic microorganisms found predominantly in aquatic environments

Benthic: associated with the seafloor

Euphotic zone: the zone at ~0–200-m depth, where there is enough light for sustained photosynthetic production; also referred to as the photic zone

Light is another cyclic cue that is relevant for the rhythmicity of organisms, and its penetrance is an important factor for the definition of marine habitats (**Figure 2**). In habitats accessible by light, the outlined astronomical photocycles (**Figure 1**) define basic patterns of rhythmicity that can be used by marine organisms. However, position—especially water depth, but also distance to the coast—strongly impacts the overall amount and spectral quality of the light (Austin & Petzold 1986). Moreover, the biological rhythmicity itself can have secondary effects on light. For instance, seasonal phytoplankton blooms significantly affect light penetrance to deeper habitats. In addition, many marine organisms move not only horizontally (either actively or passively) but also in depth, and thereby shift between habitats. Such vertical migrations can span several hundred meters within a single day (Brierley 2014). For planktonic organisms, this phenomenon, known as diel vertical migration (DVM), is likely under circadian clock control (Häfker et al. 2017). Besides plankton, many other marine organisms exhibit vertical migrations, including top predators such as fish, squids, and whales (Chambault et al. 2021, Christiansen et al. 2019, Gilly et al. 2006, Sims et al. 2005). To date, nothing is known about how the entrainment mechanisms of any potential endogenous oscillator adapted to the drastic environmental changes that occur during such vertical migrations.

Besides light and temperature, additional cues such as salinity, mechanical forces, and pressure or magnetic field changes in marine habitats (Aguzzi et al. 2011, Hewson-Browne 1973) can provide a rhythmic framework unparalleled on land. It is therefore obvious that research on terrestrial model systems can only provide limited mechanistic insights into the chronobiology of marine species. To understand more about these mechanisms, biological analyses of marine species amenable to functional molecular investigations need to be interconnected with long-term measurements of environmental parameters. For instance, systematic long-term quantification of light conditions in a benthic habitat and corresponding laboratory experiments with molecular readouts have unraveled a new role of UVA light in seasonal adjustments (Veedin Rajan et al. 2021).

3. BIOLOGICAL RHYTHMS AND CLOCKS IN MARINE ALGAE

3.1. Rhythms in the Life of Marine Algae

The word alga subsumes highly diverse aquatic photosynthetic species widely distributed in the euphotic zone (**Figure 2**). Derived from a series of endosymbiotic events (Blaby-Haas & Merchant 2019, Brodie et al. 2017), algae are positioned throughout the major groups of the eukaryotic tree of life (**Figure 3**). Phytoplankton, also known as microalgae, play a crucial ecological role in the marine environment, producing at least 50% of the world's oxygen and primary organic biomass (Field et al. 1998).

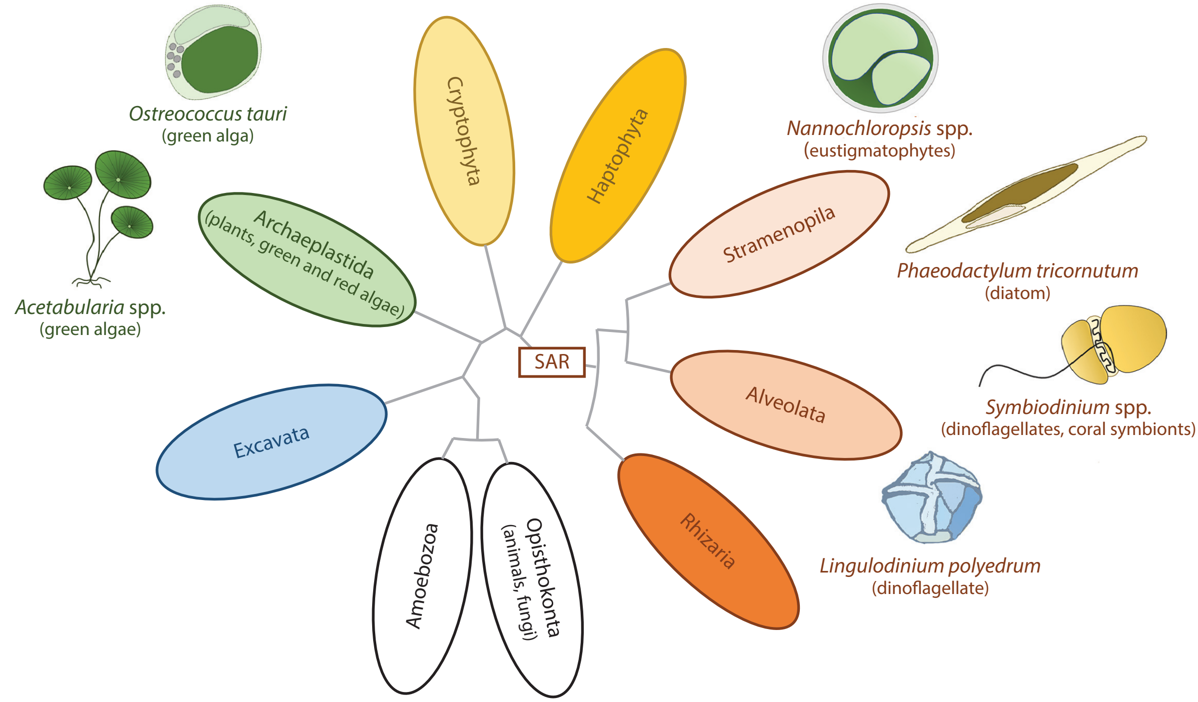

Figure 3

Established and emerging marine microalgal model systems for chronobiology and their evolutionary positions in the eukaryotic tree of life. Groups that include microalgae are colored. The SAR clade, comprising Stramenopila, Alveolata, and Rhizaria, is highlighted. Figure based on information reported by Brodie et al. (2017).

Supplemental Material >

A variety of biological rhythms have been described in algae. Strong diurnal and circadian regulation of gene expression has been described under laboratory conditions in different taxa (**Supplemental Table 1** and references therein), and diurnal rhythmicity of gene expression has been recently found in plankton communities from the natural environment (Coesel et al. 2021, Kolody et al. 2019). Rhythmic cell division is well documented for algae (e.g., Sweeney & Hastings 1958; **Supplemental Table 1** and references therein), as in plants (Fung-Uceda et al. 2018) and animals (Matsuo 2003), suggesting that this circadian function is critical for environmental adaptations.

For algae, light serves not only as an environmental information source but also as the primary source of energy for photosynthesis. Consistent with this notion, endogenous daily rhythms of photosynthetic activity and related processes have been described in most algae (**Supplemental Table 1** and references therein), suggesting that the tight temporal control of energy metabolism by a circadian clock is advantageous for algae, as previously shown for plants (Dodd et al. 2005). Photosynthesis may, in turn, represent an input for the regulation of the algal circadian clock itself, as already shown in plants (Haydon et al. 2017) and similar to food cues in animals (Asher & Sassone-Corsi 2015).

