

## Commentary

# Long days and long nights: an integrative study reveals survival strategies of an Antarctic diatom during the cold and dark polar winter

The vast majority of photosynthetic organisms on Earth have evolved under a circadian cycle, with many cellular processes being regulated by the predictable patterns of day and night. Polar algal species living in Arctic and Antarctic aquatic habitats are faced with bizarre light environments of continuous light during the short summer months and 24-h darkness during the winter, that is one long day transitioning into one long, cold night. It is well known that polar phytoplankton survive the winter and return in the summer to form blooms. In an article published in this issue of *New Phytologist*, Joli *et al.* (2024, 2193–2208) use an integrative approach to dissect how an Antarctic marine diatom not only survives the long, dark polar winter, but also recovers rapidly upon the onset of summer.

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Diatoms are a dominant phytoplankton species of polar marine habitats and contribute significantly to primary production. Standing winter communities of diatoms, as well as community dynamics during the abrupt shift from winter to the annual ice break-up in the summer, are thought to contribute significantly to summer blooms (Niemi *et al.*, 2011). Diatom communities are negatively impacted by climate-related change. For example, in the western Antarctic Peninsula, over time cryptophyte populations are replacing diatoms (Mendes *et al.*, 2023).

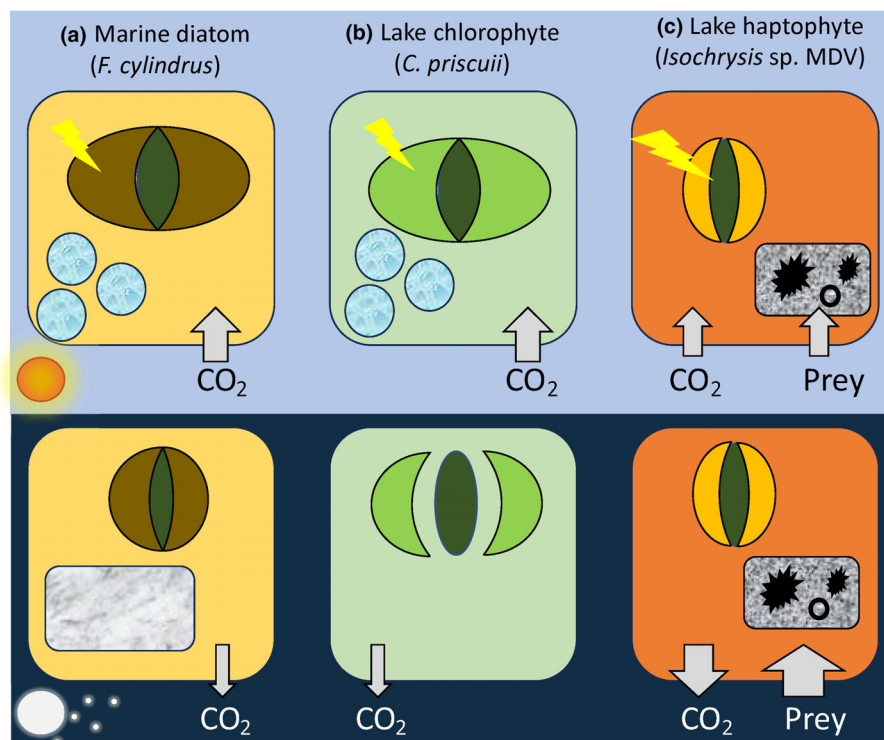
Hypometabolism, or ‘physiological fasting’, is a common phenomenon among hibernating mammals as a winter survival strategy: it involves a massive rewiring of the metabolism to severely limit energy consumption (Heldmaier *et al.*, 2004). Mammalian

hibernation is of interest in human physiology: many potential problems faced by hibernating animals mimic human diseases, such as cardiovascular function, kidney failure, muscle wasting, and osteoporosis (Berg von Linde *et al.*, 2015). While the ramping down of metabolism has been reported several times in overwintering polar algae (e.g. Baldisserotto *et al.*, 2005; Lacour *et al.*, 2019), the phenomenon of hypometabolism has not been considered for nonmammalian overwintering lifeforms. Joli *et al.* pose an interesting hypothesis that overwintering diatoms, specifically the Antarctic diatom *Fragilariopsis cylindrus*, rely on a hibernation-like metabolism to shore up their odds of survival during the long, cold and dark polar night. Phytoplankton from polar regions share a critical challenge with overwintering mammals: severe limitation of their primary energy source. For Antarctic and Arctic phytoplankton, this energy loss is directly due to the sun dropping below the horizon for 4–6 months.

