

Advances in Polar Ecology

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POLAR NIGHT

Marine Ecology

Life and Light in the Dead of Night

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Advances in Polar Ecology

In recent years, the polar regions have received increased scientific and public interest. Both the Arctic and Antarctic have been recognized as key regions in the regulation of the global climate and polar ecosystems have been identified to be particularly susceptible to the ongoing environmental changes. Consequently, the international efforts in polar research have been enhanced considerably, and a wealth of new findings is being produced at a growing rate by the international community of polar researchers. The aim of the book series *Advances in Polar Ecology* is to foster the progress in the scientific knowledge about the polar and sub-polar regions of both hemispheres by contributing to the fast and wide-ranging dissemination of novel scientific information gained from recent studies of sea, freshwater and land biota among polar researchers, environmental managers and policy makers. *Advances in Polar Ecology's* broad ecology-oriented scope encompasses environmental and biological research of both recent and past ecosystems. The Series offers an outlet to publish contributions (monographs, edited works, conference proceedings, etc.) addressing scientific topics that need more comprehensive and in-depth analysis than the length of typical journal articles allow for. These include, but are not limited to, thorough accounts of the current status of active research areas of wide importance that outline promising perspectives for future research. An international editorial board oversees the rigorous peer review that all contributions will be subjected to.

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Chapter 8

Biological Clocks and Rhythms in Polar Organisms



Kim S. Last, N. Sören Häfker, Vicki J. Hendrick, Bettina Meyer, Damien Tran, and Fabio Piccolin

Abstract Biological clocks are universal to all living organisms on Earth. Their ubiquity is testament to their importance to life: from cells to organs and from the simplest cyanobacteria to plants and primates, they are central to orchestrating life on this planet. Biological clocks are usually set by the day–night cycle, so what happens in polar regions during the Polar Night or Polar Day when there are periods of 24 hours of darkness or light? How would a biological clock function without a timekeeper cycle? This chapter details evidence that biological clocks are central to structuring daily and seasonal activities in organisms at high latitudes. Importantly, despite a strongly reduced or absent day–night cycle, biological clocks in the Polar Night still appear to be regulated by background illumination. Here we explore

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evidence for highly cyclic activity, from behaviour patterns to clock gene expression, in copepods, krill and bivalves. The ultimate goal will be to understand the role of endogenous clocks in driving important daily and seasonal life cycle functions and to determine scope for plasticity in a rapidly changing environment.

Keywords Biological clock · Bivalves · *Calanus finmarchicus* · *Chlamys islandica* · Circadian · Copepods · *Euphausia superba* · Genes · *Mytilus edulis* · Mussels · Krill

8.1 What Are Biological Clocks?

8.1.1 Molecular Underpinnings of Biological Clocks

Biological clocks are highly accurate molecular machines, continuously adjusting behaviour, metabolism and clock-controlled gene activity (Dunlap 1999). The most commonly studied clock is called the circadian clock and will, under laboratory conditions, generate a rhythm of about 24 hours. It gets its name from the Latin *circa* meaning ‘about’ and *dies* which means a ‘day’, and it measures the time of day much like any watch (Halberg et al. 1960). Although precise, it is usually just a bit fast or slow relative to astronomical time, hence the prefix ‘circa’.

The circadian clock is usually located in a distinct part of the brain. In mammals, it is close to where the optic nerves cross, a region called the suprachiasmatic nucleus (SCN) (Inouye and Kawamura 1979), and in fruit flies (*Drosophila melanogaster*), it is in the brains’ ventral neurons (Rieger et al. 2006). It synchronizes a multitude of other clocks in cells, tissues and organs often via hormonal control (in mammals: melatonin) (Foulkes et al. 1997). The clock itself is a molecular machine which constitutes positive and negative feedback loops between circadian clock genes and the clock proteins they express, primarily entrained by the light–dark cycle (Pittendrigh and Minis 1964); for further details, see Box 8.1.

8.1.2 General Characteristics and Ultimate Significance of Clocks

The circadian clock has a number of important characteristics. First, it is primarily set by the day–night cycle through *entrainment*; without this, the clock gradually desynchronizes, and rhythmic behaviour is lost (Pittendrigh and Minis 1964). Secondly, the clock *free-runs* in the laboratory (Roberts 1960). This means that in the absence of the day–night cycle (or any other cyclic environmental cues), the workings of the clock can be observed through rhythmic expression at the behavioural, physiological or molecular levels, that is an organism will continue to show rhythmic behaviour such as active/resting phases even in the absence of external

signals. This endogenous response is termed a *rhythm* and will eventually decrease or dampen which, depending on the species under investigations, may take from days to months. Any signal which entrains the clock is termed a *zeitgeber*, from the German word which means ‘time-giver’ (Aschoff and Pohl 1978). While the day–night light cycle is a common zeitgeber, others include cyclic food provision (Stephan 2002) and social cues (Mistlberger and Skene 2004). Finally, the clock is temperature compensated which is especially important in timekeeping in animals which cannot regulate their own body temperature other than by behavioural means (*poikilotherms*). The ultimate function of the clock is to allow organisms to *anticipate* rather than simply to *react* to future events, promoting survival and enhancing fitness. This will confer advantages through scheduling of biological functions at the appropriate time of the daily environmental cycle (extrinsic advantage), coordination of internal physiology (intrinsic advantage) and the role of the clock in responses to seasonal changes. Their importance is illustrated by the effect of fitness of mice with deviant circadian periods in populations living in a seminatural environment (Spoelstra et al. 2016). Mice with near 24-hour rhythms survive longer and reproduced more than mice with rhythms shortened by a mutation in the circadian clock allele. Similarly, in plants with deviant clocks, flowering times are affected with consequent loss of fitness (Green et al. 2002).

Finally, it is important to consider that when an organism is studied in the wild, one cannot exclude that it is responding to the exogenous environmental (e.g. day/night) cycle directly, that is without involvement of the endogenous circadian clock. It is only when organisms are brought into the laboratory and their behaviour or clock genes show circadian rhythms under free-running conditions (i.e. constant light or dark and temperature) that we can say for certain that a circadian clock is extant.

8.1.3 *Complex Environments Require Complex Clocks*

We have seen how the circadian clock is centrally important to synchronizing the behavioural and physiological rhythms of organisms and therefore highly adaptive to terrestrial organisms living in a 24-hour world. In the marine environment, however, organisms also experience other cycles of different durations. The Earth and moon spin about a common centre of gravity resulting in various geophysical cycles to which organisms have evolved biological clocks with matched synchronicity (for review of these, see Naylor (2010)). Organisms living in tidal habitats may have circatidal clocks (with a ~12.4-hour period matching that of the tides) or circasemilunar clocks (with a ~14-day period matching that of the spring/neap tidal cycle). Others synchronize to moonlight and possess circalunar clocks (with a ~29-day period matching the lunar phase cycle) which are often important in synchronizing reproductive events. Finally, the circannual clock synchronises to the seasons (with a ~365-day period matching 1 year). Although non-circadian types of biological clocks have been well described at the behavioural and physiological levels, our understanding of their molecular mechanisms is still rudimentary (de la Iglesia and Johnson 2013; Raible et al. 2017; Lincoln 2019).

8.1.4 *Clock Rhythms in Polar Regions*

The Polar Day or Night provides two time periods during which solar cycles are difficult to detect or are masked by other external factors. This is because the sun is either permanently above or below the horizon and light from the moon, aurora and stars contribute more or less significantly to the daily light field (as detailed in Chap. 3). When below the horizon, extended periods of civil, nautical and astronomical twilight occur, the effects of which are unknown on the circadian clocks of polar organisms. Indeed there is limited information even on the irradiance threshold or role of spectral composition in circadian clock entrainment, surprising considering their importance eliciting behavioural and physiological responses (Miljeteig et al. 2014, Båtnes et al. 2015, Cohen et al. 2015). Polar organisms therefore not only need to detect the presence/absence of light, but also have to use the extreme polar photoperiods (the length of the day or night) and varying light intensities/spectra to entrain any putative circadian clock.

