



**HAL**  
open science

## Rhythms and Clocks in Marine Organisms

N Sören Häfker, Gabriele Andreatta, Alessandro Manzotti, Angela Falciatore,  
Florian Raible, Kristin Tessmar-Raible

► **To cite this version:**

N Sören Häfker, Gabriele Andreatta, Alessandro Manzotti, Angela Falciatore, Florian Raible, et al..  
Rhythms and Clocks in Marine Organisms. Annual Review of Marine Science, pp.509-538, 2022,  
10.1146/annurev-marine-030422-113038 . hal-03944242

**HAL Id: hal-03944242**

**<https://hal.science/hal-03944242>**

Submitted on 17 Jan 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

*Annual Review of Marine Science*  
**Rhythms and Clocks in  
 Marine Organisms**

N. Sören Häfker,<sup>1,2,\*</sup> Gabriele Andreatta,<sup>1,2,\*</sup>  
 Alessandro Manzotti,<sup>3,\*</sup> Angela Falciatore,<sup>3</sup>  
 Florian Raible,<sup>1,2</sup> and Kristin Tessmar-Raible<sup>1,2,4,5</sup>

<sup>1</sup>Max Perutz Labs, University of Vienna, Vienna BioCenter, Vienna, Austria;  
 email: florian.raible@univie.ac.at, kristin.tessmar@mfl.ac.at

<sup>2</sup>Research Platform “Rhythms of Life,” University of Vienna, Vienna BioCenter, Vienna, Austria

<sup>3</sup>Laboratoire de Biologie du Chloroplaste et Perception de la Lumière chez les Microalgues,  
 UMR 7141, CNRS, Sorbonne Université, Institut de Biologie Physico-Chimique, Paris, France;  
 email: angela.falciatore@ibpc.fr

<sup>4</sup>Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven,  
 Germany

<sup>5</sup>Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University  
 of Oldenburg, Oldenburg, Germany

**ANNUAL  
 REVIEWS CONNECT**

[www.annualreviews.org](http://www.annualreviews.org)

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Annu. Rev. Mar. Sci. 2023. 15:509–38

First published as a Review in Advance on  
 August 26, 2022

The *Annual Review of Marine Science* is online at  
[marine.annualreviews.org](http://marine.annualreviews.org)

<https://doi.org/10.1146/annurev-marine-030422-113038>

Copyright © 2023 by the author(s). This work is licensed under a Creative Commons Attribution 4.0 International License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See credit lines of images or other third-party material in this article for license information.

\*These authors contributed equally to this article

**Keywords**

endogenous oscillators, environmental cycles, climate change, circadian, circatidal, circalunar, circannual, algae, animals

**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

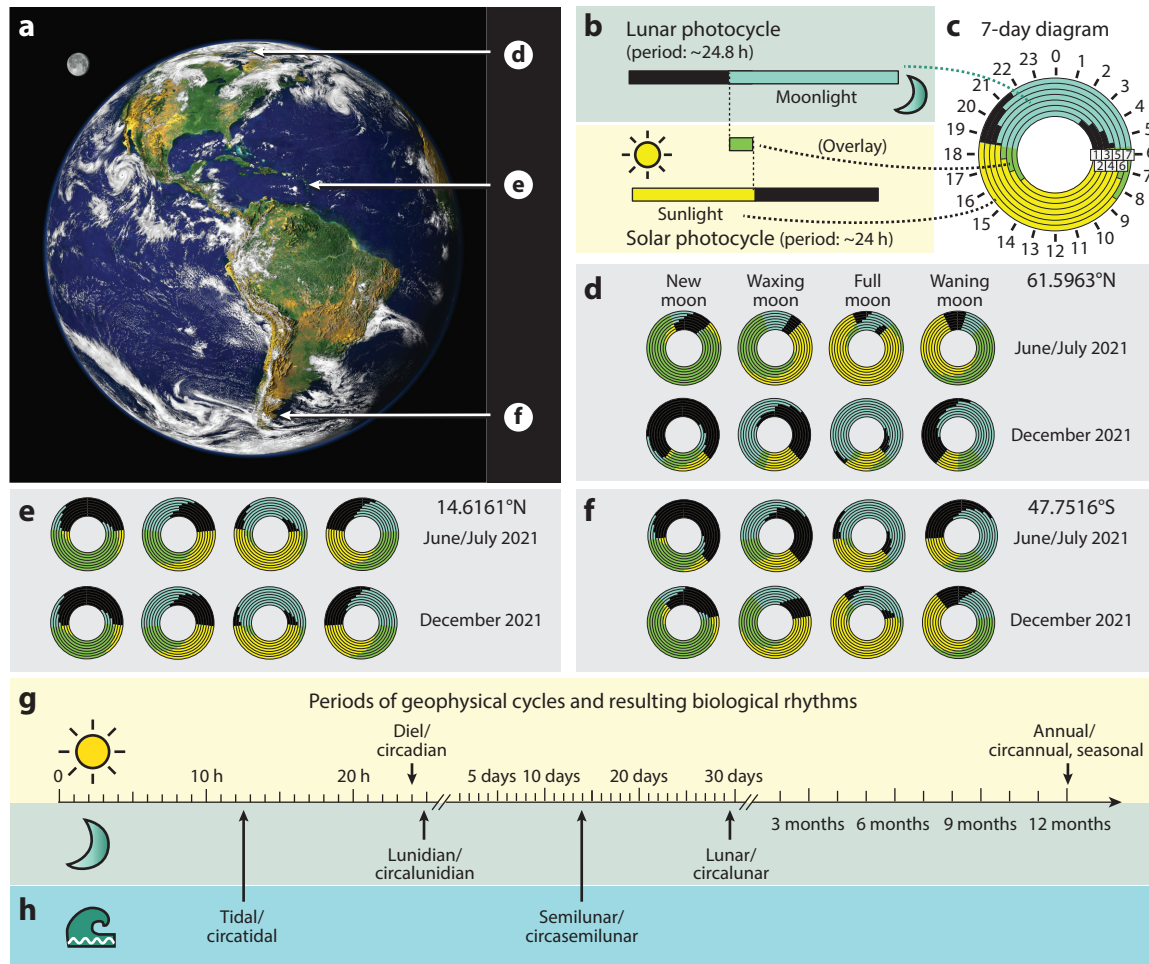
## 1. CYCLES OF THE SUN AND MOON CAUSE A MULTITUDE OF BIOLOGICAL RHYTHMS

“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 1a**) 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 1g,b**). Furthermore, these cycles differ depending on geographic location (**Figure 1b-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 1g,b**). 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, Kritika & 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).

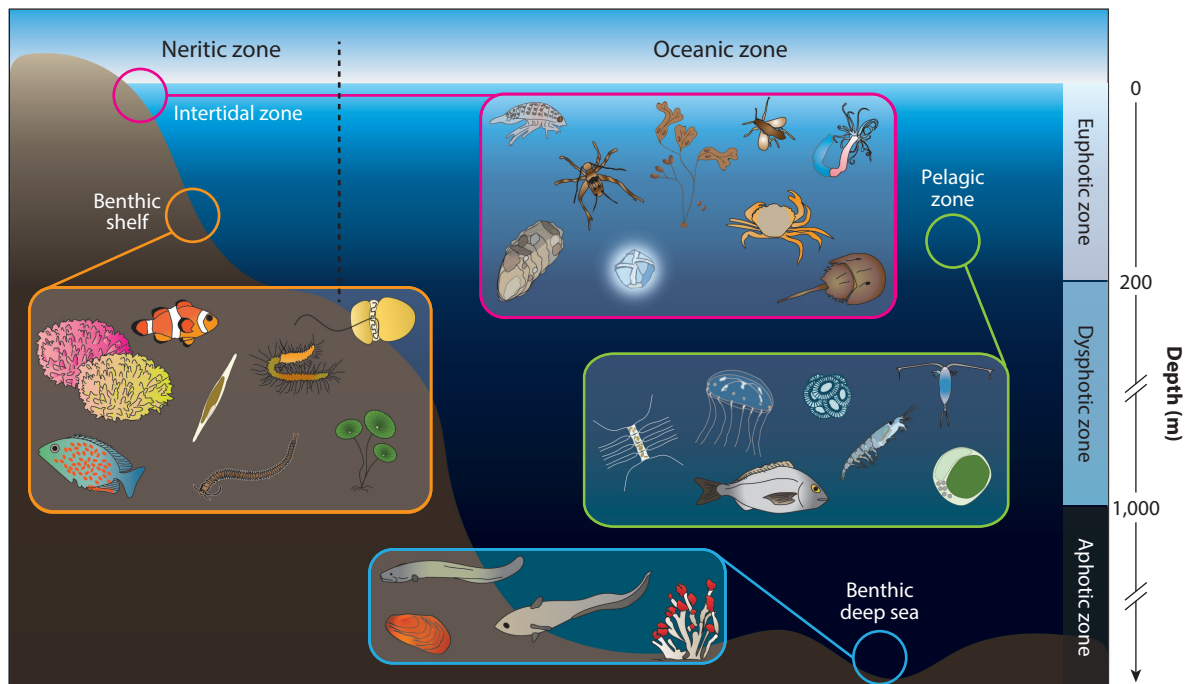
Whether a rhythm is endogenous needs to be experimentally determined. A hallmark of inner oscillators is a free-running biological rhythm that is maintained even under environmental



**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. (b) 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**

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,

### **Free-running**

#### **biological rhythm:**

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

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.