*Fragilariopsis cylindrus* is a model diatom species for cold adaptation of photosynthesis (Mock *et al.*, 2017) and is a significant member of Antarctic marine phytoplankton communities (Lizotte, 2001). Joli *et al.* used an integrative approach to dissect polar night survival of *F. cylindrus* at the level of transcriptomics, microscopy, biochemistry, and photobiology. Cultures stopped dividing 3 d into the 86-d polar night treatment; total cellular carbon, nitrogen, and pigments declined by 50% by the end of the dark period. Significant subcellular arrangements were associated with long-term dark adaptation, including a reduction in thylakoid size and the development of a large vacuole. Morphological changes were accompanied by the downregulation of photophysiology and carbon fixation; although, photosystem II photochemistry potential remained high throughout the dark treatment. In addition, significant changes in the transcriptome favored metabolism associated with autophagy processes. Autophagy appears to be a major survival strategy in the polar diatom to remobilize energy reserves to maintain energy homeostasis by slow metabolism of molecules such as energy-rich fatty acids. The large vacuole provides a location for these processes and protects other cellular components from oxidative damage (Fig. 1a).

Transition from polar winter conditions to summer is an abrupt and potentially stressful environment for polar phytoplankton. Following the incubation under winter conditions, *F. cylindrus* was returned to conditions that mimic the ice break-up during the transition from winter to summer. Upon reintroduction to summer conditions, *F. cylindrus* relied on the activation of photoprotection followed by rapid onset of photosynthetic activity. However, even before summer, there is evidence that the diatom keeps photosynthetic processes primed throughout the winter. The production of chlorophyll precursors in the dark appears to contribute to the rapid onset of photosynthesis when light returns. Conversely, pre-emptive transcription of photoprotective light harvesting genes is likely to contribute to the activation of transient

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**Fig. 1** Preparation for the long polar winter among Antarctic phytoplankton. (a) The Antarctic marine diatom, *Fragilariopsis cylindrus*, acclimates to the polar night by rewiring its carbon metabolism and forming a large vacuole, which allows it to switch to a hibernation-like state of hypometabolism (Joli *et al.*, 2024, in this issue of *New Phytologist*, 2193–2208). (b) The Antarctic lake chlorophyte, *Chlamydomonas priscuii*, switches its photosynthetic apparatus to a downregulated state during the polar night, similar to the overwintering process in evergreen trees (Morgan-Kiss *et al.*, 2006, 2016). Both strategies allow the Antarctic marine and lake phytoplankton to rapidly switch back to light energy capture and carbon fixation when the sun returns. (c) However, mixotrophic algae, such as the Antarctic lake *Isochrysis* sp. MDV, remain active in the winter by switching from photosynthesis to predation, dominating lake phytoplankton communities throughout the winter months (Li *et al.*, 2016; Patriarche *et al.*, 2021).

photoprotection while photosynthesis is jumpstarted during the first few days of summer.

Preparation for the long polar winter, as well as winter survival, has been studied in other Antarctic phytoplankton species. In the Antarctic lake green alga, *Chlamydomonas priscuii*, studies under laboratory controlled and *in situ* incubation experiments have revealed that it maintains its major photosynthetic apparatus during the polar winter, albeit in a functionally downregulated state, in a physiological process resembling overwintering in evergreen trees (Morgan-Kiss *et al.*, 2005; Morgan-Kiss *et al.*, 2006; Fig. 1b). An *in situ* incubation experiment performed within the native environment (Lake Bonney, McMurdo Dry Valleys, Antarctica) showed that the expression of the reaction center and carbon fixation genes was gradually downregulated in transplanted *C. priscuii* cultures during the transition from summer to winter (Morgan-Kiss *et al.*, 2016). These trends in the isolate fit well with responses to the polar night transition in native communities of chlorophytes, which are obligate photosynthetic microorganisms (Kong *et al.*, 2012). By contrast, mixotrophic phytoplankton in Antarctic lakes, including the cryptophyte *Geminigera* sp. and a haptophyte *Isochrysis* sp., remain active during the winter by switching to bacteriovorous heterotrophic metabolism (Li *et al.*, 2016; Patriarche *et al.*, 2021; Fig. 1c).