The first evidence of large-scale circadian-type behaviour in polar marine organisms came from a study in 2008 by Berge et al., which showed that diel vertical migration (DVM) of zooplankton occurred during the Polar Night (as described in Chap. 5). This study challenged the paradigm that DVM did not occur during the Polar Night. Using chronobiological methods, the strength of DVM was determined in different depth layers revealing that DVM only occurred around 50 m, as shown in Fig. 8.1.

It was later demonstrated (Last et al. 2016) that although the DVM observed in December was within the circadian range (defined here as within 20–28 hours), closer analysis of periodicity at higher temporal resolution revealed the period to be ~24.8 hours, the same as a lunidian day (i.e. the period of one rotation of the Earth around its axis with respect to the moon). This response was termed daily lunar vertical migration (LVM-day) and only occurred during December during the full moon period but was shown to be common across the Arctic Ocean as monthly lunar vertical migrations (LVM-month).

Evidence that zooplankton migrate during the Polar Night suggests an ability for detection and response to very low light intensities. However, acoustic data can only reveal migrations at the population level, and so, it is still largely unknown which organisms respond to moon- or sunlight at this time. The implication that a circadian clock is maybe present in migrating zooplankton was tantalizing and indirectly resulted in a number of behavioural and molecular studies of polar marine organisms capable of parsing between exogenous responses and endogenous rhythms.

Here, we build on previous chapters to discuss the underlying mechanisms and entrainment of biological clocks by light (Chap. 3) and their adaptive significance in copepods and krill (Chap. 5) and bivalves (Chap. 6), in an environment which, to the human eye at least, is devoid of clear light signals for large parts of the year.

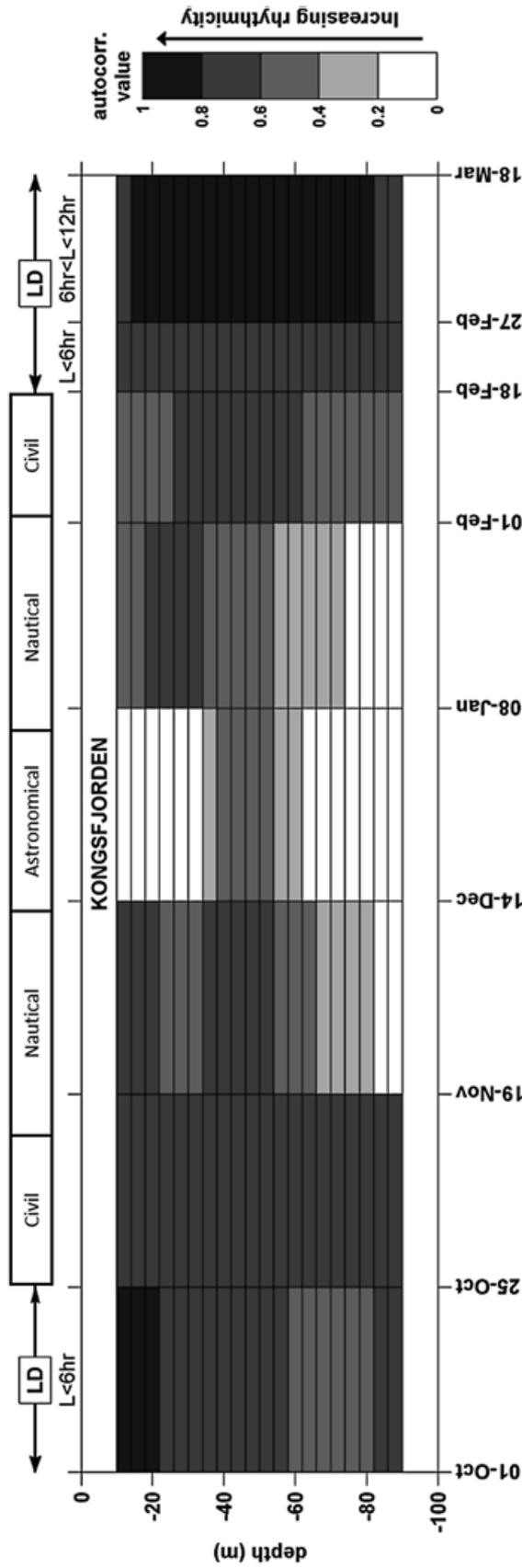


Fig. 8.1 DVM signal strength and depth centred during the Polar Night in Kongsfjorden, Svalbard. LD, light dark (difference between day and night in hours) and defined twilight periods. Each box represents a specific depth and time interval. Rhythmicity has been calculated using autocorrelation statistics (autocorr.) where the darker the shading at any particular depth, the more synchronized the 24-hour DVM signal. All shaded boxes have a detectable DVM signal that is significant above a 99 per cent confidence interval. White boxes indicate no detectable DVM signal. (Adapted from Berge et al. (2008))

8.2 Biological Clocks in the Copepod *Calanus finmarchicus*

8.2.1 Circadian Clocks and Cycles

The copepod *Calanus finmarchicus*, like many other planktonic organisms, performs DVM. It is very abundant in the boreal, Atlantic and Arctic seas and its life cycle is well described (as detailed in Chap. 5). Importantly for the study of circadian clock gene expression, molecular resources are available making transcription analysis routines possible (Lenz et al. 2014). Thus in 2017, Häfker et al. provided the first evidence of endogenous clock gene cycling in *C. finmarchicus* collected from a boreal fjord in Scotland, the United Kingdom. In the laboratory and under free-running conditions, *C. finmarchicus* showed circadian rhythms of DVM, respiration and most core circadian clock genes: clock, period1, period2, timeless, cryptochrome2 and clockwork orange (for details, see Box 8.1). Convincingly, most of these genes also cycled in animals taken directly from the wild, though the level of expression was slightly less rhythmic in animals collected from deep water (50–140 m) relative to those collected from shallow water (0–50 m). The observation that clock gene cycling also occurred in the deeper water was surprising, given that light attenuation and scattering in this fjord are extremely high below 20 m (Cohen et al. 2019), and so, it would be completely dark, at least to the human eye. At both depths, peak expression of clock genes generally occurred at either sunset or sunrise, coinciding with peak migration times in the wild. While the mechanistic connection between the circadian clock and behaviour/physiology still remains elusive, the high degree of correlation between clock gene expression and DVM is striking.

Circadian clock control of the behaviour and physiology of *C. finmarchicus* may increase fitness by optimizing the temporal trade-off between feeding and predator avoidance, especially when environmental drivers are weak or absent such as in deep water or during the Polar Night (Häfker et al. 2017). The clock will provide a time sense so that animals can anticipate the cyclic diel changes of their environment and prepare accordingly, a highly adaptive trait (Sharma 2003). In copepods, this includes the accumulation of ATP reserves for the energy-demanding ascent to surface waters at sunset, the production of digestion enzymes in advance to process as much food as possible during their limited nocturnal feeding time in surface waters, and the anticipation of sunrise which enables the copepods to return to depth before light levels become sufficient for visual predators to hunt.

