

cyanobacteria, fungi and mammals, and has been demonstrated to regulate the expression of a CCM gene in another diatom, *Phaeodactylum tricoratum*⁷.

It is not immediately obvious why genes involved in the CCM and photorespiration are co-regulated. Cells regulate their CCM to maintain an intracellular concentration of CO₂ that saturates Rubisco by ~80%^{8,9}. Correspondingly, downregulation of the CCM in response to high CO₂ should have little effect on the intracellular CO₂ to O₂ ratio, resulting in no change in the rate of photorespiration. The reduction of photosynthesis might possibly lower the rate of photorespiration, either through a lower production of O₂ or because of a lower Rubisco concentration. However, lower rates of photosynthesis are only observed in acclimated cells whereas photorespiratory and CCM genes respond both in the short and long-term CO₂ response.

Downregulation of the CCM at elevated CO₂ has commonly been observed¹⁰ and is speculated to be an energy-saving strategy⁴, though the mechanism of regulation has previously been uncertain. As growth was kept constant

in this experiment, the energy saved by downregulation of the CCM may partly explain the lower rate of respiration observed, although high CO₂ may also decrease respiration due to other reasons, such as changing pH¹¹.

According to this interpretation it may be respiration, not photosynthesis, that directly responds to CO₂, and photosynthesis is thus reduced as cells cannot grow any faster in nitrogen-limited continuous cultures. In the field, growth rates are not fixed and net photosynthesis and growth could actually increase. A reduction of respiration at high CO₂ has been observed in the field, along with increased growth¹¹. Hence in the future increasing CO₂ concentrations could result in either increased growth or constant growth but at a lower metabolic cost, depending on nutrient limitation.

The research by Hennon and colleagues³ highlights the need to gain a fundamental understanding of the metabolic response of phytoplankton to changing CO₂ concentrations. This will allow us to tease apart the complex and often contradictory physiological results observed in the field and in the laboratory. Furthermore,

Hennon and colleagues³ have identified key CO₂ signalling pathways and components controlling the expression of CCM and photorespiratory genes, which can now be looked for in other, less well understood phytoplankton species. □

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Published online: 15 June 2015

ARCTIC PERMAFROST

Microbial lid on subsea methane

Submarine permafrost thaw in the Arctic has been suggested as a trigger for the release of large quantities of methane to the water column, and subsequently the atmosphere — with important implications for global warming. Now research shows that microbial oxidation of methane at the thaw front can effectively prevent its release.

Brett F. Thornton and Patrick Crill

Methane gas has a high global warming potential on sub-century timescales, and release of currently trapped methane could drive rapid climate change¹. Thus the possibility of substantial amounts of this greenhouse gas reaching the atmosphere has attracted attention — both in scientific and policy discussions. A potentially important source could be methane trapped within permafrost, including subsea sources that may be extensive and unstable. Staggering amounts of methane are thought to exist below the Russian Arctic shelf seas, mostly associated with shallow gas hydrates (solid ice-like structures encapsulating gas molecules) beneath and within the permafrost. Writing in the *Journal of Geophysical Research: Biogeosciences*, Pier Paul Overduin and

colleagues report on a sediment core retrieved from beneath the shallow waters (4 m depth) of the southern Laptev Sea, a location inundated only 540 years ago, thus offering insight into sedimentation, thawing, and other processes that affect the inner shelf since sea levels began to rise at the end of the last glaciation. A suite of biogeochemical data directly related to methane dynamics in this setting is presented for the first time, showing methane gas is consumed by microbes before it can reach the overlying ocean².

The effects of the thawing of long-submerged permafrost on marine methane are manifold. Freeze-locked organic carbon becomes available to microbes as permafrost thaws, and the resulting greenhouse gases may be released to

overlying sediments. The permafrost itself may act as a low-permeability physical barrier to upward migration of gases from deeper sources. Alternatively, methane may be frozen into the permafrost as gas hydrates and is released at the moment of permafrost thaw. (For the study considered here², pressures at the depth limit of the core (52 m) are too low for gas hydrate stability, although they could exist at greater depths³).

In recent years, interest has focused on the wide, shallow Siberian continental shelf seas, which were inundated after the end of the Last Glacial Maximum resulting in preservation of relict terrestrial permafrost under portions of these shelves⁴. Shallow areas such as those investigated by Overduin *et al.* are a prime location for

emissions of methane from the seafloor to the atmosphere: shallow waters allow easier diffusive or bubble transfer⁵, and large amounts of organic-rich sediments provide a ready substrate for methane-producing microbes. Indeed, high summertime concentrations of methane have been reported in these waters⁶. Understanding the sources of this gas and the dynamics of its exchange is vital to knowing if this carbon, mobilized as methane, has the potential to substantially contribute to atmospheric greenhouse warming.