Input:
a cue involved in the entrainment process

Periodic changes in algal photosynthetic metabolism also impact symbiotic associations with animal partners. These associations supply the heterotroph host with organic products of photosynthesis to match energy needs and are especially relevant in waters where nutrient levels are low (Muller et al. 2009). In corals that facultatively host the photosynthetic dinoflagellate

Symbiodinium sp., the dinoflagellate's photosynthesis follows endogenously regulated circadian rhythms. These rhythms persist during association with the coral hosts, unlike other circadian processes, such as cell division and motility, which are rhythmic only in free-living algae (Sorek et al. 2013). In turn, the aposymbiotic anemone *Aiptasia diaphana* shows dominant circatidal transcriptional dynamics, but these dynamics change to predominantly circadian patterns when anemones are associated with the symbiont (Sorek et al. 2018).

Supplemental Material >

In different algae, the circadian clock also contributes to the regulation of population behavior (**Supplemental Table 1**). Phytoplankton exhibit diurnal vertical migrations (Sournia 1975) but on a much smaller scale than zooplankton (see also Section 4). Endogenous rhythms of bioluminescence (Hastings & Sweeney 1957) and cellular aggregation (Hastings & Sweeney 1957, Roenneberg & Morse 1993, Roenneberg et al. 1989) have also been described.

Algae also exhibit moon-related cycles. Migratory rhythms in intertidal sediments synchronized with diurnal and tidal cycles have been reported in different diatom species (Mitbavkar & Anil 2004, Round & Palmer 1966), and semidiurnal (12-h) gene expression periodicity has been documented in the diatom *Seminavis robusta* (Bilcke et al. 2021), likely reflecting adaptations to the tides in coastal ecosystems. Sexual reproduction is another process tangled with moon rhythms in algae. Multicellular algae have long been known to show synchronous gamete release patterns following lunar or semilunar periodicity (Andersson et al. 1994, Brawley & Johnson 1992).

Rhythmicity in algae also extends to cycles of longer period length: The composition and dynamics of phytoplanktonic populations exhibit strong seasonal patterns. Different taxa show seasonal bursts (algal blooms) in a specific area, generally interspersed with periods of apparent absence from the water column. External cues such as nutrients, light, and predators (Reynolds 2006); photoperiodic variations; and temperature changes (Lambert et al. 2019) can act as important drivers of community dynamics. In some cases, there is even evidence for endogenous control on an annual scale, as in kelp (belonging to the stramenopiles), where growth is under circannual control (**Supplemental Table 1** and references therein). Moreover, the activation of resting cysts of dinoflagellates from the genus *Alexandrium* appears to follow an internal, circannual timing system (Matrai et al. 2005). The discovery of biannual patterns of sexual reproduction in the marine diatom *Pseudo-nitzschia multistriata* (D'Alelio et al. 2010) additionally highlights the robust long-term organization of the phytoplanktonic life cycle. Research into the dissection of the mechanisms that orchestrate algal rhythmicity on different timescales is not only scientifically promising but also of tremendous relevance for ocean ecosystems.

3.2. Elucidation of Timekeeping Mechanisms in Marine Algae

As outlined above, a variety of ecologically crucial biological rhythms have been described in algae. By contrast, far less information is available on the underlying algal timekeepers. Below, we briefly summarize the available knowledge on the molecular clock of these models (**Figure 3**; **Supplemental Table 2**).

Important insights into algal timing systems were derived from research on the picoeukaryote *Ostreococcus tauri*, the smallest known free-living marine eukaryote (Courties et al. 1994). The small genome of this green alga (13 Mb) harbors a minimal timekeeper that is formed by only two transcription factors: TOC1 and CCA1 (Corellou et al. 2009). Both factors are homologous to central circadian clock components of land plants (Creux & Harmer 2019) and of the freshwater green alga *Chlamydomonas reinhardtii* (Petersen et al. 2022). CCA1 is also conserved in the thermoacidophilic red alga *Cyanidioschyzon merolae* (Miyagishima et al. 2014). This indicates that critical TTFL components might have a common origin in Archaeplastida.

Temperature compensation: buffering against temperature changes that enables endogenous oscillators to function independently of the Le Bel–Van 't Hoff rule

Regarding the SAR (Stramenopila, Alveolata, and Rhizaria) supergroup, information on the circadian clock is emerging from the study of diatoms, prominent aquatic microalgae that evolved by secondary endosymbiosis (Falciatore et al. 2020). Remarkably, the genomes of these algae lack clear homologs of the circadian clock components of bacteria, plants, or animals, with the exception of cryptochromes and casein kinases (Farré 2020, Poliner et al. 2019) (see below). A survey for rhythmic transcription factors of the diatom *Phaeodactylum tricornutum* identified proteins with basic helix-loop-helix (bHLH) and PAS domains as putative circadian clock components (Annunziata et al. 2019), reminiscent of animal circadian clocks that make use of bHLH/PAS domain transcription factors (Gekakis 1998). The additional presence of RITMO1-like proteins in other stramenopiles (e.g., *Nannochloropsis* and *Ectocarpus*), as well as in alveolates (Annunziata et al. 2019, Farré 2020), is consistent with a circadian function of these transcription factors among SAR organisms. Another putative regulator of the diatom circadian clock is the animal-like blue-light sensor cryptochrome/photolyase 1 of *P. tricornutum* (*Pt*-CPF1). This protein and its *O. tauri* ortholog can function as transcriptional repressors in mammalian cell culture by interacting with the mammalian core circadian clock component CLOCK:BMAL (Coesel et al. 2009, Heijde et al. 2010). This suggests a conserved involvement of cryptochrome/photolyase in circadian TTFL processes of animals and algae. However, while *Ot*-CPF1 is functionally involved in the maintenance of the *O. tauri* circadian clock, this alga lacks bHLH-PAS transcription factors, as do other Archaeplastida (Heijde et al. 2010), pointing to possible limitations in the interpretation of heterologous cell culture studies.

Studies in algae have also helped reveal the existence of transcription-independent oscillators. Initial insights derived from the enucleated unicellular green algae *Acetabularia* spp. (Mergenhagen & Schweiger 1975, Sweeney & Haxo 1961) were followed by the discovery of endogenous bioluminescence rhythmicity in the dinoflagellate *Lingulodinium polyedrum* (formerly *Gonyaulax polyedra*) (Hastings 2007; Morse et al. 1989a,b). In this alga, luciferase bioluminescence is regulated via a transcription-independent mechanism that relies on an RNA-binding protein named circadian-controlled translational regulator (CCTR). CCTR represses the translation of luciferin-binding protein (LBP) in a circadian fashion, by rhythmically binding a target sequence in the 3′ untranslated region of the respective mRNA (Mittag et al. 1994). Moreover, work on *O. tauri* identified rhythmic oxidation of peroxiredoxin (PRX) (Bouget et al. 2014, O'Neill et al. 2011). PRX rhythms persist in constant darkness, a condition under which *O. tauri* transcription stops. PRX rhythms are conserved across many kingdoms of life, including cyanobacteria, archaea, fungi, and animals (Edgar et al. 2012, O'Neill et al. 2011). Given the role of PRX in the detoxification of reactive oxygen species by-products of cellular metabolism, it has been proposed that the evolutionary origin of circadian timekeeping might be linked to diel cycles of redox stress and that more species-specific TTFL clockworks evolved independently later in the different eukaryotic lineages (Edgar et al. 2012).