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).

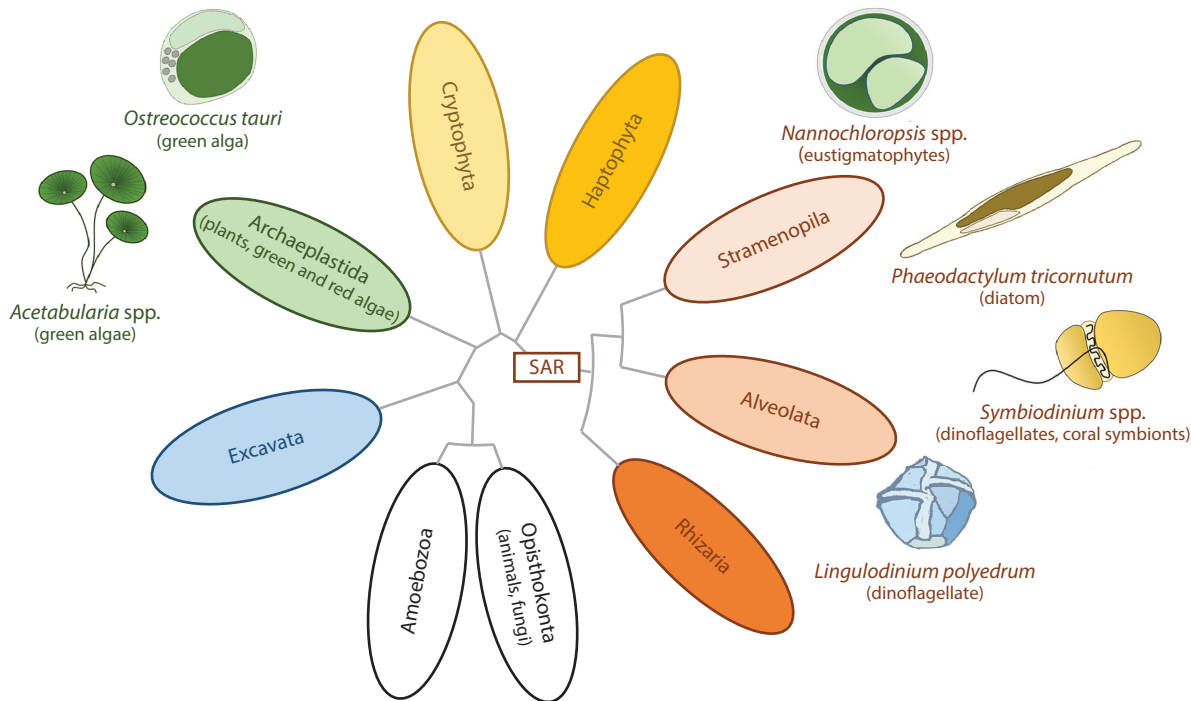
---

**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

---



**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).

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).

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

**Supplemental Material** >

**Input:**

a cue involved in the entrainment process

*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).

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 tricorutum* 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. tricorutum* (*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.

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.

## 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, Tørling 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

---

#### 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

---

**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, *Benthoosema 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 (Andrzejczek 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 retinæ 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 (*Bathymodiulus 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 1g,b; Supplemental Tables 2 and 3**).

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 hawaiiensis* (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 *Apteronomobius asabinai*, 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-Opn1, 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<sup>2+</sup>]-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

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).

Supplemental Material >

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.

Circa(semi)lunar clocks might rely on (a) oscillators with a periodicity of  $\sim 15$  or  $\sim 30$  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  $\sim 15$  or  $\sim 30$  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 multimer 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).

---

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

---

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).

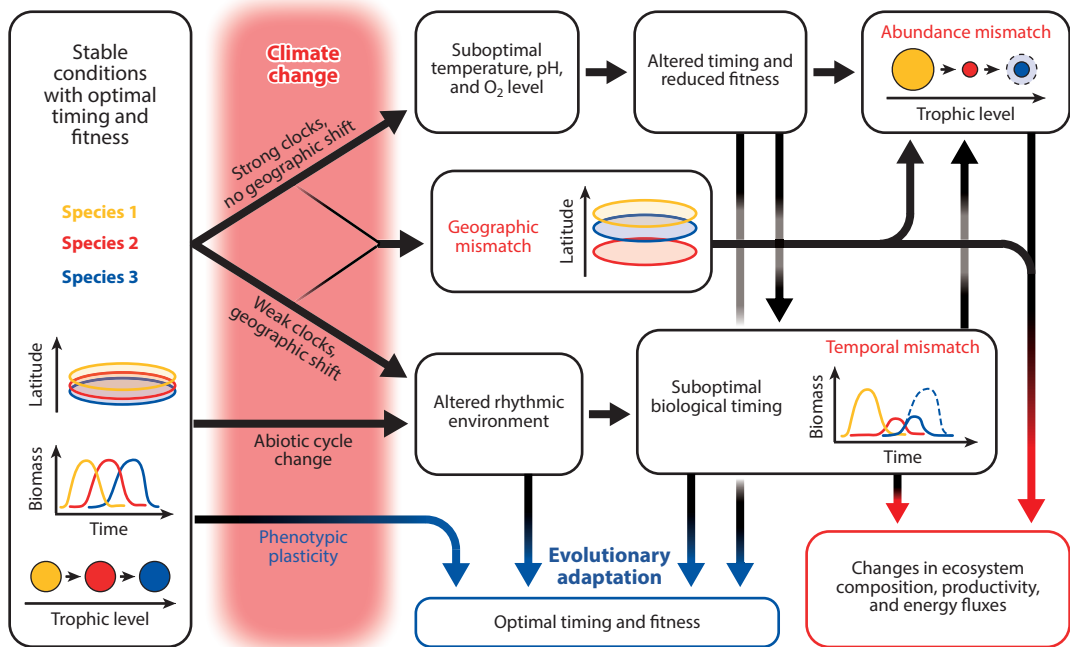
Other evidence for favorable plasticity in timing stems from the Arctic and North Atlantic *Calanus* complex. The boreal copepod *C. finmarchicus* maintained its population size throughout the Last Glacial Maximum, while its Arctic congener *C. glacialis* experienced an ~1,000-fold increase in population 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<sub>2</sub> 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<sub>2</sub>, 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 (Lieberman 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<sub>2</sub> 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 disproportionately affect these regions due to higher CO<sub>2</sub> 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 sub-optimal 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<sub>2</sub> 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.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We apologize to colleagues whose work could not be cited due to space limitations.

Research in A.F.'s laboratory is supported by the Fondation Bettencourt Schueller (Coups d'élan pour la recherche française 2018), the Initiative d'Excellence program (grant DYNAMO, ANR-11-LABX-0011-01), the Agence Nationale de la Recherche (ANR)—Deutsche Forschungsgemeinschaft (DFG) grant DiaRhythm (KR1661/20-1), and the ANR grant ClimaClock (ANR-20-CE20-0024). Research in F.R.'s and K.T.-R.'s laboratories is funded by the European Research Council (ERC) under the European Community's Seventh Framework Program (FP7/2007–2013) through ERC grant 260304 (F.R.) and ERC grant 337011 (K.T.-R.), Horizon 2020 Program ERC grant 81995 (K.T.-R.), the Distinguished Professorship program of the

Helmholtz Society (K.T.-R.), the research platforms Rhythms of Life (F.R. and K.T.-R.) and Single-Cell Genomics of Stem Cells (F.R.) of the University of Vienna, an Austrian Science Fund [Fonds zur Förderung der Wissenschaftlichen Forschung (FWF)] START award (project Y413, K.T.-R.), FWF projects P28970 (K.T.-R.) and I2972 (F.R.), and FWF grant F78 (F.R. and K.T.-R.). N.S.H. was supported by a Lise Meitner Excellence Fellowship from the FWF (M2820).

