

# Iron levels unexpectedly limit bacterial growth in the ocean's twilight zone

Microbial growth at depths of 200–500 metres has been found to be limited by iron, a key micronutrient. To meet their iron requirement, bacteria inhabiting the twilight zone manufacture siderophores – molecules that scavenge trace amounts of iron from seawater.

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## The problem

In the sunlit surface ocean, known as the euphotic zone, phytoplankton fix carbon dioxide into organic matter. This process, called ocean productivity, is regulated by the supply of key nutrients, such as nitrate, phosphate and iron<sup>1</sup>. Most organic matter is remineralized (degraded) to release carbon dioxide, usually within a few days of synthesis. However, a fraction of organic matter made in the euphotic zone escapes remineralization and sinks into the ocean's interior, delivering organic substrates that fuel the metabolism of deep-sea food webs.

The transfer of organic matter to the deep ocean acts as a biologically driven pump that removes carbon from the atmosphere and stores it in deep seawater and sediments. The strength of this biological carbon pump (BCP) is one of the principal factors that set the amount of carbon the ocean can absorb. Measuring the rates and processes that influence the BCP is difficult, because rates are low and hard to measure, and the main processes change from location to location<sup>2</sup>.

## The discovery

The global distribution of iron and other biologically essential nutrients in the ocean has been the focus of a collaborative, decades-long effort by marine scientists working under the umbrella of the international GEOTRACES programme. GEOTRACES was designed to provide high-quality data that can be used in the coming decades to understand climate-driven changes in ocean biogeochemistry. As part of a GEOTRACES expedition to the eastern Pacific Ocean, we measured the abundance and distribution of small molecules called siderophores in the upper 1,000 metres of the water column. Siderophores are synthesized by bacteria when environmental concentrations of iron are low enough to limit bacterial growth. Bacteria release the siderophores into seawater, where they form strong complexes with dissolved iron. The iron–siderophore complex is then taken into bacteria through specialized membrane transporters (Fig. 1), thereby relieving iron limitation<sup>3</sup>.

As expected, siderophore concentrations in the eastern Pacific were high in surface waters of the subpolar gyre (the large circular current between 42° N and 55° N) and equatorial areas, which are two ecosystems known to be chronically iron deficient. However, siderophore concentrations were also high at depths of between 200 m and 500 m, a region of the water column not thought to be affected by nutrient concentrations. We collected

seawater from these depths and found that bacteria in these samples rapidly took up siderophores that we labelled with the rare iron-57 isotope. After removing the iron-57 from the siderophore–iron complexes, the siderophores were excreted back into the seawater, where they could form complexes with more iron (Fig. 1). Our experiments showed that bacteria living immediately below the euphotic zone – where the flux of sinking organic matter is highest – are deficient in iron and use siderophores to enhance iron uptake. Iron deficiency and siderophore-facilitated iron uptake characterize the bacterial community at depths of 200–500 m across much of the eastern Pacific.

## The implications

Small changes in the depth at which sinking carbon is remineralized can translate into large changes in the timescales over which carbon is stored in the deep ocean. Iron limitation leads to slower growth and a lower growth efficiency (the fraction of carbon allocated to biomass relative to the fraction of carbon remineralized to carbon dioxide), both of which could have substantial impacts on the ocean's BCP<sup>4</sup>.

Over the past few decades, marine biogeochemists have devoted considerable effort to understanding the patterns and consequences of nutrient limitation on productivity in the euphotic zone. Because nutrient concentrations increase considerably just below the euphotic zone, nutrients were not thought to affect bacterial production in the dark ocean. Our study suggests otherwise, indicating that nutrient limitation extends well below the euphotic zone into the deep ocean. To fully understand how nutrients shape marine biogeochemical cycles, experiments and observations previously made near the surface need to be expanded to include the twilight zone (depths of 200–500 m), the region of the water column most crucial for the ocean's BCP.

