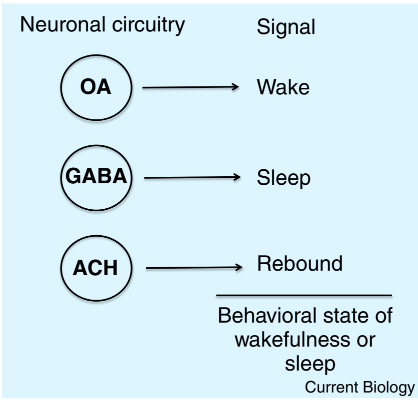

Figure 1. Regulation of rebound sleep by a group of cholinergic wake-promoting neurons.
The neurotransmitter octopamine (OA) represents a wake-promoting signal, and activation of octopaminergic circuitry does not lead to rebound sleep [1]. Sleep-promoting neurons, such as gama-aminobutyric acid (GABA) neurons, regulate baseline amounts of sleep [16]. Acetylcholine (ACH) neurons are unique in that activation of select cholinergic neurons leads to wakefulness followed by rebound sleep. Since they respond to sleep pressure they are interacting with, or are a component of, a sleep homeostat. The behavioral state of sleep or wake is a net result of output signals from different sleep-regulating circuits.

overpowers arousal, even if life is threatened. This is evident in everyday life, when people fall asleep while driving.

Seidner *et al.* identified a novel cholinergic circuit that can induce wakefulness, trigger sleep and participate in short-term memory. Evidence that certain cholinergic neurons might satisfy criteria for being homeostat neurons is increasing, but many more questions remain. Mapping of wake- and sleep-promoting neurons and their connections is an approach that can be done in *Drosophila*, which will help us understand the mechanism behind the sleep homeostat. Future studies of homeostatic sleep regulation in flies is likely going to lead to new, exciting discoveries with applications that will make not only flies sleep better.

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Marine Ecology: A Wonderland of Marine Activity in the Arctic Night

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Studies carried out on a wide variety of Arctic species during the polar night reveal continued feeding, growth and reproduction, changing our view of this period from one of biological stasis to a time of continued high activity levels.

“Once I lived in polar night, burned summer fat for winter light.” This evocative image from Naomi Replansky’s poem *Changes of Climate* encapsulates what has been the prevailing scientific view of how marine life at the poles survives the long period of continual darkness. At its extreme, this period can last over 100 days (Figure 1) with the lack of light ceasing the ability of algae, at the base of the food chain, to photosynthesise and grow. Summertime at the poles, when the ice thins and breaks, and light penetrates the upper water column, provides a bonanza of nutrient-replete primary production. Reserves built up from consuming these rich food banks are the fuel that polar marine animals rely on to outlast the long, barren period of winter darkness. Few scientists questioned that the only viable strategy to survive such a long period of deprivation was to become quiescent, limit movement and metabolism, and make reserves last until light and primary productivity return. Writing in a recent issue of *Current Biology*, however, Berge and colleagues [1] were unconvinced that marine communities in the high Arctic entered such a dormant state. Through a series of studies examining many different aspects of the Arctic marine ecosystem, they have uncovered numerous examples of continued activity, reproduction, feeding and growth during the polar night.

Berge and colleagues carried out their work over three consecutive winters, targeting the second half of the 117 day long polar night. Studies of the zooplankton community revealed organisms in the midst of the reproductive phase of their life-cycles. Abundant species, such as the copepod *Calanus* spp., which were believed to spend most of the winter at great depth in an inactive state, were found to have already mated and were heading back to the surface layers. The early larval stages of a number of other zooplankton species were also commonly found, including those of a variety of benthic species. If these communities had ever been asleep, it appears that they had already woken up again by mid-winter and were preparing themselves for the return of first light, many weeks hence.