As in other organisms, the circadian clock of algae is entrained by cyclic environmental signals. Physiological analyses provide evidence that blue and red light play an important role in entrainment (e.g., Poliner et al. 2019, Roenneberg & Hastings 1988) (**Supplemental Table 2**). Diverse blue-light-absorbing proteins have been identified in the genomes of algal model systems, and their involvement in circadian regulation has been demonstrated in some species. By contrast, red/far-red-light-sensitive phytochromes have been found only in some diatom species (Fortunato et al. 2016), possibly due to the strong attenuation of long wavelengths underwater.

Supplemental Material >

In addition to light, fundamental concepts in the temperature compensation of the circadian oscillators arose from early studies on the bioluminescence of *L. polyedrum* (Hastings & Sweeney 1957). More recent studies on circadian clock features of *Nannochloropsis* spp. (Poliner et al. 2019) and of coral-symbiotic algae (Sorek & Levy 2012) support this notion. The pathways implicated in these mechanisms, however, remain to be elucidated.

Conventional circadian clock: molecular oscillators driving diel rhythms, based mainly on a TTFL and defined sets of additional components; the involved molecules are typically conserved within one eukaryote phylum but rarely beyond

Core (circadian) clock genes: genes that are part of a central (circadian) oscillatory network; since molecular mechanisms are known only for the circadian clock, the terms clock genes and circadian clock genes are often used synonymously

Ultradian rhythm: a rhythm that occurs with a periodicity shorter than ~24 h

4. ANIMAL MODELS FOR MARINE CHRONOBIOLOGY

In this section, we present examples of prominent rhythmic phenomena, as well as animal models that have helped to start disentangling a variety of marine biological timers. We especially cover the naturally highly relevant interplay of solar and lunar timing cues.

4.1. Vertical Migrations in the Pelagic Zone

One of Earth's largest regular biomass movements is the DVM of marine plankton (Brierley 2014). This highly heterogeneous group of species represents a key component of the ocean food network. Zooplankton commonly migrate to the water surface at dusk and return to depths at dawn, which is thought to represent a balance between feeding needs and predator avoidance (Fortier et al. 2001, van Haren & Compton 2013).

Although solar light is the main reported stimulus synchronizing DVM (Kaartvedt 2010, van Haren & Compton 2013), moonlight also affects its rhythm, especially during polar nights, when periodicity shifts from the solar cycle (~24 h) to the lunidian cycle (~24.8 h) (Gilly et al. 2006; Kaartvedt 2010; Last et al. 2016, 2020). Solar and lunar eclipses (Strömberg et al. 2002, Tarling et al. 1999), as well as other phenomena that presumably influence local light intensities (e.g., storms and clouds), also affect the dynamics of vertical migrations (Omand et al. 2021). Notably, DVMs persist during the darkest part of the polar night (Berge et al. 2009, 2015; Last et al. 2020) and in the deep sea (van Haren & Compton 2013), suggesting the existence of an endogenous oscillator coordinating these migration events.

Among the marine models that are used to investigate the molecular mechanisms of DVM are the northern and Antarctic krill (*Meganyctiphanes norvegica* and *Euphausia superba*, respectively) (Cohen et al. 2021, Piccolin et al. 2020) and the copepod *Calanus finmarchicus* (Häfker et al. 2017). Studies of these organisms are consistent with an involvement of the conventional circadian clock in DVM regulation (Biscontin et al. 2017, Häfker et al. 2017, Teschke et al. 2011). Putative core circadian clock genes of both krill and *Calanus* species show a diel/circadian transcriptional oscillation both in the field and in laboratory light–dark (LD) and dark–dark (DD) conditions (Häfker et al. 2017, Teschke et al. 2011). Transcriptional dynamics (including core circadian clock gene expression) showed not only ~24-h rhythms even under the polar midnight sun in *C. finmarchicus*, but also several ultradian rhythm patterns (including circatidal frequencies) in ice-covered areas (Hüppe et al. 2020, Payton et al. 2020). DVM rhythms of the Antarctic krill consistently shifted from ~24 h in LD conditions to ~12 h in DD conditions (Piccolin et al. 2020). Approximately 50% of the krill transcriptome oscillated with an ~24-h rhythm in LD conditions, while under DD conditions, the dominant molecular signature exhibited frequencies of ~12–15 h (~40% of the transcripts) (Biscontin et al. 2019). Taken together, these data indicate a possible plastic nature of a circatidal/circadian/circalunidian clock in zooplankton and/or polar species (for more details, see below).

Whereas DVMs occur at any latitude, another type of vertical migration, but with an annual period, occurs mostly in temperate and polar regions and is typically associated with diapausing strategies. In copepods, a facultative diapause occurs during times of low productivity in autumn and winter. Individuals migrate to great depths, where they then spend several months (Baumgartner & Tarrant 2017, Lenz & Roncalli 2019). Despite several phenotypic and (high-throughput) gene expression studies (Baumgartner & Tarrant 2017, Häfker et al. 2018b, Lenz & Roncalli 2019), the underlying mechanisms are still unclear, including the question of whether

Pelagic: associated with the water column

Plasticity (of an oscillator): variability in the period length of an endogenous oscillator; it can be read out on any output level (molecular, physiological, or behavioral)

one or more endogenous oscillators or direct environmental/physiological cues are responsible for this annual rhythm. Similarly, season-dependent signatures have been identified in the transcriptome of the Antarctic krill (*E. superba*) when the species enters winter quiescence, a state of metabolic rate depression (Höring et al. 2021), but the driving forces remain to be determined. Considering the key position of copepods and krill in pelagic food webs, understanding the factors and mechanisms driving their diel and seasonal rhythms is highly relevant (for a discussion of adaptability, see Section 5).

The regular migrations of zooplankton communities often drive similar phenomena in their mesopelagic and epipelagic predators, such as fish and sharks. Indeed, DVMs have been documented in the European hake, *Merluccius merluccius* (De Pontual et al. 2012); the glacier lantern fish, *Benthosema glaciale* (Dypvik et al. 2012a,b); the Pacific cod, *Gadus macrocephalus* (Nichol et al. 2013); the Japanese eel, *Anguilla japonica* (Chow et al. 2015); the jumbo squid, *Dosidicus gigas* (Gilly et al. 2006); and the deep-water bluntnose sixgill shark, *Hexanchus griseus* (Coffey et al. 2020). Modern strategies, including pop-up satellite transmitters and machine learning approaches, facilitate the assessment of diel, seasonal, or other migratory dynamics in larger animals, such as eels (Chang et al. 2020), bigeye threshers (*Alopias superciliosus*) (Coelho et al. 2015), whale sharks (Andrzejaczek et al. 2021), and sperm whales (Chambault et al. 2021). There are also many rhythms and possible endogenous oscillators that critically determine interactions within and among marine species that await mechanistic analyses.