The high-permeability sandy sediments in the borehole described by Overduin *et al.* give rise to a high water content, which allows for the development of ice-bonded permafrost — the top of which was identified about 25 m below the seafloor (Fig. 1). The entire core has warmed approximately 10 °C since marine inundation resulting in permafrost thaw in the warmer, upper section. This permitted efficient intrusion of seawater into sediment pore space, reaching as deep as the thaw front. Because of the high sulphate concentrations in the intruding seawater, released methane was mostly destroyed by anaerobic microbial oxidation in the overlying sediments. The effectiveness of this process in reducing sediment methane emissions to the ocean at the boundary layer is widely known⁷, but was thought to be negligible further below in the sediments due to limited sulphate availability. Anaerobic oxidation of methane requires an alternate electron acceptor other than oxygen, and in marine systems this is usually sulphate⁸. The reaction produces sulphide and the methane is oxidized to CO₂, which contributes to the formation of carbonates in the sediments near methane seeps⁹. Overduin and colleagues show the seawater intrusion and supply of sulphate is sufficient to keep pace with the release of methane from the thawing permafrost below, fuelling an efficient microbial biofilter that prevents it from reaching the atmosphere (Fig. 1).

These results have substantial ramifications for explaining the large enhancements of seawater methane that have been observed in the Laptev Sea⁶. In particular, it now seems less likely that the reported large plumes of methane bubbles and high seawater concentrations in shallow areas of that region⁵ are due to release from deep, ice-bonded permafrost. Alternate possibilities to explain the seafloor sources of these bubbles (observed

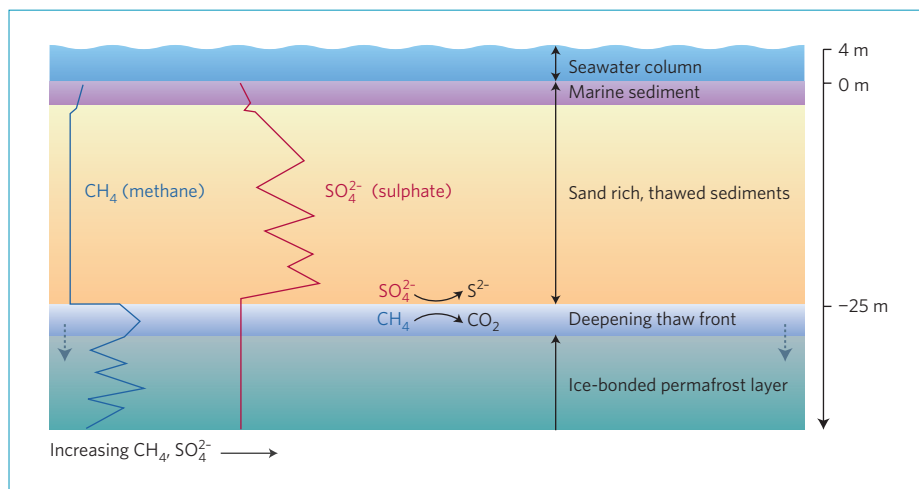


Figure 1 | Anaerobic oxidation of methane at a subsea permafrost thaw front. A core from the southern Laptev Sea revealed dramatically lower methane in the unfrozen sediment within the top 25 m of the core, compared to methane frozen into the deeper, ice-bonded permafrost. An order of magnitude drop in methane concentration, along with an increase in sulphate concentrations on crossing the thaw boundary, shown in stylized form here, all indicate efficient sulphate-driven anaerobic oxidation of methane⁸, producing CO₂ and sulphide (S₂⁻). Overduin *et al.* suggest a methane release rate from the thawing permafrost of 121 ± 64 mg m⁻² yr⁻¹; however, this methane is oxidized at the deepening thaw front (indicated by the dotted grey arrows), never migrating higher in the sediment.

by sonar) include: deeper gas sources that find clear channels to the seabed¹⁰, possibly through unfrozen taliks (thawed regions within permafrost)¹¹, local faulting or shallower sources related to *in situ* methane production in sediments rich in recently deposited organic carbon¹².

The data presented illustrate rapid oxidation of methane once it enters the thawed sediment overlying the permafrost. They remind us that upward diffusion of this gas through the sediments requires navigation past an efficient biological filter both in the sea¹³ — and as reported by Overduin *et al.*, in the sediment — before it can reach the atmosphere. This study² only considers a single nearshore area of the Laptev Sea, albeit in a region of high reported concentrations of seawater methane, so we need to be careful extrapolating these results across the Arctic region. Will areas with low permeability sediments overlying subsea permafrost differ? And, if thawing permafrost is not the dominant methane source to these waters, what is? Understanding methane sources and sinks, and their total impact on the Arctic carbon cycle in a warming climate, in Siberian shelf seas will require similar studies from other sites across the

region. Now that anaerobic oxidation has been shown to occur at the thaw front of subsea permafrost, a re-examination of methane dynamics may be required for shallow Arctic shelves that still host relict permafrost. □

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