## LITERATURE CITED

- Aguzzi J, Company JB, Costa C, Menesatti P, Garcia JA, et al. 2011. Activity rhythms in the deep-sea: a chronobiological approach. *Front. Biosci. Landmark Ed.* 16:131–50
- Andersson S, Kautsky L, Kalvas A. 1994. Circadian and lunar gamete release in *Fucus vesiculosus* in the atidal Baltic Sea. *Mar. Ecol. Prog. Ser.* 110:195–201
- Andreatta G, Tessmar-Raible K. 2020. The still dark side of the moon: molecular mechanisms of lunar-controlled rhythms and clocks. *J. Mol. Biol.* 432:3525–46
- Andrzejczek S, Vély M, Jouannet D, Rowat D, Fossette S. 2021. Regional movements of satellite-tagged whale sharks *Rhincodon typus* in the Gulf of Aden. *Ecol. Evol.* 11:4920–34
- Annunziata R, Ritter A, Fortunato AE, Manzotti A, Cheminant-Navarro S, et al. 2019. bHLH-PAS protein RITMO1 regulates diel biological rhythms in the marine diatom *Phaeodactylum tricorutum*. *PNAS* 116:13137–42
- Arboleda E, Hartenstein V, Martinez P, Reichert H, Sen S, et al. 2018. An emerging system to study photo-symbiosis, brain regeneration, chronobiology, and behavior: the marine acel *Symsagittifera roscoffensis*. *BioEssays* 40:e1800107
- Arboleda E, Zurl M, Waldherr M, Tessmar-Raible K. 2019. Differential impacts of the head on *Platynereis dumerilii* peripheral circadian rhythms. *Front. Physiol.* 10:900
- Aschoff J. 1960. Exogenous and endogenous components in circadian rhythms. *Cold Spring Harb. Symp. Quant. Biol.* 25:11–28
- Aschoff J. 1965. Circadian rhythms in man. *Science* 148:1427–32
- Asher G, Sassone-Corsi P. 2015. Time for food: the intimate interplay between nutrition, metabolism, and the circadian clock. *Cell* 161:84–92
- Atkinson A, Harmer RA, Widdicombe CE, McEvoy AJ, Smyth TJ, et al. 2015. Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Prog. Oceanogr.* 137:498–512
- Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss CS, et al. 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat. Clim. Change* 9:142–47
- Austin RW, Petzold TJ. 1986. Spectral dependence of the diffuse attenuation coefficient of light in ocean waters. *Opt. Eng.* 25:471–79
- Ayalon I, Rosenberg Y, Benichou JIC, Campos CLD, Sayco SLG, et al. 2020. Coral gametogenesis collapse under artificial light pollution. *Curr. Biol.* 31:413–19
- Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, et al. 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Mar. Biol.* 90:379–94
- Baghel KK, Pati AK. 2015. Pheromones as time cues for circadian rhythms in fish. *Biol. Rhythm Res.* 46:659–69
- Baillon S, Hamel J-F, Mercier A. 2014. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. *PLOS ONE* 9:e111519
- Baumgartner MF, Tarrant AM. 2017. The physiology and ecology of diapause in marine copepods. *Annu. Rev. Mar. Sci.* 9:387–411
- Berge J, Cottier F, Last KS, Varpe Ø, Leu E, et al. 2009. Diel vertical migration of Arctic zooplankton during the polar night. *Biol. Lett.* 5:69–72
- Berge J, Geoffroy M, Daase M, Cottier F, Priou P, et al. 2020. Artificial light during the polar night disrupts Arctic fish and zooplankton behaviour down to 200 m depth. *Commun. Biol.* 3:102
- Berge J, Renaud PE, Darnis G, Cottier F, Last K, et al. 2015. In the dark: a review of ecosystem processes during the Arctic polar night. *Prog. Oceanogr.* 139:258–71
- Bilcke G, Osuna-Cruz CM, Silva MS, Poulsen N, Bulankova P, et al. 2021. Diurnal transcript profiling of the diatom *Seminavis robusta* reveals adaptations to a benthic lifestyle. *Plant J.* 107:315–36

- Biscontin A, Martini P, Costa R, Kramer A, Meyer B, et al. 2019. Analysis of the circadian transcriptome of the Antarctic krill *Euphausia superba*. *Sci. Rep.* 9:13894
- Biscontin A, Wallach T, Sales G, Grudziecki A, Janke L, et al. 2017. Functional characterization of the circadian clock in the Antarctic krill, *Euphausia superba*. *Sci. Rep.* 7:17742
- Blaby-Haas CE, Merchant SS. 2019. Comparative and functional algal genomics. *Annu. Rev. Plant Biol.* 70:605–38
- Bouget F-Y, Lefranc M, Thommen Q, Pfeuty B, Lozano J-C, et al. 2014. Transcriptional versus non-transcriptional clocks: a case study in *Ostreococcus*. *Mar. Genom.* 14:17–22
- Bradshaw WE, Holzapfel CM. 2001. Genetic shift in photoperiodic response correlated with global warming. *PNAS* 98:14509–11
- Brawley SH, Johnson LE. 1992. Gametogenesis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. *Br. Phycol. J.* 27:233–52
- Brenna A, Albrecht U. 2020. Phosphorylation and circadian molecular timing. *Front. Physiol.* 11:612510
- Brierley AS. 2014. Diel vertical migration. *Curr. Biol.* 24:R1074–76
- Brodie J, Chan CX, De Clerck O, Cock JM, Coelho SM, et al. 2017. The algal revolution. *Trends Plant Sci.* 22:726–38
- Brun P, Stamieszkin K, Visser AW, Licandro P, Payne MR, Kiørboe T. 2019. Climate change has altered zooplankton-fuelled carbon export in the North Atlantic. *Nat. Ecol. Evol.* 3:416–23
- Buhr ED, Yoo S-H, Takahashi JS. 2010. Temperature as a universal resetting cue for mammalian circadian oscillators. *Science* 330:379–85
- Caballes CF, Pratchett MS. 2017. Environmental and biological cues for spawning in the crown-of-thorns starfish. *PLOS ONE* 12:e0173964
- Chabot CC, Ramberg-Pihl NC, Watson WH. 2016. Circalunidian clocks control tidal rhythms of locomotion in the American horseshoe crab, *Limulus polyphemus*. *Mar. Freshw. Behav. Physiol.* 49:75–91
- Chabot CC, Watson WH III. 2010. Circatidal rhythms of locomotion in the American horseshoe crab *Limulus polyphemus*: underlying mechanisms and cues that influence them. *Curr. Zool.* 56:499–517
- Chambault P, Fossette S, Heide-Jørgensen MP, Jouannet D, Vély M. 2021. Predicting seasonal movements and distribution of the sperm whale using machine learning algorithms. *Ecol. Evol.* 11:1432–45
- Chang Y, Dall’Olmo G, Schabetsberger R. 2020. Tracking the marine migration routes of South Pacific silver eels. *Mar. Ecol. Prog. Ser.* 646:1–12
- Chen C, Buhl E, Xu M, Croset V, Rees JS, et al. 2015. *Drosophila* Ionotropic Receptor 25a mediates circadian clock resetting by temperature. *Nature* 527:516–20
- Chivers WJ, Walne AW, Hays GC. 2017. Mismatch between marine plankton range movements and the velocity of climate change. *Nat. Commun.* 8:14434
- Choquet M, Hatlebakk M, Dhanasiri AKS, Kosobokova K, Smolina I, et al. 2017. Genetics redraws pelagic biogeography of *Calanus*. *Biol. Lett.* 13:20170588
- Choquet M, Smolina I, Dhanasiri AKS, Blanco-Bercial L, Kopp K, et al. 2019. Towards population genomics in non-model species with large genomes: a case study of the marine zooplankton *Calanus finmarchicus*. *R. Soc. Open Sci.* 6:180608
- Choquet M, Smolina I, Hoarau G. 2021. No evidence for hybridization in *Calanus*: reply to the comment by Parent et al. *Limnol. Oceanogr.* 66:3603–6
- Chow S, Okazaki M, Watanabe T, Segawa K, Yamamoto T, et al. 2015. Light-sensitive vertical migration of the Japanese eel *Anguilla japonica* revealed by real-time tracking and its utilization for geolocation. *PLOS ONE* 10:e0121801
- Christiansen S, Titelman J, Kaartvedt S. 2019. Nighttime swimming behavior of a mesopelagic fish. *Front. Mar. Sci.* 6:787
- Coelho R, Fernandez-Carvalho J, Santos M. 2015. Habitat use and diel vertical migration of bigeye thresher shark: overlap with pelagic longline fishing gear. *Mar. Environ. Res.* 112:91–99
- Coesel SN, Durham BP, Groussman RD, Hu SK, Caron DA, et al. 2021. Diel transcriptional oscillations of light-sensitive regulatory elements in open-ocean eukaryotic plankton communities. *PNAS* 118:e2011038118