4.2. Rhythms in the Deep Sea

The deep sea had long been considered an arrhythmic environment with low and steady biological rates due to its darkness, low average temperatures (below 4°C), high pressure, and food availability that is either limited or driven by spontaneous hydrothermal vent activity caused by plate tectonics. Chronobiological studies require either long(er)-term or repeated measurements while ensuring that those measurements do not distort the results. Indeed, it takes several hours just to bring samples on board, and camera observations generate unnatural light exposure, both of which have complicated studies of possible temporal components in deep-sea life.

However, evidence for environmental rhythms (such as seabed currents with periodic changes in velocity and direction, as well as temperature changes) is emerging (Wagner et al. 2007). Deep-sea tidal changes (internal tides) occur when coastal or surface tides propagate vertically across water layers with different properties (often cold and warm, respectively), along the water column (Garrett 2003). The advance of observatory technology and long-term infrastructure investments identified tidal (Cuvelier et al. 2017), diel, lunar (Mercier et al. 2011), and seasonal rhythms in different categories of animal life, covering behavior, growth rates, abundance, and reproduction (Aguzzi et al. 2011, Baillon et al. 2014).

At a molecular level, circatidal oscillations in melatonin levels from isolated pineal glands and retinae were observed in deep-sea fish (Wagner et al. 2007). Transcriptome sequencing from vent crabs and mussels started to set up resources to understand the molecular mechanisms underlying the adaptation to extreme hydrothermal vent habitats, including conventional animal core circadian clock genes (Hui et al. 2017, Zheng et al. 2017). Such transcriptomic sequencing combined with repeated deep-sea on-site organism fixation and behavioral observations under red light allowed the identification of correlational tidal signatures in the behavior and transcriptome of the gill tissue of the vent mussel (*Bathymodiolus azoricus*) (Mat et al. 2020). Notably, the putative core circadian clock genes *period*, *timeless*, and *cry1* (a *dCry/L-Cry* ortholog) exhibited approximate tidal rhythms in field samples (Mat et al. 2020), suggesting the plasticity of the ~24-h oscillator. Similarly, putative core circadian clock genes showed daily and/or tidal oscillations in the Iceland scallop (*Chlamys islandica*) during equinox and polar night (Perrigault et al. 2020).

4.3. A Plastic Clock to Time Daily and Tidal Rhythms

In the marine environment, behavior and physiology are often synchronized with relatively short environmental cycles (in the range of hours). These comprise tidal (∼12.4 h), diel (∼24 h), and lunidian (∼24.8 h) cycles, including the examples given above as well as many others (Andreatta & Tessmar-Raible 2020, Rock et al. 2022) (**Figure 1*g*,*h***; **Supplemental Tables 2 and 3**).

Supplemental Material >

Tidal variations at the coast cause remarkably regular but drastic changes in immersion, temperature, salt concentrations, oxygen and food availability, and so on. As it is of the utmost importance for organisms to not be surprised by those environmental changes, circatidal clock mechanisms to anticipate the imminent tidal variation provide a large adaptive advantage (Rock et al. 2022). Circatidal locomotor rhythms have been described in a variety of animal taxa, such as crustaceans (Mehta & Lewis 2000, Naylor 1996, Palmer 1991, Williams 1998), insects (Evans 1976; Foster & Moreton 1981; Satoh 2017; Satoh et al. 2006, 2008), *Limulus* (Chabot & Watson 2010, Chabot et al. 2016), polychaetes (Last et al. 2009), acoel worms (Arboleda et al. 2018), limpets (Schnytzer et al. 2018), and fish (Pülmanns et al. 2018). Valve-opening activity rhythms in the oyster *Crassostrea gigas* shifted from a predominantly circadian (∼24 h) to circatidal (∼12.4 h) pattern under DD laboratory conditions, suggesting control by both the environment and an endogenous circatidal oscillator (Perrigault & Tran 2017). Diel and tidal rhythms have also been documented in the amphipod *Parhyale hawaiensis* (Hunt 2016, Ramos et al. 2019) and the starlet sea anemone (*Nematostella vectensis*) (Hendricks et al. 2012, Oren et al. 2015). The dominance of either circadian or circatidal activity rhythms in *Nematostella* depends on light conditions (blue/green light or red light/DD, respectively) (Leach & Reitzel 2020).

The current data on circatidal oscillators have been debated as evidence for different models. Indeed, circatidal rhythms could rely on (*a*) a unimodal circatidal clock (∼12.4 h), which exists independently from the circadian clock (Naylor 2010) and does not even need to interact with the latter (Williams 1998); (*b*) the superposition of two unimodal antiphase circalunidian (∼24.8 h) clocks (Palmer 2000); or (*c*) a single bimodal clock orchestrating both circadian and circatidal rhythms (∼24 h and ∼12.4 h, respectively) (Enright 1976, Mat et al. 2014, Tran et al. 2020).

Analyses of the plasticity of the conventional circadian oscillator and possible other oscillatory mechanisms in the diel/lunidian/tidal range have thus been of particular interest. Functional molecular investigations of the isopod *Eurydice pulchra* revealed an at least partial dissociation of circadian and circatidal oscillations (Zhang et al. 2013) and predominantly circatidal rhythms in metabolic dynamics (O'Neill et al. 2015). Similarly, in the cricket *Apteronemobius asahinai*, several genes involved in metabolic processes cycled in the transcriptome predominantly in a circatidal fashion, yet presumptive core circadian clock genes showed no evident rhythmicity (Satoh & Terai 2019). Furthermore, RNA interference–mediated downregulation of the core circadian clock genes *period* and *clock* in the cricket revealed impaired circadian but not circatidal rhythms in this species (Takekata et al. 2012, 2014), in line with RNA interference experiments targeting the *period* gene in *E. pulchra* (Zhang et al. 2013). These findings suggest that if molecular overlaps between circadian and circatidal oscillators exist, they might be only partial.

Dominant circadian signatures have been observed in mussels at both the transcript and protein levels in natural and simulated tidal environments (Connor & Gracey 2011, Elowe & Tomanek 2021). Oyster classical circadian clock genes showed circatidal expression in the field, a signature maintained under DD conditions, but became diel in animals exposed to LD cycles under laboratory conditions (Tran et al. 2020). These results are very similar to observations of transcriptional core circadian clock gene oscillations in the Antarctic krill under different conditions, where the changes also matched with alterations in DVM behavior and metabolism (Piccolin et al. 2020).

Peripheral circadian clocks: circadian oscillators that are present in (almost) all (animal) tissues; evidence from terrestrial (mouse, *Drosophila*) and marine (*Platynereis*) models shows that these clocks are coordinated by a central brain oscillator

Although these findings do not resolve the circatidal oscillator riddle, they indicate a plastic clock machinery that operates on timescales in the range of hours and differentially integrates environmental cues (e.g., light and tides). Independent input pathways might modulate the period length of the endogenous oscillator(s) by acting on different molecular loops of what at present is considered the conventional circadian clock. These loops could resonate with either circadian or circatidal frequency, depending on the dominant environmental input. Additionally, such a scenario might be confined to specific cells, with others maintaining a classical circadian period. Finally, it is possible that the ticking of a still elusive metabolic oscillator is at the core of circatidal rhythms, directly or indirectly modulating oscillations of conventional core circadian clock genes.