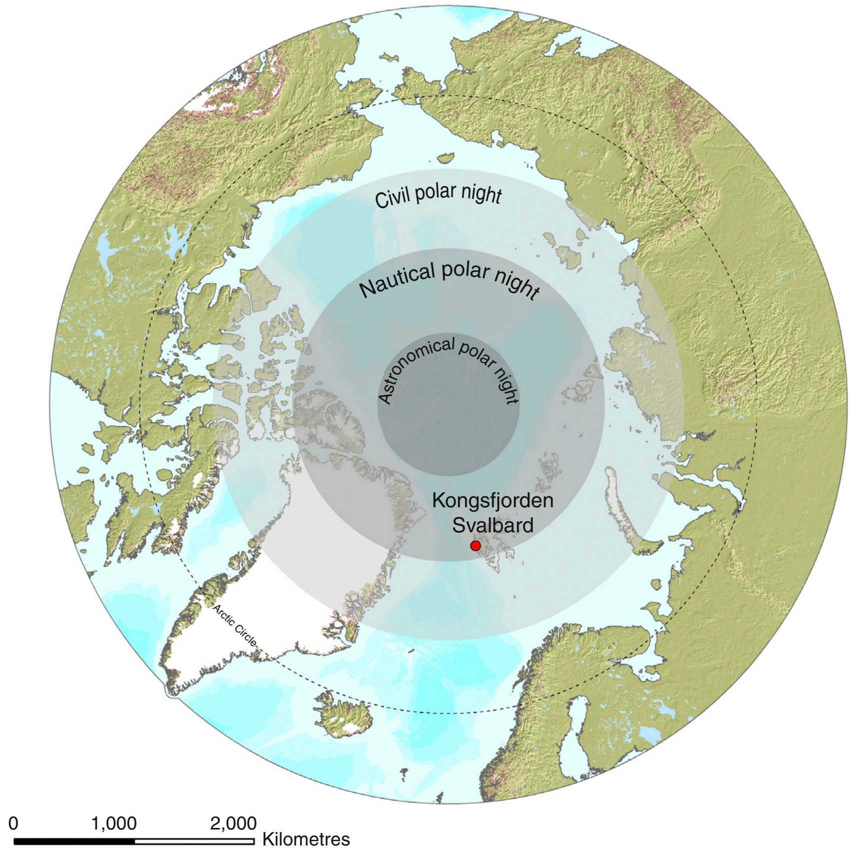

Figure 1. Area of the Arctic that experiences the polar night, in which the sun remains below the horizon for the entire 24 h cycle.
The duration of polar night conditions and the degree of darkness depend on latitude. Within the region of civil polar night, the sun lies below the horizon between 1 November until 30 January but there remains a faint glow of light visible (twilight) around midday. In the region of nautical polar night period, there is no trace of natural twilight but there is a faint glow of light around midday as a result of refraction. Kongsfjorden, where most of the present observations were made, lies within the nautical polar night zone and experiences these conditions for 116 days. The region where all visible twilight is absent is called the astronomical polar night region, and this state of darkness may last there for up to 11 weeks. (Map: Oliva Martin-Sanchez.)

Nevertheless, these observations may not be as surprising as they first seem. Summertime in polar environments is short and organisms need to make the most of the warmer, food-rich conditions by having everything in place right from the start. Laying eggs in advance of this period will ensure that the newly hatched larvae have the maximum period within which to grow and accumulate resources to endure the next winter to come. However, this requires parents to have sufficient resources themselves to meet the significant energetic demands of reproduction when there is little food around. This strategy has been termed ‘capital breeding’, meaning the use of bodily reserves to fuel reproduction [2]. It necessitates an even greater effort to accumulate resources during the previous summer, at greater risk of attracting predators. The alternative is ‘income breeding’, where reproduction relies on concurrent food intake. Evolutionary models have predicted that the reproductive fitness of those eggs laid right at the start of the polar season should be considerably higher, thus favouring the capital breeding strategy [3]. What Berge and colleagues [1] found was evidence of capital breeding in action.

They also found numerous examples of continued activity and growth in the marine community throughout the polar night. Respiration rates of *Calanus* spp. at the surface were comparable if not higher than rates measured during summer. Similarly, the respiration rates of species in the sediment measured in January were similar to those measured at the same stations at different times of year and other Arctic locations in the summer. Growth rates of the filter feeder *Chlamys islandica* (Iceland scallop) were found to continue at summertime rates in half the specimens examined. Deployments of baited traps, with time-lapse cameras, revealed a species-rich and active shallow water scavenging community during the polar night, comprised of gastropods, amphipods and crabs.