- Coesel SN, Mangogna M, Ishikawa T, Heijde M, Rogato A, et al. 2009. Diatom PtCPF1 is a new cryptochrome/photolyase family member with DNA repair and transcription regulation activity. *EMBO Rep.* 10:655–61
- Coffey DM, Royer MA, Meyer CG, Holland KN. 2020. Diel patterns in swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill (*Hexanchus griseus*). *PLOS ONE* 15:e0228253
- Cohen JH, Last KS, Charpentier CL, Cottier F, Daase M, et al. 2021. Photophysiological cycles in Arctic krill are entrained by weak midday twilight during the Polar Night. *PLOS Biol.* 19:e3001413
- Cohen JH, Screen JA, Furtado JC, Barlow M, Whittleston D, et al. 2014. Recent Arctic amplification and extreme mid-latitude weather. *Nat. Geosci.* 7:627–37
- Connor KM, Gracey AY. 2011. Circadian cycles are the dominant transcriptional rhythm in the intertidal mussel *Mytilus californianus*. *PNAS* 108:16110–15
- Conover RJ. 1965. Notes on the molting cycle, development of sexual characters and sex ratio in *Calanus hyperboreus*. *Crustaceana* 8:308–20
- Corellou F, Schwartz C, Motta J-P, Djouani-Tahri EB, Sanchez F, Bouget F-Y. 2009. Clocks in the green lineage: comparative functional analysis of the circadian architecture of the picoeukaryote *Ostreococcus*. *Plant Cell* 21:3436–49
- Courties C, Vaquer A, Troussellier M, Lautier J. 1994. Smallest eukaryotic organism. *Nature* 370:255
- Creux N, Harmer S. 2019. Circadian rhythms in plants. *Cold Spring Harb. Perspect. Biol.* 11:a034611
- Cuvelier D, Legendre P, Laës-Huon A, Sarradin P-M, Sarrazin J. 2017. Biological and environmental rhythms in (dark) deep-sea hydrothermal ecosystems. *Biogeosciences* 14:2955–77
- d'Alcalá MR, Conversano F, Corato F, Licandro P, Mangoni O, et al. 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. *Sci. Mar.* 68(S1):65–83
- D'Alelio D, d'Alcalá MR, Dubroca L, Sarn D, Zingone A, Montresor M. 2010. The time for sex: a biennial life cycle in a marine planktonic diatom. *Limnol. Oceanogr.* 55:106–14
- Davies TW, Duffy JP, Bennie J, Gaston KJ. 2014. The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* 12:347–55
- de Lima CDM, Göndör A. 2018. Circadian organization of the genome. *Science* 359:1212–13
- De Pontual H, Jolivet A, Bertignac M, Fablet R. 2012. Diel vertical migration of European hake *Merluccius merluccius* and associated temperature histories: insights from a pilot data-storage tagging (DST) experiment. *J. Fish Biol.* 81:728–34
- Deagle BE, Faux C, Kawaguchi S, Meyer B, Jarman SN. 2015. Antarctic krill population genomics: apparent panmixia, but genome complexity and large population size muddy the water. *Mol. Ecol.* 24:4943–59
- Deutsch C, Ferrel A, Seibel B, Pörtner H-O, Huey RB. 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–35
- Dixson DL, Munday PL, Jones GP. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* 13:68–75
- Dodd AN, Salathia N, Hall A, Kévei E, Tóth R, et al. 2005. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Science* 309:630–33
- Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, et al. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philos. Trans. R. Soc. B* 362:67–94
- Durant JM, Molinero J-C, Ottersen G, Reygondeau G, Stige LC, Langangen Ø. 2019. Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. *Sci. Rep.* 9:15213
- Dypvik E, Klevjer TA, Kaartvedt S. 2012a. Inverse vertical migration and feeding in glacier lanternfish (*Bentosema glaciale*). *Mar. Biol.* 159:443–53
- Dypvik E, Røstad A, Kaartvedt S. 2012b. Seasonal variations in vertical migration of glacier lanternfish, *Bentosema glaciale*. *Mar. Biol.* 159:1673–83
- Edgar RS, Green EW, Zhao Y, van Ooijen G, Olmedo M, et al. 2012. Peroxiredoxins are conserved markers of circadian rhythms. *Nature* 485:459–64
- Elowe C, Tomanek L. 2021. Circadian and circatidal rhythms of protein abundance in the California mussel (*Mytilus californianus*). *Mol. Ecol.* 30:5151–63
- Enright JT. 1976. Plasticity in an isopod's clockworks: Shaking shapes form and affects phase and frequency. *J. Comp. Physiol.* 107:13–37

- Evans WG. 1976. Circadian and circatidal locomotory rhythms in the intertidal beetle *Thalassotrechus barbarae* (Horn): Carabidae. *J. Exp. Mar. Biol. Ecol.* 22:79–90
- Fabry VJ, McClintock JB, Mathis JT, Grebmeier J. 2009. Ocean acidification at high latitudes: the bellwether. *Oceanography* 22(4):160–71
- Falciatore A, Jaubert M, Bouly J-P, Bailleul B, Mock T. 2020. Diatom molecular research comes of age: model species for studying phytoplankton biology and diversity. *Plant Cell* 32:547–72
- Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR. 2009. Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5:18–39
- Farré EM. 2020. The brown clock: circadian rhythms in stramenopiles. *Physiol. Plant.* 169:430–41
- Feng Z, Ji R, Ashjian C, Campbell R, Zhang J. 2017. Biogeographic responses of the copepod *Calanus glacialis* to a changing Arctic marine environment. *Glob. Change Biol.* 24:e159–70
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–40
- Fogarty ND, Marhaver KL. 2019. Coral spawning, unsynchronized. *Science* 365:987–88
- Fortier M, Fortier L, Hattori H, Saito H, Legendre L. 2001. Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *J. Plankton Res.* 23:1263–78
- Fortunato AE, Jaubert M, Enomoto G, Bouly J-P, Raniello R, et al. 2016. Diatom phytochromes reveal the existence of far-red-light-based sensing in the ocean. *Plant Cell* 28:616–28
- Foster WA, Moreton RB. 1981. Synchronization of activity rhythms with the tide in a saltmarsh collembolan *Anurida maritima*. *Oecologia* 50:265–70
- Fulton J. 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Board Can.* 30:811–15
- Fung-Uceda J, Lee K, Seo PJ, Polyn S, De Veylder L, Mas P. 2018. The circadian clock sets the time of DNA replication licensing to regulate growth in *Arabidopsis*. *Dev. Cell* 45:101–113.e4
- Gardner JPA. 1997. Hybridization in the sea. In *Advances in Marine Biology*, Vol. 31, ed. JHS Blaxter, AJ Southward, pp. 1–78. San Diego, CA: Academic
- Garrett C. 2003. Internal tides and ocean mixing. *Science* 301:1858–59
- Gekakis N. 1998. Role of the CLOCK protein in the mammalian circadian mechanism. *Science* 280:1564–69
- Gerkema MP, Davies WIL, Foster RG, Menaker M, Hut RA. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proc. R. Soc. B* 280:20130508
- Gilly WF, Markaida U, Baxter CH, Block BA, Boustany A, et al. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser.* 324:1–17
- Goldman B, Gwinner E, Karsch FJ, Saunders D, Zucker I, Gall GF. 2004. Circannual rhythms and photoperiodism. In *Chronobiology: Biological Timekeeping*, ed. JC Dunlap, JJ Loros, PJ DeCoursey, pp. 107–42. Sunderland, MA: Sinauer
- Häfker NS, Meyer B, Last KS, Pond DW, Hüppe L, Teschke M. 2017. Circadian clock involvement in zooplankton diel vertical migration. *Curr. Biol.* 27:2194–201.e3
- Häfker NS, Teschke M, Hüppe L, Meyer B. 2018a. *Calanus finmarchicus* diel and seasonal rhythmicity in relation to endogenous timing under extreme polar photoperiods. *Mar. Ecol. Prog. Ser.* 603:79–92
- Häfker NS, Teschke M, Last KS, Pond DW, Hüppe L, Meyer B. 2018b. *Calanus finmarchicus* seasonal cycle and diapause in relation to gene expression, physiology, and endogenous clocks. *Limnol. Oceanogr.* 63:2815–38
- Häfker NS, Tessmar-Raible K. 2020. Rhythms of behavior: Are the times changin'? *Curr. Opin. Neurobiol.* 60:55–66
- Hairston NG, Kearns CM. 1995. The interaction of photoperiod and temperature in diapause timing: a copepod example. *Biol. Bull.* 189:42–48
- Hastings JW. 2007. The *Gonyaulax* clock at 50: translational control of circadian expression. *Cold Spring Harb. Symp. Quant. Biol.* 72:141–44
- Hastings JW, Sweeney BM. 1957. On the mechanism of temperature independence in a biological clock. *PNAS* 43:804–11
- Hauenschild C. 1960. Lunar periodicity. *Cold Spring Harb. Symp. Quant. Biol.* 25:491–97
- Haydon MJ, Mielczarek O, Frank A, Román A, Webb AAR. 2017. Sucrose and ethylene signaling interact to modulate the circadian clock. *Plant Physiol.* 175:947–58