Evidence that at least the conventional circadian clock can function individually in cells of marine organisms (i.e., as a peripheral circadian clock) is well documented for the chromatophores of the annelid *Platynereis dumerilii*. These cells oscillate on molecular and phenotypic levels independently of the worms' central head oscillator (Arboleda et al. 2019). Moreover, work on the integration of solar and lunar light cues for the exact timing of the spawning hour provided further insight on the plasticity of the conventional circadian clock in *P. dumerilii*. At least in mature worms, this clock can change its period length depending on exposure to either naturalistic sunlight or a combination of naturalistic (full/waning) moonlight and sunlight. This circadian/circalunidian plasticity allows the worms to spawn exactly at the darkness window between sunset and moonrise, the exact time of which changes across the month (Zurl et al. 2022). Functional genetic analyses demonstrate that the combination of two light receptors, L-CRY and r-Opsin1, is critical for the correct interpretation of light valence (i.e., sun- or moonlight) and moon phase (Zurl et al. 2022). Notably, the light-dependent plasticity of the ∼24-h clock period length has long been observed across a wide range of aquatic and terrestrial organisms, including humans (Aschoff 1960, 1965), but its biological relevance had remained unclear. Studies under more naturalistic conditions, including those of marine organisms, will provide a better understanding of oscillators that time specific hours.

The plasticity of the ∼24-h clock not within the same individual but among different individuals provides the basis for the marine midge *Clunio marinus* to adapt its hour of adult emergence to local tidal regimes. To find the best substrate for zygote deposition, *C. marinus* emerges at the lowest low tide (Neumann 1966, 1968, 1988). However, the exact hours of the lowest low tide vary predictably along the coast (Kaiser et al. 2021). Polymorphisms in the *CaMKII.1* gene cause differential splicing and subsequent functional differences of the [Ca^{2+}]-dependent kinase. Those variances result in different circadian clock periods and ultimately in distinct emergence times, which match the local tidal conditions (Kaiser et al. 2016).

In summary, the plasticity of ∼24-h oscillators could be sufficient to explain rhythms in the tidal, diel, and lunidian range.

4.4. Timing Reproduction with an Inner Calendar

Supplemental Material >

Below, we briefly focus on approximately monthly and approximately semimonthly cycles (Andreatta & Tessmar-Raible 2020). In animals, circasemilunar (semimonthly) and circalunar (monthly) rhythms have been well documented (Andreatta & Tessmar-Raible 2020, Raible et al. 2017, Tessmar-Raible et al. 2011) (**Supplemental Table 3**). For several species, including annelids (*P. dumerilii* and *Typosyllis prolifera*), molluscs (e.g., *Haliotis asinina*), crustaceans (e.g., *E. pulchra*), insects (e.g., *C. marinus*, *Clunio tsushimensis*, and *Pontomyia oceana*), and fishes (e.g., *Fundulus heteroclitus*, *Fundulus grandis*, and *Oncorhynchus mykiss*), these rhythms have been shown to persist in the absence of (semi)monthly cues and hence to be controlled by endogenous oscillators (Kaiser & Neumann 2021). For some, the entraining stimuli are known, and for annelids, insects, and fishes, evidence for temperature compensation has been provided (Kaiser & Neumann 2021).

Here, we consider lunar and semilunar rhythms (and their underlying oscillators) as output modifications of the same mechanisms, because studies have shown that both periods can variably occur within the same insect and worm laboratory strains, depending on the entraining light conditions (Kaiser et al. 2021, Poehn et al. 2022). Importantly, however, this does not necessarily imply that the oscillatory mechanisms are the same across species.

Output: a biological process whose rhythmicity is regulated by an endogenous oscillator

Circa(semi)lunar clocks might rely on (*a*) oscillators with a periodicity of ∼15 or ∼30 days, (*b*) rhythms generated by the superposition of a circadian and a circatidal or circalunidian clock (the beat hypothesis), and (*c*) a circadian cycle countermechanism with a periodicity of ∼15 or ∼30 days (the frequency demultiplication hypothesis) (Kaiser & Neumann 2021). The latter two mechanisms imply that each circadian clock change would also influence the (semi)monthly oscillator, while an independent circa(semi)lunar oscillator would provide more flexibility for independent adjustments of diel and monthly timing. There have been many correlational studies on the transcript level and some on the protein level (reviewed in detail in Andreatta & Tessmar-Raible 2020), but the molecular mechanisms remain an open question.

The first knockout studies on an organism with a circa(semi)lunar oscillator, the marine annelid *P. dumerilii*, suggested that the worms' cryptochrome L-Cry is critical to provide the organism with information on whether light is coming from the sun or the moon, and as such, it functions as a natural light interpreter or valence detector (Poehn et al. 2022). Depending on the light intensity and/or spectrum, *Pdu*-L-Cry assumes distinct biochemical moonlight and sunlight states that coincide with distinct subcellular (stable nuclear versus cytoplasmic/nuclear degradation, respectively) localizations. Biochemically, L-Cry reaches its full moonlight state only under at least 6 h of naturalistic moonlight, allowing it to discriminate not only between sunlight and moonlight but also between moon phases (Poehn et al. 2022). This enables the system to work independently of photoperiods and is in line with classical work that showed that nocturnal light duration, not its exact timing, is relevant (Hauenschild 1960). Interestingly, the specific biochemical moonlight state properties of L-Cry are not present in its ortholog dCry in the diurnal/crepuscular insect *Drosophila melanogaster*, which does not possess a moon-controlled (semi)monthly oscillator (Zurl et al. 2022). It will be attractive to test cryptochromes of other species with moonlight-controlled rhythms for their biochemical and cellular properties. This is particularly interesting for corals due to the long-standing proposal that a cryptochrome is involved in lunar light-controlled spawning synchronization (Levy et al. 2007). Reef-building corals have been extensively studied for their extremely precise spawning, which often occurs only once per year (Babcock et al. 1986), highlighting the required complex coordination of diel, monthly, and annual cues (Wuitchik et al. 2019). While this complex multitimer coordination is likely widespread, the reefs' ecological relevance makes corals critical model systems to study the anthropogenic impacts on the timing of fundamental physiological and behavioral aspects of marine organisms (Fogarty & Marhaver 2019).

5. MARINE RHYTHMS AND CLOCKS UNDER CLIMATE CHANGE

In this section, we review past and present effects of climate change on biological rhythms and elaborate how climate effects on rhythms and timing systems can affect fitness, species interactions, and ecosystem functioning. We discuss how organismic plasticity and the genetic adaptability of timing systems might favorably impact species survival in an environment where cyclic conditions change (Häfker & Tessmar-Raible 2020).

Artificial light at night is another important and historically unprecedented anthropogenic environmental stressor. Nocturnal light pollution by, for example, human settlements can affect various aspects of biological rhythmicity in marine habitats (Ayalon et al. 2020, Berge et al. 2020).