As circadian clocks are not perfectly precise, but have to be entrained by the diel light–dark cycle on a regular basis, it might be expected that DVM would cease during long periods when there is no more day–night cycle such as during the Polar Day or Polar Night. Studies have shown, however, that during the Polar Day when the upper water layers are permanently illuminated, DVM becomes desynchronized within the population of zooplankton yet continues at the individual level (Cottier et al. 2006; Darnis et al. 2017). Similarly, DVM has been shown to continue during the Polar Night and is either driven exogenously or entrained by the sun (Berge

et al. 2015; Hobbs et al. 2018) or the moon (Last et al. 2016), whichever is the stronger signal. DVM of zooplankton has also been documented in the deep sea (as a proxy for another environment without overt solar signals), yet the mechanisms of entrainment are not understood (van Haren and Compton 2013). Noteworthy is that cycling clock gene expression in *C. finmarchicus* has only been demonstrated during the Polar Day, but not the Polar Night, as shown in Fig. 8.2 in animals collected from Kongsfjorden (Häfker et al. 2018a).

Copepods in early diapause (September; for details, see Chap. 5) which were collected below 200 m, where light levels were probably below their visual detection limit (Båtnes et al. 2015), still showed cycling of some clock genes (*per1* was not significant). This indicated that the clock was running endogenously without light entrainment at a time when the copepods had just descended to depth, suggesting that the physiological switch to the diapause state happens after the descent to deeper water layers (Freese et al. 2017, Häfker et al. 2018a,b). The persistent rhythmicity during the Polar Day, at a time when the sun is permanently above the horizon, suggests that changes in spectral irradiance and intensity with solar altitude are sufficient to entrain the clock. Depending on light attenuation in the water column, an organism in the epipelagic zone may therefore still be able to perceive distinct ‘photoperiods’ that will vary with depth and with visual sensitivity of the organism (for further discussion, see Chap. 3).

Whilst the mechanism of photoperiodic detection and circadian clock entrainment during the Polar Day is still unknown, the observation of clock gene cycling at this time suggests that clock functioning requires only subtle changes in solar irradiance. However during the Polar Night, *C. finmarchicus* showed no clock gene cycling (Fig. 8.2). This may be attributed to the lack of sufficient light intensity/spectrum at this time or to the physiological state of diapause which could actively switch off clock gene cycling (Häfker et al. 2018b). Where DVM or LVM of *C. finmarchicus* is observed during the Polar Night using acoustics (Berge et al. 2008; Last et al. 2016), we suggest the behaviour is primarily exogenously driven by sun- or moonlight, respectively, although light strong enough to evoke a direct response may also have the potential to entrain a biological clock, although this would require testing.

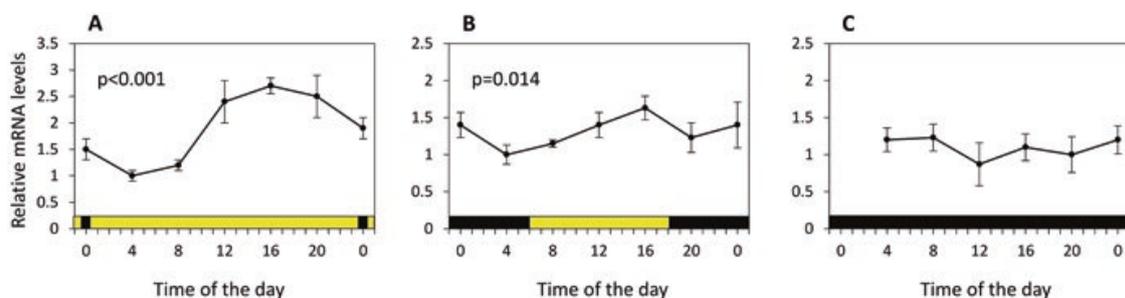


Fig. 8.2 Diel clock gene expression of the period1 (*per1*) gene in (a), August (active phase); (b), September (early diapause); and (c), January (late diapause). Colour bars indicate day (yellow) and night (black). Expression of *per1* gene was analysed for 24 hour rhythmicity with RAIN analysis with significant 24 hour cycling ($p < 0.001$) in August. (Adapted from Häfker et al. (2018a))

8.2.2 Seasonal Clocks

For a large part of the year, the majority of the population of *C. finmarchicus* migrates to deep water undergoing a form of hibernation, or diapause. At this time, they are inactive, show reduced metabolic activity and survive on their lipid storages without feeding (noteworthy however is that not all copepods do this; for details, see Chap. 5). Calanoid copepod diapause has been investigated for more than a century, but the factors controlling the initiation and termination of this important life phase remain elusive (Baumgartner and Tarrant 2017). Since circadian clocks are intrinsically linked to photoperiodism (Schultz and Kay 2003, Goto 2013) and diapause in *C. finmarchicus* occurs at a specific time of the year depending on location, we suggest the potential of circadian clock involvement and diapause regulation via photoperiod measurement.

Classically, the lipid stores of copepods have been considered to have a major role in diapause with the expectation that diapause is initiated once the animals reach a certain lipid threshold, enabling them to survive the foodless time of diapause at depth (Rey-Rassat et al. 2002). Conversely, the gradual depletion of the lipid stores over time is expected to result in the triggering of emergence of diapause once reserves fall below a critical value. Diapause ‘lipid threshold’ hypotheses do, however, struggle to explain why, particularly at lower latitudes, some animals at the copepodite CV stage (for details, see Chap. 5) either enter diapause or mature and produce another generation (cohort). If the lipid stores were the factor triggering diapause, all animals should descend to depth. Similarly, a gradual depletion of lipids cannot be considered a precise timer for diapause emergence, conflicting with the observations that the ascent from diapause in winter/spring is often strongly synchronized within a given *C. finmarchicus* population (Baumgartner and Tarrant 2017).

As copepods typically overwinter at depth where light or other seasonal cues are unavailable or reduced, an argument is made in favour of seasonal/circannual clocks in regulating diapause timing as has been described for various insects (Meuti and Denlinger 2013). The circadian clock of *C. finmarchicus* remains functional during extremely long photoperiods in summer (Häfker et al. 2018a), and it is likely that the same is true for the polar-adapted species *C. glacialis* and *C. hyperboreus*. Thus, the circadian clock could be used to determine the seasons based on photoperiod and the use of a critical day length in diapause initiation. As sufficient lipid storages are still crucial to survive diapause, it is probable that a certain lipid threshold has to be reached before photoperiod induction takes place (Häfker et al. 2018b).

For diapause emergence triggers however, photoperiod is an unlikely cue due to the lack of light at diapause depth which is usually, in *C. finmarchicus*, >200 m. The synchronized emergence in the absence of any seasonal cue points towards the existence of an endogenous circannual timing mechanism. Indeed, very early studies on *C. hyperboreus* and another *Calanus* species showed that animals collected from the field and kept in constant darkness in the laboratory still emerged from diapause in synchrony with their conspecifics in the field several months later (Conover 1965,