- Heijde M, Zabulon G, Corellou F, Ishikawa T, Brazard J, et al. 2010. Characterization of two members of the cryptochrome/photolyase family from *Ostreococcus tauri* provides insights into the origin and evolution of cryptochromes. *Plant Cell Environ.* 33:1614–26
- Hendricks WD, Byrum CA, Meyer-Bernstein EL. 2012. Characterization of circadian behavior in the starlet sea anemone, *Nematostella vectensis*. *PLOS ONE* 7:e46843
- Hewson-Browne RC. 1973. Magnetic effects of sea tides. *Phys. Earth Planet. Inter.* 7:167–86
- Hölker F, Bolliger J, Davies TW, Giavi S, Jechow A, et al. 2021. 11 pressing research questions on how light pollution affects biodiversity. *Front. Ecol. Evol.* 9:896
- Höring F, Biscontin A, Harms L, Sales G, Reiss CS, et al. 2021. Seasonal gene expression profiling of Antarctic krill in three different latitudinal regions. *Mar. Genom.* 56:100806
- Höring F, Teschke M, Suberg L, Kawaguchi S, Meyer B. 2018. Light regime affects the seasonal cycle of Antarctic krill (*Euphausia superba*): impacts on growth, feeding, lipid metabolism, and maturity. *Can. J. Zool.* 96:1203–13
- Horn M, Mitesser O, Hovestadt T, Yoshii T, Rieger D, Helfrich-Förster C. 2019. The circadian clock improves fitness in the fruit fly, *Drosophila melanogaster*. *Front. Physiol.* 10:1374
- Howard EM, Penn JL, Frenzel H, Seibel BA, Bianchi D, et al. 2020. Climate-driven aerobic habitat loss in the California Current System. *Sci. Adv.* 6:eaay3188
- Huffeldt NP. 2020. Photic barriers to poleward range-shifts. *Trends Ecol. Evol.* 35:652–55
- Hughes AR, Hanley TC, Moore AF, Ramsay-Newton C, Zerebecki RA, Sotka EE. 2019. Predicting the sensitivity of marine populations to rising temperatures. *Front. Ecol. Environ.* 17:17–24
- Hui M, Song C, Liu Y, Li C, Cui Z. 2017. Exploring the molecular basis of adaptive evolution in hydrothermal vent crab *Austinoegræa alayseae* by transcriptome analysis. *PLOS ONE* 12:e0178417
- Hunt BJ. 2016. *Advancing molecular crustacean chronobiology through the characterisation of the circadian clock in two malacostracan species, Euphausia superba and Parhyale hawaiensis*. PhD Thesis, Univ. Leicester, Leicester, UK
- Hüppe L, Payton L, Last K, Wilcockson D, Ershova E, Meyer B. 2020. Evidence for oscillating circadian clock genes in the copepod *Calanus finmarchicus* during the summer solstice in the high Arctic. *Biol. Lett.* 16:20200257
- IPCC (Intergov. Panel Clim. Change). 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switz.: IPCC
- Jenouvrier S, Caswell H, Barbraud C, Holland M, Strøeve J, Weimerskirch H. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *PNAS* 106:1844–47
- Jesus TF, Moreno JM, Repolho T, Athanasiadis A, Rosa R, et al. 2017. Protein analysis and gene expression indicate differential vulnerability of Iberian fish species under a climate change scenario. *PLOS ONE* 12:e0181325
- Johnson CH, Golden SS. 1999. Circadian programs in cyanobacteria: adaptiveness and mechanism. *Annu. Rev. Microbiol.* 53:389–409
- Jónasdóttir SH, Visser AW, Richardson K, Heath MR. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *PNAS* 112:12122–26
- Jorda G, Marbà N, Bennett S, Santana-Garçon J, Agusti S, Duarte CM. 2020. Ocean warming compresses the three-dimensional habitat of marine life. *Nat. Ecol. Evol.* 4:109–14
- Kaartvedt S. 2010. Diel vertical migration behaviour of the northern krill (*Meganyctiphanes norvegica* Sars). In *Advances in Marine Biology*, Vol. 57, ed. GA Tarling, pp. 255–75. San Diego, CA: Academic
- Kaartvedt S, Titelman J. 2018. Planktivorous fish in a future Arctic Ocean of changing ice and unchanged photoperiod. *ICES J. Mar. Sci.* 75:2312–18
- Kahru M, Brotas V, Manzano-Sarabia M, Mitchell BG. 2010. Are phytoplankton blooms occurring earlier in the Arctic? *Glob. Change Biol.* 17:1733–39
- Kaiser TS, Neumann D, Heckel DG, Berendonk TU. 2010. Strong genetic differentiation and postglacial origin of populations in the marine midge *Clunio marinus* (Chironomidae, Diptera). *Mol. Ecol.* 19:2845–57
- Kaiser TS, Neumann J. 2021. Circalunar clocks—old experiments for a new era. *BioEssays* 43:2100074

- Kaiser TS, Poehn B, Szkiba D, Preussner M, Sedlazeck FJ, et al. 2016. The genomic basis of circadian and circalunar timing adaptations in a midge. *Nature* 540:69–73
- Kaiser TS, von Haeseler A, Tessmar-Raible K, Heckel DG. 2021. Timing strains of the marine insect *Clunio marinus* diverged and persist with gene flow. *Mol. Ecol.* 30:1264–80
- Keith SA, Maynard JA, Edwards AJ, Guest JR, Bauman AG, et al. 2016. Coral mass spawning predicted by rapid seasonal rise in ocean temperature. *Proc. R. Soc. B* 283:20160011
- Kolody BC, McCrow JP, Allen LZ, Aylward FO, Fontanez KM, et al. 2019. Diel transcriptional response of a California Current plankton microbiome to light, low iron, and enduring viral infection. *ISME J.* 13:2817–33
- Krittika S, Yadav P. 2020. Circadian clocks: an overview on its adaptive significance. *Biol. Rhythm Res.* 51:1109–32
- Lambert S, Tragin M, Lozano J-C, Ghiglione J-F, Vaulot D, et al. 2019. Rhythmicity of coastal marine picoeukaryotes, bacteria and archaea despite irregular environmental perturbations. *ISME J.* 13:388–401
- Last KS, Bailhache T, Kramer C, Kyriacou CP, Rosato E, Olive PJW. 2009. Tidal, daily, and lunar-day activity cycles in the marine polychaete *Nereis virens*. *Chronobiol. Int.* 26:167–83
- Last KS, Häfker NS, Hendrick VJ, Meyer B, Tran D, Piccolin F. 2020. Biological clocks and rhythms in polar organisms. In *Polar Night Marine Ecology: Life and Light in the Dead of Night*, ed. J Berge, G Johnsen, JH Cohen, pp. 217–40. Cham, Switz.: Springer
- Last KS, Hobbs L, Berge J, Brierley AS, Cottier F. 2016. Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic winter. *Curr. Biol.* 26:244–51
- Leach WB, Reitzel AM. 2020. Decoupling behavioral and transcriptional responses to color in an eyeless cnidarian. *BMC Genom.* 21:361
- Lenz PH, Roncalli V. 2019. Diapause within the context of life-history strategies in calanid copepods (Calanoida: Crustacea). *Biol. Bull.* 237:170–79
- Levy O, Appelbaum L, Leggat W, Gothlif Y, Hayward DC, et al. 2007. Light-responsive cryptochromes from a simple multicellular animal, the coral *Acropora millepora*. *Science* 318:467–70
- Liberman R, Fine M, Benayahu Y. 2021. Simulated climate change scenarios impact the reproduction and early life stages of a soft coral. *Mar. Environ. Res.* 163:105215
- Maor R, Dayan T, Ferguson-Gow H, Jones KE. 2017. Temporal niche expansion in mammals from a nocturnal ancestor after dinosaur extinction. *Nat. Ecol. Evol.* 1:1889–95
- Mat AM, Massabuau J-C, Ciret P, Tran D. 2014. Looking for the clock mechanism responsible for circatidal behavior in the oyster *Crassostrea gigas*. *Mar. Biol.* 161:89–99
- Mat AM, Sarrazin J, Markov GV, Apremont V, Dubreuil C, et al. 2020. Biological rhythms in the deep-sea hydrothermal mussel *Bathymodiolus azoricus*. *Nat. Commun.* 11:3454
- Matrai P, Thompson B, Keller M. 2005. Circannual excystment of resting cysts of *Alexandrium* spp. from eastern Gulf of Maine populations. *Deep-Sea Res. II* 52:2560–68
- Matsuo T. 2003. Control mechanism of the circadian clock for timing of cell division in vivo. *Science* 302:255–59
- Mehta TS, Lewis RD. 2000. Quantitative tests of a dual circalunidian clock model for tidal rhythmicity in the sand beach isopod *Cirolana cookii*. *Chronobiol. Int.* 17:29–41
- Melle W, Runge J, Head E, Plourde S, Castellani C, et al. 2014. The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits. *Prog. Oceanogr.* 129:244–84
- Menegazzi P, Dalla Benetta E, Beauchamp M, Schlichting M, Steffan-Dewenter I, Helfrich-Förster C. 2017. Adaptation of circadian neuronal network to photoperiod in high-latitude European drosophilids. *Curr. Biol.* 27:833–39
- Mercier A, Sun Z, Baillon S, Hamel J-F. 2011. Lunar rhythms in the deep sea: evidence from the reproductive periodicity of several marine invertebrates. *J. Biol. Rhythms* 26:82–86
- Mergenhagen D, Schweiger HG. 1975. Circadian rhythm of oxygen evolution in cell fragments of *Acetabularia mediterranea*. *Exp. Cell. Res.* 92:127–30
- Meyer B, Freier U, Grimm V, Groeneveld J, Hunt BPV, et al. 2017. The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. *Nat. Ecol. Evol.* 1:1853–61
- Mitbavkar S, Anil AC. 2004. Circadian migratory rhythms of benthic diatoms in a tropical intertidal sand flat: influence of irradiance and tides. *Mar. Biol.* 145:9–20