Artificial light at night is not directly connected to climate change, and for conciseness, we do not cover it here; we instead refer readers to other reviews that address this important topic in appropriate detail (e.g., Davies et al. 2014, Hölker et al. 2021).

5.1. Changes of Marine Rhythms in the Past

Earth has gone through numerous climate changes. It is difficult to deduce how biological rhythms responded to such changes, as fossils do not provide temporal information. They might, however, provide information about lifestyles (e.g., diurnal versus nocturnal, based on eye size) or—if sufficient DNA is recoverable—about putative clock genes and their sequence evolution. One famous example comes from nocturnal mammals, which, likely after the decline of dinosaurs, occupied new temporal niches in all environments, including the oceans. The spread of activity across the day–night cycle allowed for greater diversity (Gerkema et al. 2013, Maor et al. 2017).

The last major change in environmental conditions was the warming after the Last Glacial Maximum (20,000 years before present) and the associated retreat of the polar ice caps. Population analysis in the marine midge *C. marinus* showed that the species' habitat-specific, genetically encoded circadian and circa(semi)lunar rhythmicity (see Section 4) likely evolved between the Last Glacial Maximum and 8,000 years before present from a single population that spread throughout the European coast (Kaiser et al. 2010). Along the European Atlantic coast, these midges have adapted to different temporal niches, characterized by the monthly and diel combination of the lowest low tides optimal for adult emergence and zygote deposition (Kaiser et al. 2016, 2021).

Other evidence for favorable plasticity in timing stems from the Arctic and North Atlantic *Calanus* complex. The boreal copepod *C. finmarchicus* maintained its population size throughout the Last Glacial Maximum, while its Arctic congener *C. glacialis* experienced an ~1,000-fold increase in population size since the Last Glacial Maximum (Provan et al. 2009, Weydmann et al. 2018). This was likely due to the increased availability of shelf habitats, which *C. glacialis* prefers. Although it is not possible to prove past changes in copepod rhythmicity, it is likely that since the last ice age, species of the *Calanus* complex experienced major latitudinal shifts and thus adapted to changes in light conditions (e.g., photoperiod) and other rhythmic cues.

Thus, the rhythms and endogenous oscillators of marine organisms can adapt to environmental changes. However, it remains unclear how much time is required for such adaptations and how they affect and are affected by population sizes. The answers are likely species specific.

5.2. Present-Day Climate Effects on Marine Rhythmicity

Since the end of the eighteenth century, Earth's climate has been experiencing major changes, at least partially caused by anthropogenic CO_2 emissions (IPCC 2014). These changes affect marine life through at least three major factors: (*a*) increases in water temperatures and associated decreases in polar sea ice cover, (*b*) decreases in water pH due to the uptake of atmospheric CO_2, and (*c*) expansion of marine oxygen minimum zones (OMZs) (**Figure 4**). While various studies have addressed the impacts of this deadly trio on, for example, physiology, ecosystem composition, and fluxes, the effects on biological rhythms and possible inner timing systems have been addressed to a much lesser extent.

5.2.1. Temperature changes. Warming of tropical waters affects the synchronized mass spawning of reef-forming corals. Gamete maturation and release in these cnidarians show seasonal, lunar, and diel coordination that is also reflected in corresponding rhythmic transcriptome changes (Oldach et al. 2017, Wuitchik et al. 2019) and circadian rhythmicity (Oren et al. 2015, Sorek et al. 2014). The seasonal phase of coral spawning is set primarily by a summer increase in

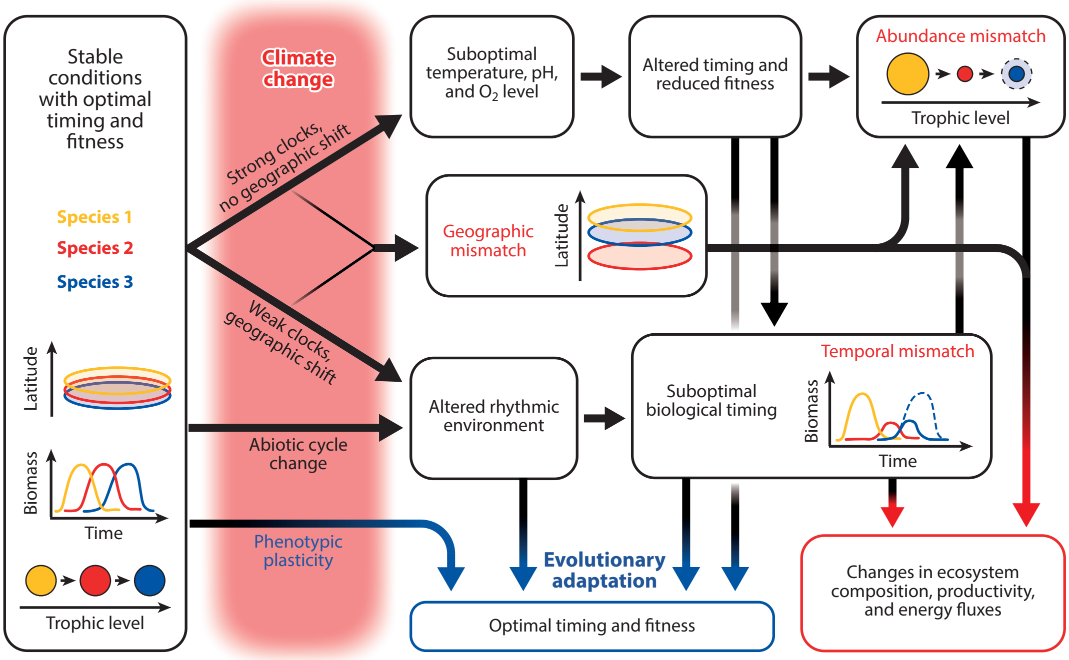

Figure 4

Climate change effects on timing and how they could impact species interactions and ecosystems. Changes in abiotic factors (here temperature, pH, and oxygen) and/or the rhythmic environment create suboptimal conditions, forcing responses that can differ among species. A simplified three-species system illustrates mismatches, with species 2 (*red*, intermediate trophic level) affected most severely. Dashed lines indicate the potential of species 3 (*blue*, higher trophic level) if species 2 were not affected. The enlarged cycle for species 1 (*yellow*, lower trophic level) in the abundance mismatch scenario illustrates the reduced top-down control by species 2. In the more complex natural environment, other species may compensate for, benefit from, or suffer under some of the interspecies mismatches.

water temperature (Keith et al. 2016). Besides desynchronization by artificial light (Ayalon et al. 2020), the overall increase in ocean temperature has been suggested to cause temporal desynchronization of gamete release in Red Sea corals. This implies that increasing temperatures threaten coral reefs not only through direct effects (e.g., bleaching) but likely also through the disturbance of (reproductive) rhythms (**Figure 4**).