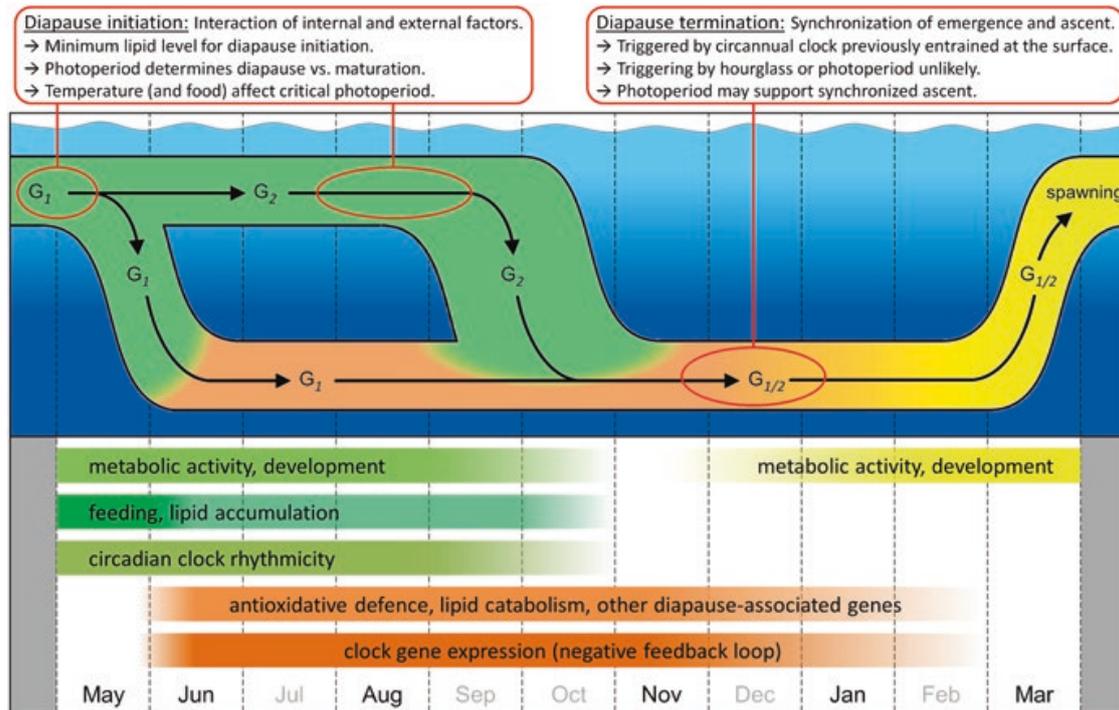


Fig. 8.3 Seasonal life cycle and gene expression of *C. finmarchicus* exemplified for a boreal habitat where copepods produce two generations per year (G_1 and G_2). Red boxes summarize possible mechanisms of diapause initiation/termination. Bars in the lower panel indicate seasonal gene expression patterns. (Figure adapted from Häfker et al. (2018b))

Fulton 1973). Although the mechanism of this is still unclear, circannual rhythms have been described in several terrestrial species maintaining time with astonishing precision (Goldman et al. 2004). It has been suggested that for the boreal *C. finmarchicus* and its Arctic congener species, photoperiods perceived during the summer when the animals are near the surface of the ocean may entrain their circannual clock (Häfker et al. 2018b). This would provide a temporal cue to trigger emergence in winter in the midst of the Polar Night in readiness of moulting and reproduction.

Aside from the physiological changes associated with diapause (Chap. 5), this phase of the *C. finmarchicus* seasonal cycle is also characterized by distinct changes in gene expression patterns as detailed in Fig. 8.3.

Copepods active in surface waters and those that recently descended to diapause depth show high expression of genes related to metabolic activity, development, digestion and lipid accumulation, reflecting migration to phytoplankton-rich water, growth and accumulation of lipid stores for overwintering. This is also the phase when circadian clock genes show diel expression rhythmicity matching the DVM that occurs at this time. At depth, copepods show major changes in gene expression, which mark the start of diapause. While the expression of the genes active in surface waters decreases, so clock gene rhythmicity ceases. Genes involved in oxidative stress responses and lipid catabolism are upregulated, reflecting the often hypoxic conditions in deep waters with behavioural inactivity fuelled by the gradual depletion of lipid storages.

Another interesting yet unexplained observation over the seasonal cycle of *C. finmarchicus* is the overall upregulation of several clock genes despite the lack of diel rhythmicity (Häfker et al. 2018a,b). Towards late autumn/early winter, there is a shift in gene expression, which signifies the start of the diapause emergence phase. Although animals still remain at depth, the expression of diapause-related genes decreases, while genes associated with metabolic activity and development increase. The initiation of the emergence phase is synchronized within the population and happens in deep waters, without any known seasonal cues and well in advance of the ascent to surface waters in spring, clearly showing ‘anticipation’ for a future behaviour/physiological state. These observations suggest that emergence is triggered by an endogenous timing where the mechanism may represent a putative circannual clock. While the mechanistic nature of such a clock is unknown, it could be related to lipid storage status and photoperiod measurement at diapause initiation (Häfker et al. 2018b). Such a mechanism, which works independent of light for certain times of the year, could ensure precise seasonal timing even under the extreme light conditions in polar marine habitats.

8.3 Biological Clocks in Krill *Euphausia superba*

8.3.1 Circadian Clocks and Cycles

Krill are very abundant in the polar oceans and are one of the preferred prey species for many marine predators throughout the year. While the most common krill species in the Arctic is *Thysanoessa* spp., the Southern Ocean is dominated by its much larger cousin the Antarctic krill, *Euphausia superba* (Fig. 8.4). Krill generally are exceedingly agile and fast swimmers, frequently congregating in large swarms making them a prime target for higher trophic predators such as fish, baleen whales and birds. From echo sounder data and net hauls, they are also considered the dominant group undergoing highly synchronized diel vertical migrations (DVM).

Whilst very little is known of the physiology and behaviour of *T. inermis*, the converse is true of *E. superba*. Studies have revealed that its success is hinged on a life cycle perfectly matched to the annual variations in day length (photoperiod), sea-ice cover and food supply. Krill show highly orchestrated annual patterns of metabolic activity, sexual maturity and lipid utilization with recent studies further revealing daily rhythms in behaviour, metabolism and gene transcription (Meyer et al. 2010). Its position as a model organism for the study of a high-latitude biological clock has, therefore, made it worthy of discussion here, although the species neither lives in the Arctic nor is exposed to permanent darkness because of Southern Ocean latitudes. However, its vertical distribution is deeper than in those of its northern cousin, with corresponding increased light attenuation, and therefore, parallels may be drawn between these polar habitats.

As is the case with many other pelagic organisms, *E. superba* undergo DVM, swimming to surface around sunset and retreating to deeper waters around sunrise.

Fig. 8.4 The Antarctic krill, *Euphausia superba*, an important food source for the majority of Southern Ocean higher trophic levels. (Photo: Carsten Pape)



This predator avoidance behaviour changes seasonally with more pronounced DVM in spring and autumn when compared to the summer. In spring and autumn, migrations are predominantly in the upper 200 m, whilst during summer, when the sun rarely dips below the horizon and food availability is high, no clear DVM pattern is observed. Instead, multiple shallow individual migrations occur in a similar manner as those seen in Arctic copepods (see Chap. 5), referred to as unsynchronized DVM. During winter, when days are exceedingly short and there is thick sea-ice cover, krill move to deeper water where they perform extensive DVM postulated to support foraging at the seafloor (Taki et al. 2005, Siegel 2005, Bernard et al. 2018).

The seasonal changes in krill DVM are not just a reflection of changing photoperiods, but are also influenced by the ontogenetic developmental of the krill. During winter, the larval stages Furcilia III to VI, which are mainly associated with the winter sea ice, show reverse DVM, rising to the surface during the day rather than at night. In the day, the larvae are closely associated with the sea ice, whereas after sunset, they are dispersed in the upper 50 m of the water column. Such behaviour has been suggested to increase the chances of finding food in patchy environments and reduces predation from visual hunters which come to the surface waters during the night (Meyer & Teschke 2016).

Clearly there are adaptive advantages to changing foraging behaviour with season and developmental stage, and it follows that physiological processes also show seasonal cycles. For instance, laboratory experiments show that the response of *E. superba* to high food concentrations during winter is dependent on appropriate changes in light regime with only long days stimulating increased feeding activity (Teschke et al. 2007). Long days also result in advancement of sexual maturity, whilst sexual regression could only be induced under short days. Photoperiodic

entrainment of metabolic processes and feeding activity, growth and time of maturity have all been interpreted as part of a comprehensive overwintering strategy to save energy during the food-depleted season (for more details, see Chap. 5). The observation that daily and seasonal behavioural/physiological cycles are so overt has led to the hypothesis that they are regulated by an endogenous timing system entrained by the seasonal Antarctic light regime (Meyer et al. 2010).