- Mittag M, Lee DH, Hastings JW. 1994. Circadian expression of the luciferin-binding protein correlates with the binding of a protein to the 3' untranslated region of its mRNA. *PNAS* 91:5257-61
- Miyagishima S, Fujiwara T, Sumiya N, Hirooka S, Nakano A, et al. 2014. Translation-independent circadian control of the cell cycle in a unicellular photosynthetic eukaryote. *Nat. Commun.* 5:3807
- Montanari SR, Hobbs J-PA, Pratchett MS, van Herwerden L. 2016. The importance of ecological and behavioural data in studies of hybridisation among marine fishes. *Rev. Fish Biol. Fish.* 26:181-98
- Morse D, Milos PM, Roux E, Hastings JW. 1989a. Circadian regulation of bioluminescence in *Gonyaulax* involves translational control. *PNAS* 86:172-76
- Morse D, Pappenheimer AM, Hastings JW. 1989b. Role of a luciferin-binding protein in the circadian bioluminescent reaction of *Gonyaulax polyedra*. *J. Biol. Chem.* 264:11822-26
- Moum JN. 2021. Variations in ocean mixing from seconds to years. *Annu. Rev. Mar. Sci.* 13:201-26
- Muller EB, Kooijman SALM, Edmunds PJ, Doyle FJ, Nisbet RM. 2009. Dynamic energy budgets in symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts. *J. Theor. Biol.* 259:44-57
- Narasimamurthy R, Virshup DM. 2021. The phosphorylation switch that regulates ticking of the circadian clock. *Mol. Cell* 81:1133-46
- Naylor E. 1996. Crab clockwork: the case for interactive circatidal and circadian oscillators controlling rhythmic locomotor activity of *Carcinus maenas*. *Chronobiol. Int.* 13:153-61
- Naylor E. 2010. *Chronobiology of Marine Organisms*. Cambridge, UK: Cambridge Univ. Press
- Neumann D. 1966. Die lunare und tägliche Schlüpfperiodik der Mücke *Clunio*: Steuerung und Abstimmung auf die Gezeitenperiodik. *Z. Vgl. Physiol.* 53:1-61
- Neumann D. 1967. Genetic adaptation in emergence time of *Clunio* populations to different tidal conditions. *Helgol. Wiss. Meeresunters.* 15:163-71
- Neumann D. 1968. Die Steuerung einer semilunaren Schlüpfperiodik mit Hilfe eines künstlichen Gezeitenzyklus. *Z. Vgl. Physiol.* 60:63-78
- Neumann D. 1988. The timing of reproduction to distinct spring tide situations in the intertidal insect *Clunio*. In *Behavioral Adaptation to Intertidal Life*, ed. G Chelazzi, M Vannini, pp. 45-54. Boston: Springer
- Nichol DG, Kotwicki S, Zimmermann M. 2013. Diel vertical migration of adult Pacific cod *Gadus macrocephalus* in Alaska. *J. Fish Biol.* 83:170-89
- Niehoff B, Madsen S, Hansen B, Nielsen T. 2002. Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. *Mar. Biol.* 140:567-76
- Oldach MJ, Workentine M, Matz MV, Fan T-Y, Vize PD. 2017. Transcriptome dynamics over a lunar month in a broadcast spawning acroporid coral. *Mol. Ecol.* 26:2514-26
- Omand MM, Steinberg DK, Stamieszkin K. 2021. Cloud shadows drive vertical migrations of deep-dwelling marine life. *PNAS* 118:e2022977118
- O'Neill JS, Lee KD, Zhang L, Feeney K, Webster SG, et al. 2015. Metabolic molecular markers of the tidal clock in the marine crustacean *Eurydice pulchra*. *Curr. Biol.* 25:R326-27
- O'Neill JS, van Ooijen G, Dixon LE, Troein C, Corellou F, et al. 2011. Circadian rhythms persist without transcription in a eukaryote. *Nature* 469:554-58
- Oren M, Tarrant AM, Alon S, Simon-Blecher N, Elbaz I, et al. 2015. Profiling molecular and behavioral circadian rhythms in the non-symbiotic sea anemone *Nematostella vectensis*. *Sci. Rep.* 5:11418
- Palmer JD. 1991. Contributions made to chronobiology by studies of fiddler crab rhythms. *Chronobiol. Int.* 8:110-30
- Palmer JD. 2000. The clocks controlling the tide-associated rhythms of intertidal animals. *BioEssays* 22:32-37
- Payton L, Noirot C, Hoede C, Hüppe L, Last K, et al. 2020. Daily transcriptomes of the copepod *Calanus finmarchicus* during the summer solstice at high Arctic latitudes. *Sci. Data* 7:415
- Peijnenburg KTCA, Goetze E. 2013. High evolutionary potential of marine zooplankton. *Ecol. Evol.* 3:2765-81
- Perrigault M, Andrade H, Bellec L, Ballantine C, Camus L, Tran D. 2020. Rhythms during the polar night: evidence of clock-gene oscillations in the Arctic scallop *Cblamys islandica*. *Proc. R. Soc. B* 287:20201001
- Perrigault M, Tran D. 2017. Identification of the molecular clockwork of the oyster *Crassostrea gigas*. *PLOS ONE* 12:e0169790
- Petersen J, Rredhi A, Szyttenholm J, Mittag M. 2022. Evolution of circadian clocks along the green lineage. *Plant Physiol.* 190:924-37