Increasing temperatures also result in a decline of polar sea ice cover and earlier ice breakup in spring or summer. Polar phytoplankton blooms start with the ice breakup, and their peaks have shifted up to 50 days forward in one decade (Kahru et al. 2010). The reduction in Antarctic sea ice has been connected to a decline in the stock of Antarctic krill (*E. superba*) (Atkinson et al. 2019, Meyer et al. 2017). In winter, krill larvae find shelter from predation at the underside of the sea ice and perform a reverse DVM, sinking into the water column after sunset and drifting with the water current to find new under-ice food patches (Meyer et al. 2017). The decrease in krill stocks could thus be due at least in part to a loss of larval daytime refuge and consequently higher predation pressure in open water habitats. Polar phytoplankton growth is strong near the ice edge due to the seeding by algae released from the melting ice. As the ice edge retreats further poleward, so do the associated blooms. Together with the aforementioned forward shift of bloom timing, this could increase migration distance and impair the timing of seasonal latitudinal migrations that benefit from polar productivity (Jenouvrier et al. 2009). Baleen whales that visit boreal and polar regions in summer apparently show some adaptive plasticity in migratory timing, but it is unclear what the underlying mechanisms are and whether they can keep pace with the ongoing shifts in productivity, on both latitudinal (Visser et al. 2011) and temporal (Kahru et al. 2010) scales (**Figure 4**). Warming in general has resulted in a latitudinal distribution shift in a variety of marine species, which, in an attempt to stay within their thermal niches, move toward the poles and thereby into habitats with more extreme rhythmic environmental conditions (Atkinson et al. 2019, Chivers et al. 2017, Kaartvedt & Titelman 2018, Melle et al. 2014, Villarino et al. 2020).

5.2.2. pH changes. The effects of ocean acidification on rhythms and clocks have hardly been investigated so far. A recent study found altered timing and synchronization in coral spawning under a combination of increased temperature and reduced pH (Liberman et al. 2021). Furthermore, reports of altered circadian clock gene expression in fish at reduced pH levels suggest a response by the circadian clock that regulates diel rhythms of osmoregulation in marine fishes (Jesus et al. 2017, Schunter et al. 2016). Ocean acidification can also impact chemical detection and brain functioning in fish (Dixson et al. 2010, Schunter et al. 2018) and could thus impair rhythm entrainment through chemical cues (e.g., pheromones) used to synchronize reproduction (Baghel & Pati 2015, Watson et al. 2003) and egg release (Caballes & Pratchett 2017, Tankersley et al. 2002). Reduced pH levels also influence DNA methylation and chromatin condensation in corals and marine fish and could thereby also affect both circadian (de Lima & Göndör 2018, Weizman et al. 2019) and circannual (Stevenson & Lincoln 2017) timing mechanisms. While the potential effects of acidification on biological clocks have long been overlooked, they clearly warrant detailed investigation.

5.2.3. Oxygen concentration changes. OMZs in the world's ocean are expanding both vertically and horizontally. Many species cannot inhabit OMZs, while others are closely associated with them. Thus, the expansion of these zones can have profound effects on species, as shown for the depth distribution of the vertically migrating jumbo squid (*D. gigas*) and other top predators in the eastern Pacific (Rosa & Seibel 2008, Stramma et al. 2012). Similar to vertical distribution shifts caused by OMZs, ocean warming can also affect vertical habitat usage due to downward shifts of thermoclines (Howard et al. 2020, Jorda et al. 2020). Vertical distribution shifts alter the experienced diel rhythms of light and other parameters (temperature, oxygen, and pressure) (**Figure 4**). This could affect the entrainment of circadian clock systems, which can regulate DVM (Häfker et al. 2017), as well as potential photoperiod-based seasonal timing (Häfker et al. 2018a, Teuber et al. 2013). Altered diel and seasonal vertical distribution patterns could further impact CO_2 sequestration to deep waters (Brun et al. 2019, Jónasdóttir et al. 2015). Additionally, horizontal OMZ spreading leads to latitudinal shifts of species specifically adapted to these zones, while species intolerant to low oxygen levels are forced to shift their habitats as well (Seibel et al. 2014, Stramma et al. 2012, Zeidberg & Robison 2007). The induced latitudinal shifts again alter the light conditions the species encounter and could thus impair diel and/or seasonal timing (**Figure 4**).

Generally, present-day temperature changes are especially pronounced at high latitudes (Cohen et al. 2014, Ducklow et al. 2007), and ocean acidification will also disproportionally affect these regions due to higher CO_2 solubility in cold water (Fabry et al. 2009). Hence, it is likely that present and future changes in marine rhythms will be especially pronounced in polar habitats (Tougeron 2021).

5.3. Adaptability of Rhythms and Clocks to Future Ocean Conditions

Climatic conditions continue to change, and marine organisms will have to respond by either adapting to them or avoiding them through distribution shifts. Changes can affect a species' rhythmic environment as well as its ability to respond to such changes (**Figure 4**). It is also important to distinguish rhythms that are direct responses to environmental changes and those that are generated by endogenous timing systems, as the responses to ecological changes will differ significantly, for example, due to temperature compensation.

5.3.1. Phenotypic adaptive capacity.

As discussed above, climate change can cause major latitudinal distribution shifts in marine species, for example, due to increasing temperatures or expanding OMZs. However, individual adaptive capacity and photoperiodic range for clock functioning (diel rhythmicity and seasonal photoperiodism) are adjusted to a given habitat (Bradshaw & Holzapfel 2001, Höring et al. 2018, Schneck & Barreto 2020) and could hinder occupation of new, higher-latitude habitats with different environmental cycles (Huffeldt 2020, Kaartvedt & Titelman 2018, Saikkonen et al. 2012). If species are unable to adjust their timing systems to the altered environment or cannot shift their distribution due to rigid timing systems, they face suboptimal environmental conditions and, as a consequence, likely reduced fitness and abundance (Deutsch et al. 2015, Hughes et al. 2019) (**Figure 4**). Furthermore, if a species does not shift its distribution, temperature can directly affect photoperiodic seasonal timing, thus altering species phenology in spite of unchanged light conditions (Hairston & Kearns 1995, Watson & Smallman 1971) (**Figure 4**). Generally, whether species exhibit distribution shifts will depend on the relative selection pressure exerted by the light environment relative to other environmental factors (Tougeron 2021).

Phenotypic rhythm and clock adaptability to altered environments is difficult to predict. Classical as well as recent work shows that circadian periods can be plastic, for instance, depending on ambient light intensities (Aschoff 1960, Zurl et al. 2022) (see Section 4) and photoperiods (Pfeuty et al. 2012, Piccolin et al. 2018).

By contrast, circadian clock genes peak at the same time under field photoperiods of 16 h (56°N) and almost 24 h (79°N) in the boreal copepod *C. finmarchicus* (Häfker et al. 2018a,b). However, a significant fraction of the *C. finmarchicus* transcriptome, including presumptive core circadian clock genes, showed semidiurnal cycling under midnight sun conditions at 82.5°N (Hüppe et al. 2020, Payton et al. 2020), due to either the different light conditions or entrainment by tidal food cues. A possible adaptation to extreme photoperiods might also be the approximately tidal period of core circadian clock gene transcript oscillations in the brain of the Antarctic krill (*E. superba*) under constant (darkness) conditions, which shifted to an ∼24-h period under light–dark cycles (Piccolin et al. 2020). It is also possible that latitudinal light changes could be compensated for behaviorally through vertical distribution adjustments.