Free-running circadian clock gene activity was first described in krill during the Antarctic summer at a time when the sun is permanently above the horizon (Mazzotta et al. 2010; Teschke et al. 2011). Mazzotta et al. (2010) showed that at this time, 8% of the transcriptome of krill displayed daily oscillations with either 12-hour or 24-hour periods. Associated with this was a progression of biochemical and physiological events throughout the day. Breakdown of energy-yielding nutrients and energy storage pathways was specifically activated in the early morning, whilst glycogen mobilization, gluconeogenesis and fatty acid catabolism were activated in the evening and throughout the night. The implication was that a significant component of the transcriptome cycling is involved in the circadian clock, at least during the summer (De Pittà et al. 2013). More detailed investigations followed, which showed that the DVM, oxygen consumption and expression of the core clock genes correlated with the light–dark cycle again persisting under constant darkness, demonstrating that the response was due to an endogenous circadian clock (Piccolin 2018). However, rhythmicity of these physiological processes was only 30%, and interindividual variation between krill was large, suggesting possible differences at the molecular level between animals with different clock gene alleles or variation in the regulation of circadian input/output pathways.

A comparison of the principal clock components in krill and their role within the circadian feedback loop with known circadian models in mammals, insects and crustaceans has shown that the krill clock exhibits both mammalian and insect features, presumably contributing to an evolutionary strategy to cope with polar environment challenges (Biscontin et al. 2017). The krill clock proteins CLK and CYC were identified as the putative positive elements of the principal feedback loop, as described for *Drosophila* (see Fig. 8.9), whereas the krill clock proteins PER, TIM and CRY2 were identified as the putative negative elements, as described for the monarch butterfly, *Danaus plexippus*, in sun compass orientation (Merlin et al. 2009).

8.3.2 Seasonal Clocks

Seasonal changes in the activity of the circadian clock and the regulation of daily metabolic output rhythms in *E. superba* were studied in a 1-year experiment in which krill were exposed to simulated seasonal photoperiodic cycles of the Southern Ocean (66°S) and to constant darkness in the absence of other environmental signals (Piccolin et al. 2018a). Food was provided ad libitum, and temperature was kept constant. In simulated early-autumn conditions, with 16 hours of light and 8 hours of darkness (LD 16:8), clock gene activity was rhythmic as seen in Fig. 8.5 B showing *per* gene (the role of *per* in the circadian clock is described in Fig. 8.9). At the same

time, the metabolic output was synchronized with the light/dark cycle, with upregulation of key metabolic genes occurring during the dark phase. Conversely, in simulated midsummer (LD 24:0) and mid-winter (LD 3:21) conditions, clock gene activity was arrhythmic as shown in Fig. 8.5 A and C, respectively, and with upregulation of key metabolic genes occurring at different times of the day.

The results suggest that only overt day–night cycles are able to entrain the circadian clock and promote the synchronization of metabolic output functions such as changes in growth, enzyme activity and oxygen consumption, much like in *C. finmarchicus* (see previous section). However, both rhythmic clock gene expression and transcriptional output were observed in wild krill caught during Polar Day in the Southern Ocean, and hence, there may be important clock entraining cues missing in the laboratory (Piccolin et al. 2018a).

Interestingly, under constant darkness, seasonal rhythms of growth, enzyme activity and gene expression were observed, suggesting the possible involvement of an endogenous circannual clock (Höring et al. 2018; Piccolin et al. 2018b). However, oxygen consumption, which represents the sum of multiple physiological processes including basal metabolism, swimming activity, growth and feeding activity, did not display a seasonal rhythm (Piccolin et al. 2018b), which was in contrast to another study by Brown et al. (2013). These differences may be explained by the timing of the experiments. Brown et al. (2013) initiated DD in early autumn (February), whereas Piccolin et al. (2018b) initiated the treatment earlier, in the austral December (early summer). It is likely that to achieve effective entrainment, the circannual clock might require exposure to a specific portion of the seasonal photoperiodic cue in phase with the endogenous circannual cycle, to provide the ‘correct’ seasonal response, as in rainbow trout, *Oncorhynchus mykiss*, and detailed with a circannual phase response curve (Randall et al. 1998). The implication here is that there is a critical photoperiodic entrainment period of the circannual clock that occurs between midsummer and early autumn. Indeed, experiments under simulated natural light conditions at 66°S revealed that oxygen consumption only started to decrease after the light-phase duration had been reduced below 16 hours, corresponding to simulated early autumn in February (Piccolin et al. 2018b). However, in krill exposed to constant darkness, the krill clock genes

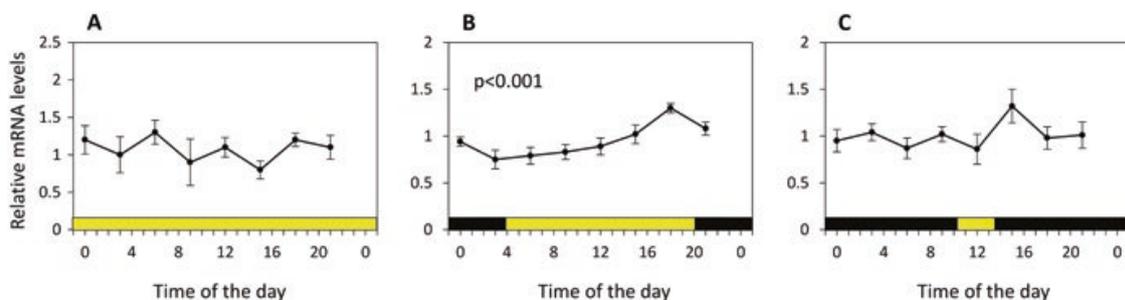


Fig. 8.5 Daily patterns of expression of the period (*per*) gene in (a), midsummer; (b), early-autumn; and (c), mid-winter. Data points represent means \pm SEM ($N = 6$). Colour bars indicate simulated day (yellow) and night (black) phases. Expression of *per* gene was analysed for 24-hour rhythmicity, and RAIN analysis with significant 24-hour cycling ($p < 0.001$) is indicated. (Adapted from Piccolin et al. 2018a)

clock, *cryptochrome2* and *timeless* showed up-regulation under such conditions, suggesting a specific link between clock-related activity and the light regime at that time of year. It therefore appears likely that a circannual clock is involved in structuring the physiological processes of krill irrespective of the exogenous seasonal light regime.

8.4 Biological Clocks in Bivalves

8.4.1 Measuring Bivalve Shell Gape Cycles

As suspension feeders, bivalves play important roles in coupling benthic–pelagic interactions, seafloor biogeochemical processes and modification of near-bed hydrodynamics. Like zooplankton, bivalves are photoperiodic, but unlike zooplankton, they either are completely sessile or only have limited capability to move. Their response to changes in light is to modify the duration and the amplitude of their valve opening. Thus, bivalve behaviour is typically studied using valvometers consisting of pairs of electrodes which are glued to the animals' shells (see Fig. 8.6). The valvometers provide a means to measure electrically, and at high frequency, the distance between the valves providing both gape activity patterns and shell growth data as the electrodes are incrementally pushed apart over time.

Monitoring valve gape behaviour is used as a proxy for gill filtration which is necessary for respiration and nutrition or as a response to environmental stressors such as pollutants (Andrade et al. 2016) or harmful algae (Tran et al. 2010). Uniquely, the valvometer system provides a means of measuring the gape activity of bivalves in their natural ecosystem over long time scales (days to years).