- Pfeuty B, Thommen Q, Corellou F, Djouani-Tahri EB, Bouget F-Y, Lefranc M. 2012. Circadian clocks in changing weather and seasons: lessons from the picoalga *Ostreococcus tauri*. *BioEssays* 34:781–90
- Piccolin F, Meyer B, Biscontin A, De Pittà C, Kawaguchi S, Teschke M. 2018. Photoperiodic modulation of circadian functions in Antarctic krill *Euphausia superba* Dana, 1850 (Euphausiacea). *J. Crustac. Biol.* 38:707–15
- Piccolin F, Pitzschler L, Biscontin A, Kawaguchi S, Meyer B. 2020. Circadian regulation of diel vertical migration (DVM) and metabolism in Antarctic krill *Euphausia superba*. *Sci. Rep.* 10:16796
- Poehn B, Krishnan S, Zurl M, Coric A, Rokvic D, et al. 2022. A Cryptochrome adopts distinct moon- and sunlight states and functions as sun- versus moonlight interpreter in monthly oscillator entrainment. *Nat. Commun.* 13:5220
- Poliner E, Cummings C, Newton L, Farré EM. 2019. Identification of circadian rhythms in *Nannochloropsis* species using bioluminescence reporter lines. *Plant J.* 99:112–27
- Provan J, Beatty GE, Keating SL, Maggs CA, Savidge G. 2009. High dispersal potential has maintained long-term population stability in the North Atlantic copepod *Calanus finmarchicus*. *Proc. R. Soc. B* 276:301–7
- Pülmanns N, Castellanos-Galindo GA, Krumme U. 2018. Tidal-diel patterns in feeding and abundance of armed snook *Centropomus armatus* from macrotidal mangrove creeks of the tropical eastern Pacific Ocean. *J. Fish Biol.* 93:850–59
- Raible F, Takekata H, Tessmar-Raible K. 2017. An overview of monthly rhythms and clocks. *Front. Neurol.* 8:189
- Ramos AP, Gustafsson O, Labert N, Salecker I, Nilsson D-E, Averof M. 2019. Analysis of the genetically tractable crustacean *Parhyale hawaiiensis* reveals the organisation of a sensory system for low-resolution vision. *BMC Biol.* 17:67
- Régnier T, Gibb FM, Wright PJ. 2019. Understanding temperature effects on recruitment in the context of trophic mismatch. *Sci. Rep.* 9:15179
- Renaud PE, Daase M, Banas NS, Gabrielsen TM, Søreide JE, et al. 2018. Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience. *ICES J. Mar. Sci.* 75:1871–81
- Reynolds C. 2006. *Ecology of Phytoplankton*. Cambridge, UK: Cambridge Univ. Press
- Rock A, Wilcockson D, Last KS. 2022. Towards an understanding of circatidal clocks. *Front. Physiol.* 13:830107
- Roenneberg T, Colfax GN, Hastings JW. 1989. A circadian rhythm of population behavior in *Gonyaulax polyedra*. *J. Biol. Rhythms* 4:89–104
- Roenneberg T, Hastings JW. 1988. Two photoreceptors control the circadian clock of a unicellular alga. *Sci. Nat.* 75:206–7
- Roenneberg T, Morse D. 1993. Two circadian oscillators in one cell. *Nature* 362:362–64
- Rosa R, Seibel BA. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *PNAS* 105:20776–80
- Round FE, Palmer JD. 1966. Persistent, vertical-migration rhythms in benthic microflora: II. Field and laboratory studies on diatoms from the banks of the River Avon. *J. Mar. Biol. Assoc. UK* 46:191–214
- Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE, Hamilton CE, et al. 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nat. Clim. Change* 2:239–42
- Saini R, Jaskolski M, Davis SJ. 2019. Circadian oscillator proteins across the kingdoms of life: structural aspects. *BMC Biol.* 17:13
- Sanchez A, Shin J, Davis SJ. 2011. Abiotic stress and the plant circadian clock. *Plant Signal. Behav.* 6:223–31
- Satoh A. 2017. Constant light disrupts the circadian but not the circatidal rhythm in mangrove crickets. *Biol. Rhythm Res.* 48:459–63
- Satoh A, Momoshita H, Hori M. 2006. Circatidal rhythmic behaviour in the coastal tiger beetle *Callytron inspecularis* in Japan. *Biol. Rhythm Res.* 37:147–55
- Satoh A, Terai Y. 2019. Circatidal gene expression in the mangrove cricket *Apteronomobius asabinai*. *Sci. Rep.* 9:3719
- Satoh A, Yoshioka E, Numata H. 2008. Circatidal activity rhythm in the mangrove cricket *Apteronomobius asabinai*. *Biol. Lett.* 4:233–36
- Schneck DT, Barreto FS. 2020. Phenotypic variation in growth and gene expression under different photoperiods in allopatric populations of the copepod *Tigriopus californicus*. *Biol. Bull.* 238:106–18

- Schnytzer Y, Simon-Blecher N, Li J, Ben-Asher HW, Salmon-Divon M, et al. 2018. Tidal and diel orchestration of behaviour and gene expression in an intertidal mollusc. *Sci. Rep.* 8:4917
- Schunter C, Welch MJ, Nilsson GE, Rummer JL, Munday PL, Ravasi T. 2018. An interplay between plasticity and parental phenotype determines impacts of ocean acidification on a reef fish. *Nat. Ecol. Evol.* 2:334–42
- Schunter C, Welch MJ, Ryu T, Zhang H, Berumen ML, et al. 2016. Molecular signatures of transgenerational response to ocean acidification in a species of reef fish. *Nat. Clim. Change* 6:1014–18
- Seibel BA, Häfker NS, Trübenbach K, Zhang J, Tessier SN, et al. 2014. Metabolic suppression during protracted exposure to hypoxia in the jumbo squid, *Dosidicus gigas*, living in an oxygen minimum zone. *J. Exp. Biol.* 217:2555–68
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD. 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J. Anim. Ecol.* 74:755–61
- Søreide JE, Leu E, Berge J, Graeve M, Falk-Petersen S. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Change Biol.* 16:3154–63
- Sorek M, Díaz-Almeyda EM, Medina M, Levy O. 2014. Circadian clocks in symbiotic corals: the duet between *Symbiodinium* algae and their coral host. *Mar. Genom.* 14:47–57
- Sorek M, Levy O. 2012. Influence of the quantity and quality of light on photosynthetic periodicity in coral endosymbiotic algae. *PLOS ONE* 7:e43264
- Sorek M, Schnytzer Y, Waldman Ben-Asher H, Caspi VC, Chen C-S, et al. 2018. Setting the pace: host rhythmic behaviour and gene expression patterns in the facultatively symbiotic cnidarian *Aiptasia* are determined largely by *Symbiodinium*. *Microbiome* 6:83
- Sorek M, Yacobi YZ, Roopin M, Berman-Frank I, Levy O. 2013. Photosynthetic circadian rhythmicity patterns of *Symbiodinium*, the coral endosymbiotic algae. *Proc. R. Soc. B* 280:20122942
- Sournia A. 1975. Circadian periodicities in natural populations of marine phytoplankton. In *Advances in Marine Biology*, Vol. 12, ed. FS Russell, M Yonge, pp. 325–89. London: Academic
- Spoelstra K, Wikelski M, Daan S, Loudon ASI, Hau M. 2016. Natural selection against a circadian clock gene mutation in mice. *PNAS* 113:686–91
- Stevenson TJ, Lincoln GA. 2017. Epigenetic mechanisms regulating circannual rhythms. In *Biological Time-keeping: Clocks, Rhythms and Behaviour*, ed. V Kumar, pp. 607–23. New Delhi: Springer
- Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, et al. 2012. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* 2:33–37
- Strelkov P, Nikula R, Väinölä R. 2007. *Macoma balthica* in the White and Barents Seas: properties of a widespread marine hybrid swarm (Mollusca: Bivalvia). *Mol. Ecol.* 16:4110–27
- Strömberg J-O, Spicer JJ, Liljebland B, Thomasson MA. 2002. Northern krill, *Meganctiphanes norvegica*, come up to see the last eclipse of the millennium? *J. Mar. Biol. Assoc. UK* 82:919–20
- Sweeney BM, Hastings JW. 1958. Rhythmic cell division in populations of *Gonyaulax polyedra*. *J. Protozool.* 5:217–24
- Sweeney BM, Haxo FT. 1961. Persistence of a photosynthetic rhythm in enucleated *Acetabularia*. *Science* 134:1361–63
- Sweeney BM, Tuffli CF, Rubin RH. 1967. The circadian rhythm in photosynthesis in *Acetabularia* in the presence of actinomycin D, puromycin, and chloramphenicol. *J. Gen. Physiol.* 50:647–59
- Takekata H, Matsuura Y, Goto SG, Satoh A, Numata H. 2012. RNAi of the circadian clock gene *period* disrupts the circadian rhythm but not the circatidal rhythm in the mangrove cricket. *Biol. Lett.* 8:488–91
- Takekata H, Numata H, Shiga S, Goto SG. 2014. Silencing the circadian clock gene *Clock* using RNAi reveals dissociation of the circatidal clock from the circadian clock in the mangrove cricket. *J. Insect Physiol.* 68:16–22
- Tankersley RA, Bullock TM, Forward RB, Rittschof D. 2002. Larval release behaviors in the blue crab *Callinectes sapidus*: role of chemical cues. *J. Exp. Mar. Biol. Ecol.* 273:1–14
- Tarling GA, Buchholz F, Matthews JBL. 1999. The effect of a lunar eclipse on the vertical migration behaviour of *Meganctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea. *J. Plankton Res.* 21:1475–88
- Teschke M, Wendt S, Kawaguchi S, Kramer A, Meyer B. 2011. A circadian clock in Antarctic krill: an endogenous timing system governs metabolic output rhythms in the euphausiid species *Euphausia superba*. *PLOS ONE* 6:e26090