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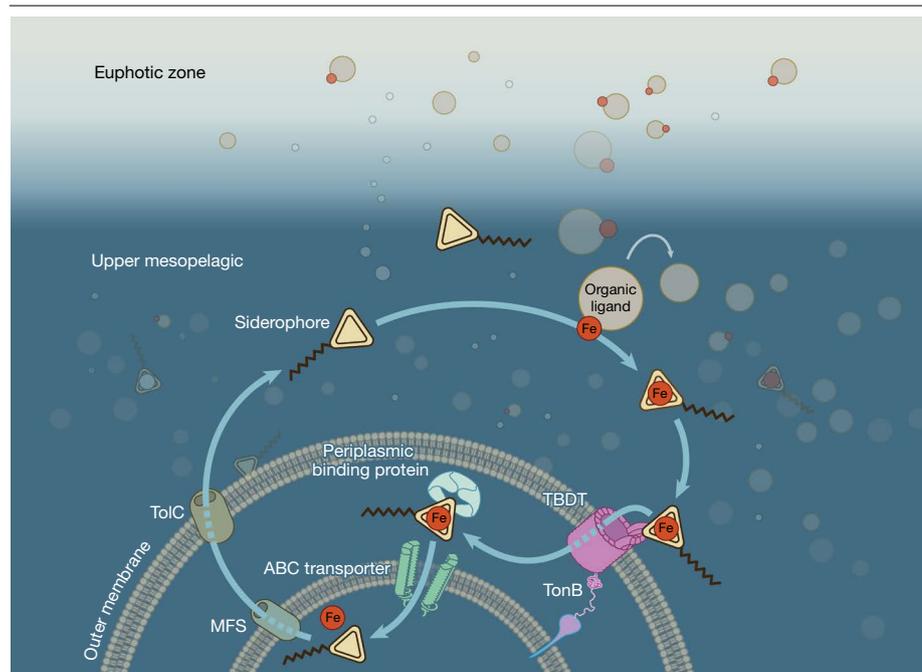
## EXPERT OPINION

**||** This exciting paper on siderophore distributions in the Pacific provides an impressively comprehensive and cohesive data set of siderophore abundance across a large-scale ocean transect. The work considerably advances our understanding of the role of siderophores in microbial iron acquisition and iron availability, with potential

for impacts on the ocean carbon cycle. The data set can also be used to develop new hypotheses that can be tested going forward.” (CC BY 4.0)

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## FIGURE



**Figure 1 | Iron-siderophore cycling in the ocean's twilight zone.** The upper mesopelagic zone is situated immediately beneath the sunlit euphotic zone of the ocean, about 200 metres below the surface. Siderophores are made in the cytoplasm of bacteria and released into seawater through major facilitator subtype (MFS) and TolC protein complexes in bacterial membranes. Once in the seawater, metal-free siderophores bind to iron ions that are weakly bound to organic ligands, and the iron-siderophore complex is transported across the bacterial outer membrane by TonB-dependent transporters (TBDTs). Then, the iron-siderophore complex binds to a periplasmic binding protein for transfer through ABC transporters into the cytoplasm, where the iron is recovered.

## BEHIND THE PAPER

Measurements of siderophores in environmental samples are extraordinarily difficult to make, and techniques have only recently been developed. We are therefore still in the early stages of understanding where and when microbes use siderophores to acquire iron. When we first set out to measure siderophores, we did not expect to find them below the euphotic zone. Our first samples taken below the euphotic zone were collected simply to test the equipment. When we found high concentrations of siderophores here, we could not explain them. The key experiments

in our work were the incubation experiments using siderophores labelled with iron-57. The siderophores disappeared from these samples after only a few days. We suspected that the siderophores were used by bacteria as a carbon, nitrogen and energy source. However, when we added iron to the sample and saw the siderophores reappear, we knew the bacteria must be using them to acquire iron.

**D.J.R.**

## REFERENCES

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## FROM THE EDITOR

This work is intriguing because it sheds new light on the factors controlling microbial metabolism in the ocean's twilight zone — the layer between the surface ocean and the deep abyss. This is important because this region of the ocean is essential for understanding the strength of the biological carbon pump that can lock carbon away in the deep ocean.

**Juliane Mössinger**, Senior Editor, *Nature*