Combined, the findings of Berge and colleagues [1] provide a new perspective into the processes that

Figure 2. The Arctic krill species *Thysanoessa inermis*.
T. inermis (25 mm) can detect the limited solar light levels during the polar night down to depths of around 30 m. (Photo: Russ Hopcroft.)

control populations of Arctic marine species. One of the major arguments is whether such systems are controlled from the bottom up, where species population size is determined by the availability of the photosynthetic organisms and nutrients or from the top down, by herbivorous consumption and predation keeping prey abundance under control. Polar marine ecosystems are believed to be primarily bottom-up controlled, as the extremely short period of summer productivity gives little time for consumers to exert any control on the rapidly growing populations of autotrophs and small heterotrophs [4]. However, what Berge and colleagues [1] show is that the activity of higher trophic levels does not grind to a halt as soon as conditions become unfavourable for primary production. The carbon fixed by the photosynthetic organisms persists in the water column for a considerable period of the winter and consumption switches from herbivorous-grazing to detritivory. Filter-feeding benthic species continue to thrive on this detrital material throughout the polar night. Planktonic larval stages may also use this material to meet their energetic demands and these larvae, in turn, are a major prey resource for carnivorous species. Larval recruitment in many polar species therefore becomes a top-down controlled process operating over the course of the polar night. It is widely understood that the relative importance of top-down and bottom-up processes varies as a function of spatial scales [5]. The evidence provided by Berge and colleagues [1] highlights how these processes in the Arctic marine environment also vary in importance over time on seasonal scales.

A particularly novel finding was that even visually guided predators continued to feed during the polar night. Many seabird species (little auks, black guillemots, Brünnich guillemots, northern fulmars, black legged kittiwakes and glaucous gulls) foraged actively on fish, krill and amphipods during this time. Also, species of pelagic and benthic fish were found with stomachs over half-full with fresh prey. Certain prey species, such as krill, are known to exhibit bioluminescence, which could attract visual predators, but this is not true of all prey species. Some predators may have alternative means of detecting prey, such as tactile and acoustic mechanisms. However, a large part of the success of these visual predators during the polar night may be explained by the availability of moonlight. With the exception of the new moon phase, the moon continually rises and sets throughout the polar night to the point where it remains above the horizon for 24 hours during full moon. It also reaches its highest altitude above the horizon during the polar night. A number of studies have shown that seabirds are responsive to moonlight during foraging, with individuals diving deeper and more frequently in brighter moon-phases [6–8]. Furthermore, the prey themselves are able to react directly to moonlight in order to reduce their risk of predation [9,10]. Hence, it is likely that both predators and prey take advantage of moonlight in place of the absent sun during the polar night.

Nevertheless, this is not the whole story because there are times when the moon is also completely absent, yet certain rhythmical behaviours continue. Valve opening in *Chlamys islandica* was found to maintain a diel rhythm, while the stereotypical 24 h cycle of upward and downward migration in the zooplankton community persisted throughout the polar night. These behaviours could be synchronised by internal clocks, but the ability of such physiological clocks to maintain a consistent rhythm without significant drift over a period in excess of 100 days is unlikely. Most biological clocks are otherwise tuned to a predictable environmental signal or '*zeitgeber*'. Even though the sun does not go above the horizon during the polar night, there remains a dynamic change in light regime with respect to intensity and spectral composition around the solar noon when the sun is at its highest elevation below the horizon. Electrophysiological tests have demonstrated that zooplankton, such as the krill *Thysanoessa inermis* (Figure 2), are capable of detecting such dim light levels down to depths of 30 m [11]. Therefore, even in the midst of the polar night, there may be sufficient light by which daily cycles can be coordinated.

The Arctic is undergoing some of the most rapid warming of any oceanic region. This may facilitate an invasion of temperate marine species as conditions become more favourable. Such an invasion threatens the structure of Arctic marine ecosystems as new competitors and predators will decrease the availability of resources and increase levels of predation mortality, respectively. However, although temperature has a powerful influence on the life-cycles and distributions of marine organisms, interactions between them are strongly dictated by the light regime. The lack of light for such a long period may inhibit many temperate visual predators from establishing themselves in the Arctic [12]. Furthermore, the extremely short productive season favours those organisms that can amass large levels of bodily reserves, which selects against the smaller body sizes typical of herbivorous zooplankton from temperate regions [13]. Hence, the unique adaptations of Arctic species towards surviving the continual darkness of the polar night may act to preserve community structure despite the ensuing rapid environmental changes.

Berge and colleagues [1] propose a re-evaluation of how the polar night is viewed. This period is not one of dormancy and the minimisation of energy loss but one of continued activity and growth. The advent of the polar night does not result in severe ramp-down in ecosystem function but is a time during which predation and scavenging become the dominant modes of energy transfer. Ultimately, the Arctic ecosystem is reliant on the phytoplankton blooms that occur during the few summer months when both nutrients and light are sufficiently available. However, not everything in this environment is time-critical and many parts of the ecosystem continue to exploit this rich food resource beyond the summer and into the polar night. What we now understand is that Arctic organisms have adapted not only to survive but to thrive during this long continual period of darkness.

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