- Tessmar-Raible K, Raible F, Arboleda E. 2011. Another place, another timer: marine species and the rhythms of life. *BioEssays* 33:165–72
- Teuber L, Schukat A, Hagen W, Auel H. 2013. Distribution and ecophysiology of calanoid copepods in relation to the oxygen minimum zone in the eastern tropical Atlantic. *PLOS ONE* 8:e77590
- Thorne LH, Nye JA. 2021. Trait-mediated shifts and climate velocity decouple an endothermic marine predator and its ectothermic prey. *Sci. Rep.* 11:18507
- Tomioka K, Matsumoto A. 2015. Circadian molecular clockworks in non-model insects. *Curr. Opin. Insect Sci.* 7:58–64
- Tougeron K. 2021. How constraining are photic barriers to poleward range-shifts? *Trends Ecol. Evol.* 36:478–79
- Tran D, Perrigault M, Ciret P, Payton L. 2020. Bivalve mollusc circadian clock genes can run at tidal frequency. *Proc. R. Soc. B* 287:20192440
- van Haren H, Compton TJ. 2013. Diel vertical migration in deep sea plankton is finely tuned to latitudinal and seasonal day length. *PLOS ONE* 8:e64435
- Veedin Rajan VB, Häfker NS, Arboleda E, Poehn B, Gossenreiter T, et al. 2021. Seasonal variation in UVA light drives hormonal and behavioural changes in a marine annelid via a ciliary opsin. *Nat. Ecol. Evol.* 5:204–18
- Villarino E, Irigoien X, Villate F, Iriarte A, Uriarte I, et al. 2020. Response of copepod communities to ocean warming in three time-series across the North Atlantic and Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 636:47–61
- Visser F, Hartman KL, Pierce GJ, Valavanis VD, Huisman J. 2011. Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Mar. Ecol. Prog. Ser.* 440:267–79
- Wagner HJ, Kemp K, Mattheus U, Priede IG. 2007. Rhythms at the bottom of the deep sea: cyclic current flow changes and melatonin patterns in two species of demersal fish. *Deep-Sea Res. I* 54:1944–56
- Wallace MI, Cottier FR, Berge J, Tarling GA, Griffiths C, Brierley AS. 2010. Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnol. Oceanogr.* 55:831–45
- Watson GJ, Bentley MG, Gaudron SM, Hardege JD. 2003. The role of chemical signals in the spawning induction of polychaete worms and other marine invertebrates. *J. Exp. Mar. Biol. Ecol.* 294:169–87
- Watson NHF, Smallman BN. 1971. The role of photoperiod and temperature in the induction and termination of an arrested development in two species of freshwater cyclopoid copepods. *Can. J. Zool.* 49:855–62
- Weizman EN, Tannenbaum M, Tarrant AM, Hakim O, Levy O. 2019. Chromatin dynamics enable transcriptional rhythms in the cnidarian *Nematostella vectensis*. *PLOS Genet.* 15:e1008397
- Weydmann A, Przyłucka A, Lubośny M, Walczyńska KS, Serrão EA, et al. 2018. Postglacial expansion of the Arctic keystone copepod *Calanus glacialis*. *Mar. Biodivers.* 48:1027–35
- Williams BG. 1998. The lack of circadian timing in two intertidal invertebrates and its significance in the circatidal/circalunidian debate. *Chronobiol. Int.* 15:205–18
- Wuitchik DM, Wang D, Pells TJ, Karimi K, Ward S, Vize PD. 2019. Seasonal temperature, the lunar cycle and diurnal rhythms interact in a combinatorial manner to modulate genomic responses to the environment in a reef-building coral. *Mol. Ecol.* 28:3629–41
- Yan J, Kim YJ, Somers DE. 2021. Post-translational mechanisms of plant circadian regulation. *Genes* 12:325
- Yerushalmi S, Green RM. 2009. Evidence for the adaptive significance of circadian rhythms. *Ecol. Lett.* 12:970–81
- Yildirim E, Curtis R, Hwangbo D-S. 2022. Roles of peripheral clocks: lessons from the fly. *FEBS Lett.* 596:263–93
- Yocum GD, Rinehart JP, Yocum IS, Kemp WP, Greenlee KJ. 2016. Thermoperiodism synchronizes emergence in the alfalfa leafcutting bee (Hymenoptera: Megachilidae). *Environ. Entomol.* 45:245–51
- Zbawicka M, Gardner JPA, Wenne R. 2019. Cryptic diversity in smooth-shelled mussels on Southern Ocean islands: connectivity, hybridisation and a marine invasion. *Front. Zool.* 16:32
- Zeidberg LD, Robison BH. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *PNAS* 104:12946–48

- Zhang L, Hastings MH, Green EW, Tauber E, Sladek M, et al. 2013. Dissociation of circadian and circatidal timekeeping in the marine crustacean *Eurydice pulchra*. *Curr. Biol.* 23:1863–73
- Zheng P, Wang M, Li C, Sun X, Wang X, et al. 2017. Insights into deep-sea adaptations and host-symbiont interactions: a comparative transcriptome study on *Bathymodiolus mussels* and their coastal relatives. *Mol. Ecol.* 26:5133–48
- Zurl M, Poehn B, Rieger D, Krishnan S, Rokvic D, et al. 2022. Two light sensors decode moonlight versus sunlight to adjust a plastic circadian/circalunidian clock to moon phase. *PNAS* 119:e2115725119



# Contents

From Stamps to Parabolas <i>S. George Philander</i> .....	1
Gender Equity in Oceanography <i>Sonya Legg, Caixia Wang, Ellen Kappel, and LuAnne Thompson</i> .....	15
Sociotechnical Considerations About Ocean Carbon Dioxide Removal <i>Sarah R. Cooley, Sonja Klinsky, David R. Morrow, and Terre Satterfield</i> .....	41
Oil Transport Following the <i>Deepwater Horizon</i> Blowout <i>Michel C. Bouffadel, Tamay Özgökmen, Scott A. Socolofsky, Vasiliki H. Kourafalou, Ruixue Liu, and Kenneth Lee</i> .....	67
Marshes and Mangroves as Nature-Based Coastal Storm Buffers <i>Stijn Temmerman, Erik M. Horstman, Ken W. Krauss, Julia C. Mullarney, Ignace Pelckmans, and Ken Schoutens</i> .....	95
Biological Impacts of Marine Heatwaves <i>Kathryn E. Smith, Michael T. Burrows, Alistair J. Hobday, Nathan G. King, Pippa J. Moore, Alex Sen Gupta, Mads S. Thomsen, Thomas Wernberg, and Dan A. Smale</i> .....	119
Global Fisheries Science Documents Human Impacts on Oceans: The <i>Sea Around Us</i> Serves Civil Society in the Twenty-First Century <i>Dirk Zeller, Maria L.D. Palomares, and Daniel Pauly</i> .....	147
Exchange of Plankton, Pollutants, and Particles Across the Nearshore Region <i>Melissa Moulton, Sutara H. Suanda, Jessica C. Garwood, Nirnimesh Kumar, Melanie R. Fewings, and James M. Pringle</i> .....	167
Nuclear Reprocessing Tracers Illuminate Flow Features and Connectivity Between the Arctic and Subpolar North Atlantic Oceans <i>Núria Casacuberta and John N. Smith</i> .....	203
The Arctic Ocean's Beaufort Gyre <i>Mary-Louise Timmermans and John M. Toole</i> .....	223



Modes and Mechanisms of Pacific Decadal-Scale Variability <i>E. Di Lorenzo, T. Xu, Y. Zhao, M. Newman, A. Capotondi, S. Stevenson, D.J. Amaya, B.T. Anderson, R. Ding, J.C. Furtado, Y. Job, G. Liguori, J. Lou, A.J. Miller, G. Navarra, N. Schneider, D.J. Vimont, S. Wu, and H. Zhang</i> .....	249
Global Quaternary Carbonate Burial: Proxy- and Model-Based Reconstructions and Persisting Uncertainties <i>Madison Wood, Christopher T. Hayes, and Adina Paytan</i> .....	277
Climate Change Impacts on Eastern Boundary Upwelling Systems <i>Steven J. Bograd, Michael G. Jacox, Elliott L. Hazen, Elisa Lovecchio, Ivonne Montes, Mercedes Pozo Buil, Lynne J. Shannon, William J. Sydeman, and Ryan R. Rykaczewski</i> .....	303
Quantifying the Ocean's Biological Pump and Its Carbon Cycle Impacts on Global Scales <i>David A. Siegel, Timothy DeVries, Ivona Cetinić, and Kelsey M. Bisson</i> .....	329
Carbon Export in the Ocean: A Biologist's Perspective <i>Morten H. Iversen</i> .....	357
Novel Insights into Marine Iron Biogeochemistry from Iron Isotopes <i>Jessica N. Fitzsimmons and Tim M. Conway</i> .....	383
Insights from Fossil-Bound Nitrogen Isotopes in Diatoms, Foraminifera, and Corals <i>Rebecca S. Robinson, Sandi M. Smart, Jonathan D. Cybulski, Kelton W. McMabon, Basia Marcks, and Catherine Nowakowski</i> .....	407
Microbial Interactions with Dissolved Organic Matter Are Central to Coral Reef Ecosystem Function and Resilience <i>Craig E. Nelson, Linda Wegley Kelly, and Andreas F. Haas</i> .....	431
Prokaryotic Life in the Deep Ocean's Water Column <i>Gerhard J. Herndl, Barbara Bayer, Federico Baltar, and Thomas Reinthaler</i> .....	461
Lipid Biogeochemistry and Modern Lipidomic Techniques <i>Bethanie R. Edwards</i> .....	485
Rhythms and Clocks in Marine Organisms <i>N. Sören Häfker, Gabriele Andreatta, Alessandro Manzotti, Angela Falciatore, Florian Raible, and Kristin Tessmar-Raible</i> .....	509

## Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at <http://www.annualreviews.org/errata/marine>