5.3.2. Evolutionary adaptation of clock and rhythms.

The speed of evolutionary adaptation depends on several factors, including overall population size, connectivity of populations, generation time, and selection pressure. Many of these factors differ strongly between marine and terrestrial habitats. Gene flow is typically considered to be stronger in the oceans due to the interconnection of water masses, reproduction through broadcast spawning, and larval dispersal via currents. The zooplankton species *C. finmarchicus* and *E. superba* both have enormous overall population sizes and inhabit vast areas of the North Atlantic and Southern Oceans, respectively. Nevertheless, *C. finmarchicus* and its congener *C. glacialis* show at best weak genetic differentiation among populations (Choquet et al. 2019, Weydmann et al. 2018), and for *E. superba* there seems to be no genetic differentiation at all (Deagle et al. 2015). While high overall population size should increase the probability of the emergence of favorable alleles and rhythmic phenotypes, the high connectivity of habitats could hinder the genetic adaptation of rhythmicity to a new local regime, as occurred in, for example, the midge *C. marinus* (Kaiser et al. 2010, 2021).

Mismatch: a dissimilarity in the distribution, timing, abundance, and so on of two or more currently interacting species that often results in fitness reduction

Low genetic differentiation among populations could be a trait of highly abundant species (e.g., *E. superba* and *Calanus* spp.), while stronger differentiation may be found between populations of less conspicuous species (Peijnenburg & Goetze 2013). This would mean that species of high abundance and ecological relevance could struggle the most to adapt their rhythmicity because the high marine connectivity hinders genetic differentiation. Understanding the timing systems and adaptability of such keystone species is thus of particular importance.

Potentially rapid evolution of new chronotypes in response to environmental changes could occur through hybridization (Kaiser et al. 2010, Strelkov et al. 2007). *C. marinus* parents from populations with differing diel emergence timing produce offspring with intermediate timing rhythms (Neumann 1967). Although less studied, hybridization seems to be just as common in marine environments as in terrestrial ecosystems (Gardner 1997) and has been reported in numerous species, including fish and bivalves (Montanari et al. 2016, Zbawicka et al. 2019). However, even for closely related species (e.g., the *Calanus* complex), hybridization is not necessarily a given (Choquet et al. 2017, 2021) and can be hindered by temporal reproductive isolation (Niehoff et al. 2002). Thus, determining the hybridization potential among closely related species and the rhythms of hybrid offspring could provide valuable insights on their adaptability to climate change.

5.3.3. Interspecies mismatches. Both generation times and timing mechanisms are species specific, and circadian clocks can show mechanistic differences among species, even when they are closely related (Menegazzi et al. 2017, Tomioka & Matsumoto 2015). It is thus likely that phenotypic adaptive capacity and the time needed to evolve chronobiological adaptations will strongly differ among species. This is even more probable if species use different timing mechanisms, as suggested for both seasonal (Baumgartner & Tarrant 2017, Goldman et al. 2004) and lunar (Kaiser & Neumann 2021) rhythms. Furthermore, as suboptimal timing results in a loss in fitness and likely reduced abundance (Dodd et al. 2005, Horn et al. 2019, Spoelstra et al. 2016, Yerushalmi & Green 2009), species with proper timing can still be affected through, for example, trophic interactions with suboptimally timed species (**Figure 4**). Moreover, latitudinal shifts can separate trophic interactors or lead to encounters between species that were previously separated (Chivers et al. 2017, Kaartvedt & Titelman 2018, Thorne & Nye 2021) (**Figure 4**). If species adjust their seasonal timing based on environmental cues (e.g., temperature, food availability, light intensity and spectrum, or photoperiod) and/or endogenous timing systems (circannual clock or hourglass timer), this can cause mismatches in response to climate change (Durant et al. 2019, Régnier et al. 2019) (**Figure 4**). For example, the onset of the Arctic phytoplankton bloom is gradually shifting to earlier dates (Kahru et al. 2010), but seasonal reproduction of the copepod *C. glacialis*, which depends on the bloom as a food source, could not adapt to changed bloom timing, resulting in a seasonal mismatch with low copepod abundance (Søreide et al. 2010). Control of *Calanus* seasonal diapause is not properly understood, but it is thought to rely on endogenous cues such as lipid content, circannual clocks (Baumgartner & Tarrant 2017, Conover 1965, Fulton 1973), and/or photoperiod (Häfker et al. 2018b).

At lower latitudes, seasonal mismatches affecting a given species could be compensated by other species becoming more abundant (Atkinson et al. 2015), but high-latitude systems are often centered on a limited number of highly abundant species, which show precisely adjusted seasonal timing due to the shorter productive period (Falk-Petersen et al. 2009). Thus, temporal mismatches might become more prominent in temperate and polar seas with high seasonality, which also harbor many of the most important commercial fisheries. Some models suggest that changes of high-latitude habitats toward possibly longer productive periods (due to higher temperatures) and smaller species with shorter generation lengths could result in increased productivity (Feng et al. 2017, Renaud et al. 2018). However, such models typically lack considerations of climate effects on the organisms' timing systems.

6. CONCLUSIONS AND OUTLOOK

Marine environments are characterized by numerous environmental cycles, and biological rhythms are central in shaping species interactions as well as ecosystem functioning and productivity. Periods span from the DVMs of pelagic organisms to the seasonal productivity rhythms of temperate and polar latitudes to moon-synchronized reproductions that result in sudden bursts of food abundance. Biological rhythms are important for organisms from the surface to the bottom of the deep sea. Many of these rhythms are under the control of endogenous timing mechanisms, and the (emerging) model species highlighted in this review have helped to identify general principles of oscillator functioning that are relevant for more than just marine habitats. Marine models have also helped to provide fundamental insights that still require further understanding, such as the existence of an ~24-h metabolic oscillator, the remarkable diversification of circadian clock systems in polyphyletic algae, the plasticity of the conventional core circadian clock in animals, and the decoding of solar versus lunar light input. It will be of increasing importance to discriminate between truly endogenous oscillator–driven rhythms and organismal rhythms that directly follow environmental changes. The impact of changing environmental cues on both types of rhythms is very different—for example, due to the presence or absence of temperature compensation and the responses to environmental cues as entrainment factors versus rhythm drivers.

Environmental changes will—either directly or indirectly—affect marine rhythms and timing systems, but to what extent they can adapt to changes and the time needed to do so are still hardly explored. Effects of climate change on marine rhythms could result in major ecosystem restructuring and changes in productivity that could also affect fishery yields and marine CO_2 storage.

It is evident that the quest for an understanding of marine rhythms must not stop at the descriptive, phenomenological level, but must move to the cellular and molecular mechanistic levels, for which model systems can pave the way. Such investigations will be crucial to better understand and predict consequences of climate change. Yet proper observations of environmental factors and biological systems will also be essential for the future, as particularly exemplified by the recent discovery of rhythms in the deep sea. After all, solid observations and descriptions are the basis from which discoveries arise—from the bottom of the deep sea to the surface of the shores.

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