This approach has been applied to fan mussel, *Pinna nobilis*, shell gape behaviour in the Mediterranean Sea (Garcia-March et al. 2008) and to oyster *Crassostrea gigas* (Tran et al. 2011), in the Atlantic revealing different rhythms correlated to moon–sun cycle interactions. In *P. nobilis*, a daily rhythm (~24 hours) of shell gape activity is evident, modulated by a moonlight rhythm (~29.5 days) with a complete absence of tidal oscillations, presumably due to the limited tides in the Mediterranean. In contrast, the dominant rhythm for *C. gigas* is that of a tidal cycle (~12.4 hours), even in

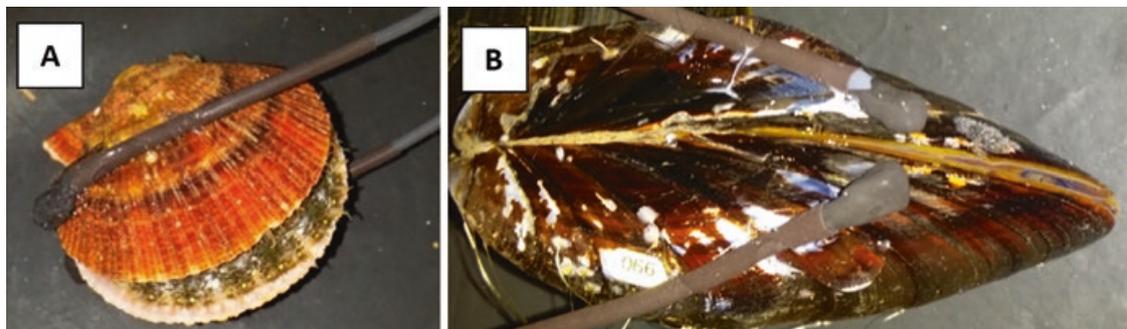


Fig. 8.6 Arctic scallop *Chlamys islandica* (a) and the blue mussel *Mytilus edulis* (b) equipped with lightweight electrodes of the high-frequency, non-invasive (HFNI) valvometer biosensor to record valve activity behaviour. (Photo credit: D. Tran)

subtidal conditions, with modulation of intensity by the neap-spring tidal cycle (~14.7 days) and the anomalistic moon cycle (~27.6 days). A weaker daily rhythm is also apparent but changes seasonally, from nocturnal in autumn and winter to diurnal in spring and summer (Payton et al. 2017a). Indeed, Payton et al. (2017a) clearly showed that the tidal, moonlight and daily rhythms are all modulated on annual time frames suggesting an interaction with a putative circannual rhythm.

Several recent long-term studies have been made possible by real-time communication with valvometers providing remarkable insights into the behaviour of some ecologically important Arctic bivalves, specifically the ocean quahog clam, *Arctica islandica*, considered as the longest-lived non-colonial animal on Earth with a longevity of >500 years (Ballesta-Artero et al. 2017); the native Arctic scallops, *Chlamys islandica*; and the blue mussel *Mytilus* spp. which is classified as a non-native species in Arctic waters.

8.4.2 Seasonal Clocks

A 3-year study was conducted on *C. islandica* in Kongsfjorden, a high Arctic fjord (Spitsbergen, Svalbard, 78° 56'N), to determine daily cycles of valve gape during the Polar Day, the Polar Night and equinoxes (Tran et al. 2016). Results revealed that the percentage of scallops within the population exhibiting a cyclic pattern in gape behaviour within the circadian range was highest during the Polar Night (76%) and lowest during the Polar Day (50%) with intermediate numbers during the equinoxes (67%). During the periods centred on the spring and autumnal equinoxes, the scallops exhibited a cycle with a period very close to 24 h, synchronized by daily light–dark alternations. During the Polar Night and Polar Day, the daily cycle was less synchronized to the exact 24-hour period. It is unclear whether the scallops reacted exogenously to light or if a functional and robust endogenous circadian clock initiated rhythmic behaviour during times when light–dark cycles were muted during the Polar Night and Day.

To better understand seasonality and potentially the role of circannual rhythmicity in shell gape behaviour and growth, a comparative assessment was made between *C. islandica* and *M. edulis* during 2 years of monitoring (2016–2018) in Svalbard (78°56'N). Figure 8.7 (upper panel) shows a typical, double-plotted actogram of an individual profile of a *C. islandica* illustrating that the scallop remained mostly open (for details, see Fig. 8.7) with an opening amplitude near the maximum throughout the 2 years. In contrast, the behaviour of a blue mussel, *M. edulis*, shows a different annual pattern of valve behaviour with strong seasonal components. The valve opening amplitude (VAO) was maximal since the beginning of the Polar Day until to the beginning of Polar Night where the activity strongly decreased until to the next Polar Day.

Even at this high latitude, *M. edulis* followed a seasonal cycle of gape activity like in other bivalves such as *A. islandica* (Ballesta-Artero et al. 2017), where shell gape activity is well correlated with food availability and, to a lesser degree, photoperiod and water temperature. There are subtle differences in behaviour how-

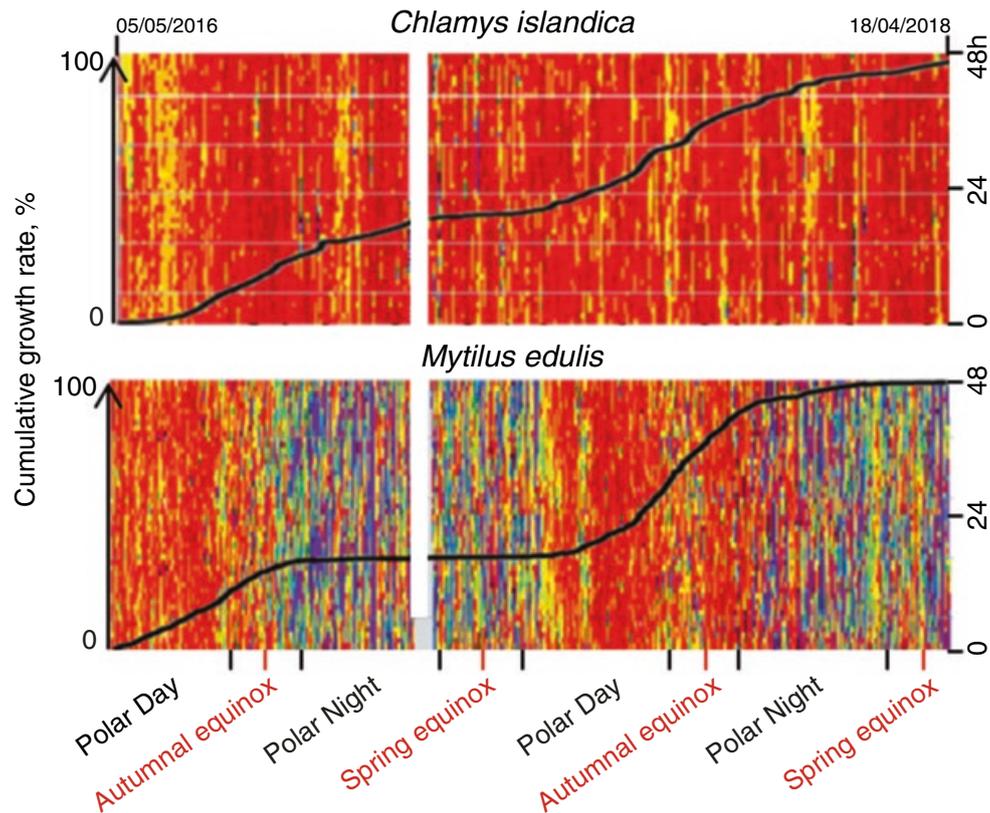


Fig. 8.7 Annual behaviour of Arctic bivalves. Double-plotted actograms of individual hourly valve opening amplitude (VOA) behaviour (right y-axis) of a *C. islandica* and a *M. edulis*. The behaviour was recorded by HFNI valvometer biosensors over 2 years (2016–2018) in the Kongsfjorden (Spitsbergen, Svalbard, 78° 56'N). Dark red and blue colours correspond to 100% and 0% of VOA, respectively. Black lines correspond to the profile of the shell growth. Left y-axis corresponds to cumulative growth; 100% corresponds to the maximal growth of shell at the end of the 2-year experiment. Unpublished data

ever; whilst *M. edulis* valve opening was maximal during the Polar Day corresponding to the summer, in *A. islandica*, this occurred during the spring. Conversely, *C. islandica* tended to keep its valves open continuously, irrespective of season, and the valve opening amplitude exhibited only a very narrow range of variation (75–80% of maximal amplitude), with no significant daily/seasonal rhythms (Tran et al. 2016). This highlights that in the scallop at least, there is an absence of any seasonal or potentially circannual cycle/rhythm of valve activity.