Joli *et al.* have shed additional light on what polar phytoplankton are doing in the dark. Their findings contribute complementary data on adjustments made to carbon metabolism to a breadth of previous work that has focused on the light harvesting side of photosynthesis. Taken together, these studies show us that, in addition to the adaptive strategies that polar algae employ to conduct photosynthesis under permanent low temperatures, Antarctic phytoplankton have a toolbox of physiological responses

to survive the long winter and hit the ground running when the sun comes over the horizon again. This information advances our understanding of important processes occurring during the winter and transition seasons when science activity is limited. Their findings are also important in the context of a rapidly changing polar ecosystem. Coastal marine Antarctic environments are threatened by warming temperatures and changes in sea ice extent. These changes will undoubtedly impact the overwinter survival of the primary producers that fuel this diverse and productive ecosystem.

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## References

- Baldissierotto C, Ferroni L, Andreoli C, Fasulo M, Bonora A, Pancaldi S. 2005. Dark-acclimation of the chloroplast in *Koliella antarctica* exposed to a simulated austral night condition. *Arctic, Antarctic, and Alpine Research* 37: 146–156.

- Berg von Linde M, Arevström L, Fröbert O. 2015. Insights from the den: how hibernating bears may help us understand and treat human disease. *Clinical and Translational Science* 8: 601–605.
- Heldmaier G, Ortmann S, Elvert R. 2004. Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory Physiology & Neurobiology* 141: 317–329.
- Joli N, Concia L, Mocaer K, Guterman J, Laude J, Guerin S, Sciandra T, Bruyant F, Ait-Mohamed O, Beguin M *et al.* 2024. Hypometabolism to survive the long polar night and subsequent successful return to light in the diatom *Fragilariopsis cylindrus*. *New Phytologist* 241: 2193–2208.
- Kong W, Ream DC, Priscu JC, Morgan-Kiss RM. 2012. Diversity and expression of RubisCO genes in a perennially ice-covered Antarctic lake during the polar night transition. *Applied and Environmental Microbiology* 78: 4358–4366.
- Lacour T, Morin P-I, Sciandra T, Donaher N, Campbell DA, Ferland J, Babin M. 2019. Decoupling light harvesting, electron transport and carbon fixation during prolonged darkness supports rapid recovery upon re-illumination in the Arctic diatom *Chaetoceros neogracilis*. *Polar Biology* 42: 1787–1799.
- Li W, Podar M, Morgan-Kiss RM. 2016. Ultrastructural and single-cell-level characterization reveals metabolic versatility in a microbial eukaryote community from an ice-covered Antarctic lake. *Applied and Environmental Microbiology* 82: 3659–3670.
- Lizotte MP. 2001. The contributions of sea ice algae to Antarctic marine primary production. *American Zoologist* 41: 57–73.
- Mendes CRB, Costa RR, Ferreira A, Jesus B, Tavano VM, Dotto TS, Leal MC, Kerr R, Islabão CA, Franco AOR. 2023. Cryptophytes: an emerging algal group in the rapidly changing Antarctic Peninsula marine environments. *Global Change Biology* 29: 1791–1808.
- Mock T, Otillar RP, Strauss J, McMullan M, Paajanen P, Schmutz J, Salamov A, Sanges R, Toseland A, Ward BJ. 2017. Evolutionary genomics of the cold-adapted diatom *Fragilariopsis cylindrus*. *Nature* 541: 536–540.
- Morgan-Kiss R, Lizotte M, Kong W, Priscu J. 2016. Photoadaptation to the polar night by phytoplankton in a permanently ice-covered Antarctic lake. *Limnology and Oceanography* 61: 3–13.
- Morgan-Kiss RM, Ivanov AG, Pocock T, Król M, Gudynaite-Savitch L, Hüner NP. 2005. The Antarctic psychrophile, *Chlamydomonas raudensis* Ettl (UWO241) (Chlorophyceae, Chlorophyta), exhibits a limited capacity to photoacclimate to red light. *Journal of Phycology* 41: 791–800.
- Morgan-Kiss RM, Priscu JC, Pocock T, Gudynaite-Savitch L, Hüner NP. 2006. Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. *Microbiology and Molecular Biology Reviews* 70: 222–252.
- Niemi A, Michel C, Hille K, Poulin M. 2011. Protist assemblages in winter sea ice: setting the stage for the spring ice algal bloom. *Polar Biology* 34: 1803–1817.
- Patriarche J, Priscu J, Takacs-Vesbach C, Winslow L, Myers K, Buelow H, Morgan-Kiss R, Doran P. 2021. Year-round and long-term phytoplankton dynamics in Lake Bonney, a permanently ice-covered Antarctic lake. *Journal of Geophysical Research: Biogeosciences* 126: e2020JG005925.

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