Since HFNI valvometry also provides a measure of shell growth from daily incremental increases between the minimum distances of electrodes when the shells are closed, seasonal patterns of growth may also be investigated. In Fig. 8.7, two typical profiles of shell growth are shown in the two species, superimposed over the valve activity behaviour. In *M. edulis*, a seasonal/circannual cycle of growth correlates to the behavioural rhythm of shell gape. The slope of shell growth rate was maximal when the valve opening amplitude was maximal during the Polar Day. In contrast, shell growth rate was minimal during the Polar Night, when valve opening amplitude was also decreased.

In *C. islandica*, the growth pattern at the annual scale was similar to *M. edulis* but with less marked variation and therefore not correlated with a circannual rhythm of valve activity. The reduced growth in the Polar Night in both these bivalves' species is in concordance with sclerochronology studies done on the Iceland cockle, *Clinocardium ciliatum*, in Greenland showing a reduction of shell growth during Polar Night (Sejr et al. 2009).

8.4.3 Circadian Clocks

The somewhat surprising finding that the highest percentage of cyclic activity in *C. islandica* was during the Polar Night warranted further investigation, specifically to understand circadian clock involvement in this response. Thus, the strength of the scallop daily gape cycle over three successive Polar Nights was assessed according to changes in light irradiance (as twilight) over the Polar Night period (Tran et al. 2016). Five periods were investigated for each of the three Polar Nights: two civil twilights, with decreasing or increasing light irradiance; two nautical twilights, with decreasing or increasing light irradiance; and astronomical twilights, the darkest twilight of the Polar Night (see Chap. 3 for twilight definitions).

The results revealed that for the population of scallops monitored, a robust daily/circadian cycle was found during the decreasing civil twilight (Fig. 8.8). Decreasing light levels during nautical twilight, however, resulted in no significant daily/circadian activity. Surprisingly, during astronomical twilight, the scallops recovered significant daily/circadian activity but out of the circadian range (here between 16 hours and 33 hours). At an individual level, animals often had a daily/circadian cycle at both increasing/decreasing civil and increasing, but not decreasing, nautical twilights. Other than during nautical twilight, a correlation was revealed between increasing light intensity in the twilights and the percentage of cyclic scallops in the circadian range. Moreover, the cycle of activity became increasingly more synchronized to 24 hours with higher irradiance during twilight.

At this stage, it was still unknown if the daily cycle of activity in *C. islandica* was simply due to an exogenous response to extremely low levels of light during the Polar Night or an actual endogenous circadian rhythm of activity. To address this question, core clock genes were sequenced from *C. islandica* which revealed close homology with those found in temperate bivalve species. To measure the clock gene expression of *C. islandica*, two field experiments were performed in Kongsfjorden during the Polar Night (January 2017) and during the autumnal equinox (September 2017). Sampling of different tissues was carried out every 2 hours during a 24-hour cycle. The results showed that the level of the clock gene expression was very low. In both periods of sampling, some clock genes were oscillating in a circadian range and were tissue-specific. During the equinox experiment, the genes *period* and *ror* in the adductor muscles, *cryptochrome 1* in the mantle and *clock* in the gills revealed cycling circadian gene expression. During the Polar Night, no clock genes were observed to oscillate in muscles, but cycling was apparent in *clock*

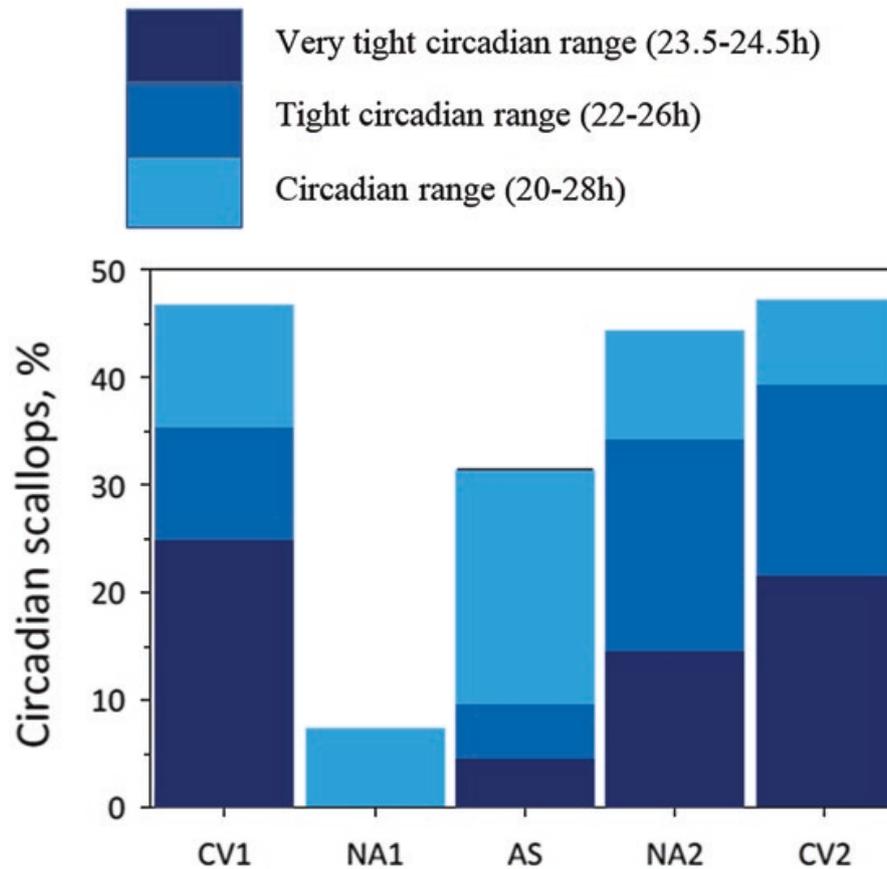


Fig. 8.8 Circadian activity of *C. islandica* ($n = 14$) during the Polar Night in Kongsfjorden (Spitsbergen, Svalbard, $78^{\circ} 56'N$). Percentage of scallops with valve behaviour in different circadian ranges according to the different twilight periods during three Polar Nights studied (2012–2015). Each Polar Night was subdivided into five periods that corresponded to different twilight periods of increasing and decreasing levels of light irradiance: the civil twilight periods (CV1, CV2), the nautical twilight periods (NA1, NA2) and the astronomical twilight periods (AS). The mean percentage represents an average for the three Polar Nights studied. (Modified from Tran et al. (2016))

and *ror* in gill tissue as well as *ror* in the mantle edge. The lack of cycling gene expression in some tissues challenges the role of clock genes in entraining all physiological and behavioural activities, especially when compared to temperate species, such as the oyster *C. gigas*, which demonstrates circadian cycling in all the core clock genes when exposed to a light–dark regime (Payton et al. 2017b).

In conclusion, recent studies in the Arctic show that bivalve molluscs are able to maintain rhythmic behaviours at daily and annual scales similar to bivalves at lower latitudes (Garcia-March et al. 2008, Tran et al. 2011, Payton et al. 2017a). Those in the Arctic appear to have adapted their behaviour to the specific light climate presumably to take advantage of the seasonal cycle of food availability. Although the molecular circadian clock machinery is present, its function at high latitudes remains to be elusive and should be the focus of further research.

8.5 Climate Change Effects on Biological Clocks in Polar Regions

By measuring photoperiod, the circadian clock synchronizes the timing of seasonal life-cycle events in response to annual cycling changes in light conditions. However, climate change-induced geographical population shifts towards higher latitudes, such as those already seen in *C. finmarchicus* (Falk-Petersen et al. 2007) and the blue mussel, *M. edulis* (Berge et al. 2005), are resulting in animals experiencing a mismatch between the thermal and the photoperiodic environments to which they are adapted (Reygondeau and Beaugrand 2011). Consequently, as the oceans warm and become more illuminated following sea ice melt, there will be trade-offs between latitudes of favourable temperature and potentially unfavourable photoperiod. Such trade-offs will be particularly pronounced in the Arctic with rapid photoperiodic change over short latitudinal ranges and increases in sea temperature predicted to be large (Beaugrand et al., 2019).

Thermal-photoperiodic mismatch due to climate change may be especially evident in the seasonal life cycles of *Calanus* spp. If diapause initiation is promoted via photoperiodic time measurement, then a critical photoperiod would induce the animals to switch from one seasonal physiological state to another. However, critical photoperiods may be affected by temperature as well as sequence variants (alleles) of circadian clock genes (Watson and Smallman 1971, Paolucci et al. 2013). While the strong selective pressure for optimal seasonal timing suggests rapid spread of 'favourable alleles', at least for terrestrial insects (Bradshaw and Holzapfel 2001, Tauber et al. 2007), it is unclear how such adaptation processes could work in marine habitats affected by large-scale displacements via ocean currents.

While all three species of *Calanus* rely on the spring phytoplankton bloom, the boreal *C. finmarchicus* does so the most (for details, see Chap. 5). Since increasing ocean temperatures are leading to earlier sea-ice breakup and earlier phytoplankton blooms (Søreide et al. 2010), the negative consequences to *C. finmarchicus* may be large if its phenology is reliant on an inflexible circadian/circannual clock. Generally, the interannual variability of the timing of the bloom is high in polar habitats due to the variability in the timing of sea ice breakup (Kahru et al. 2010). *Calanus glacialis* and *C. hyperboreus* are probably better adapted than *C. finmarchicus* to this heterogeneity (reflected in their multiyear life cycles), and *C. finmarchicus* may not, therefore, be able to fill a gap created by the poleward retreat of its polar congeners. Either way, any reduction in fitness and recruitment of *C. finmarchicus* because of thermal/photoperiodic constraints would severely affect higher trophic levels and biogeochemical cycling (Falk-Petersen et al. 2007; Jónasdóttir et al. 2015). Similar ecosystem consequences might be expected in loss of fitness in krill and, to a lesser extent, bivalves.

Copepods, krill and bivalves have adapted to the extreme polar photoperiods, and their behaviour and circadian clock expression is highly modulated by seasons and physiological state. Quite how circadian clock entrainment works during much of the Polar Night twilight periods, however, and its function in maximizing fitness has yet to be elucidated.

Box 8.1

The underlying molecular mechanism of the circadian clock is highly conserved between species and consists of autoregulatory feedback loops where gene products (proteins) switch off their own gene transcription. In invertebrates, the best-studied model for the circadian clock is *Drosophila melanogaster* (Zeng et al. 1996). Here, the two principle clock genes (*per* and *tim*) are located in the nucleus of the cell (except in mitochondria) and are ‘switched on’ or activated via clock proteins (CLOCK/CYCLE) using promoter regions (E-boxes) as depicted in Fig. 8.9.

Per and *tim* messenger ribonucleic acids (mRNA) are then used to generate clock proteins (PER and TIM) in the cell cytoplasm where another clock protein (CRY) can alter the phase of the circadian clock since it is light sensitive. CRY has the potential to degrade (phosphorylate) TIM, either slowing or speeding up the circadian clock since PER/TIM can only re-enter the nucleus if they have coupled together in a special way (they need to have formed a

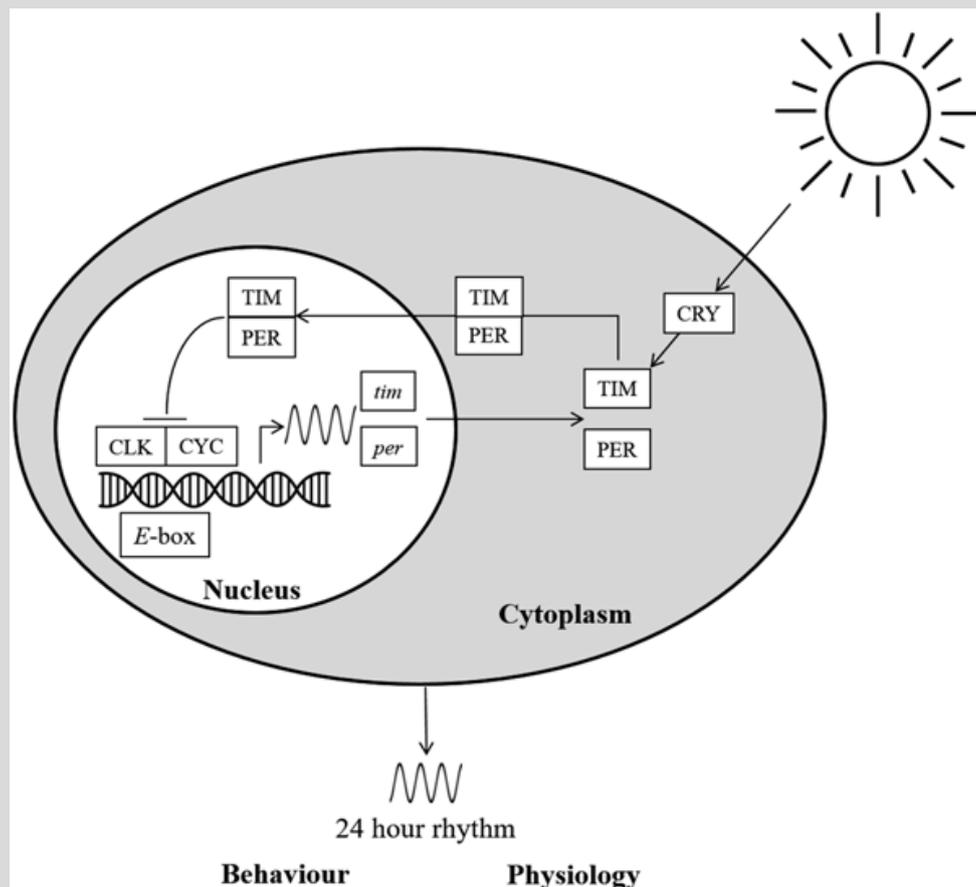


Fig. 8.9 Simplified *Drosophila* circadian clock showing molecular interactions of clock genes and proteins. Entrainment of the clock is by the day/night cycle, and the final output is a 24-hour rhythm of behaviour and physiology. The mechanism of the clock is similar between species although different genes may be recruited

(continued)

Box 8.1 (continued)

heterodimer). Once in the nucleus, they then interact with the activator clock proteins CLOCK/CYCLE, essentially ‘switching them off’. This then also switches off *per* and *tim* gene expression. Eventually after about 24 hours, the inhibitory proteins PER/TIM are depleted, and this is when the whole cycle starts again (for detailed overview of the molecular circadian clock in *Drosophila*, see Dubowy and Sehgal (2017)). Quite simply, the clock is an unseen evolutionary marvel, ticking with peaks and troughs of clock gene mRNA and their proteins, cycling through the day. The molecular machine and gene expression pathways remain largely unchanged between species, apart from a few tweaks, and a simplified proto-clock has even been documented in the earliest protozoa which first appeared in the Earth’s history over a billion years ago (Tauber et al. 2004).

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