Microbial competition for iron in the Southern Ocean

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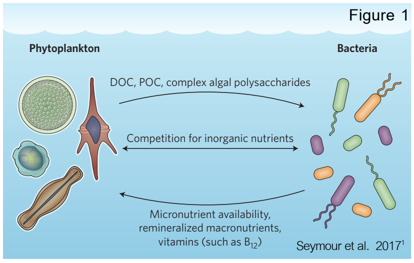
RATIONALE & SIGNIFICANCE

Iron recycling in the Ferrous Wheel at SOTS. The biogeochemical cycle of iron (Fe) and carbon (C) are linked by the Fe:C uptake ratio in phytoplankton and heterotrophic bacteria. Previous results from the Southern Ocean Time Series (SOTS) site in the autumn show that **small cells (<2.0 µm diameter) take up the most iron (Fe)**, but this size class is a **mix of heterotrophs (bacteria) and photoautotrophs (phytoplankton) that compete for this limiting resource**. Therefore, we sought to answer the question:

How much iron do heterotrophic bacteria take up compared to phytoplankton?

Answering this question is important because the fate of iron (recycled versus exported) and its efficiency in fueling primary production depend on whether bacteria or phytoplankton take it up. But competition is just one aspect of this story, as bacteria also rely on the dissolved organic carbon (DOC) released by phytoplankton and release iron-binding ligands (FeL) that can facilitate iron uptake in phytoplankton (Fig. 1).



Environmental drivers of iron and carbon uptake. **Iron uptake is also less sensitive to changes in irradiance than Carbon uptake**; the latter decreases exponentially with irradiance, suggesting that either/or: 1) Heterotrophic bacteria are responsible for much of the iron uptake in the small size fraction; 2) iron uptake in phytoplankton is less sensitive to changes in irradiance than C uptake. We thus asked:

How does light affect Fe uptake?

Possibilities include: 1) changes in the photolability of FeL complexes; 2) changes in community composition with depth (with higher heterotroph:autotroph ratios deeper in the water column); 3) physiological energetic requirements for Fe acquisition: direct for phytoplankton, indirect for heterotrophic bacteria (via DOC).

METHODS

We collected water cleanly using the Trace Metal Rosette from two sites during the SOLACE voyage on the RV *Investigator* (Dec 2020 – Jan 2021): 19 m at SOTS and from the deep biomass maximum at 83 m from a site south of the Polar Front. As previously observed, small cells took up most of the iron and large cells (> 20 µm diameter) fixed most of the carbon at both sites (Fig. 2).

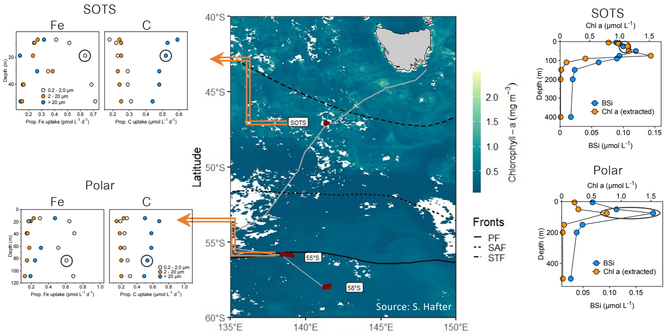


Figure 2

We exploited the difference in size between heterotrophic bacteria and phytoplankton to separate these groups using a membrane filter of appropriate porosity (0.8 µm). We performed a pre-incubation filtration to isolate the heterotrophic bacteria (< 0.8 µm) from phytoplankton and grazers and used unfiltered samples as the control (Fig. 3). We sampled the initial whole (unfiltered) and < 0.8 µm communities for community composition using flow cytometry and photosynthetic physiology using fast repetition rate fluorometry (FRRF) (2,3).

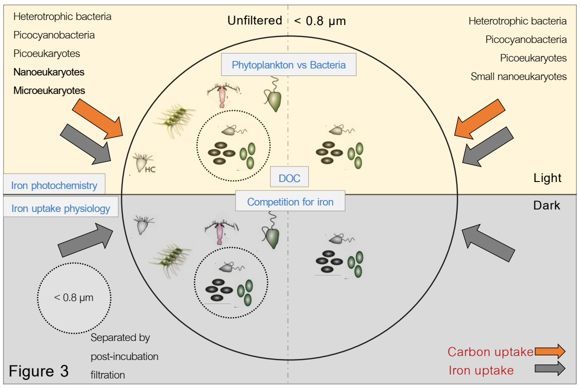
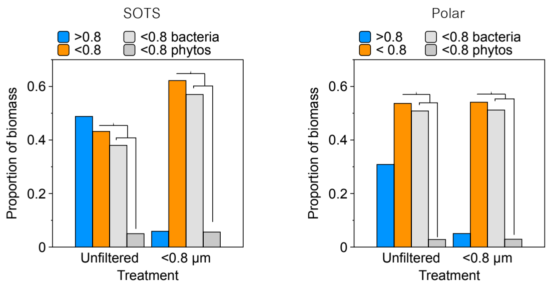


Fig. 3. Conceptual illustration of the experimental design. Treatments (size-fractions, light, dark) are in black; measurements (C and Fe uptake) are in red; variables manipulated are in blue.

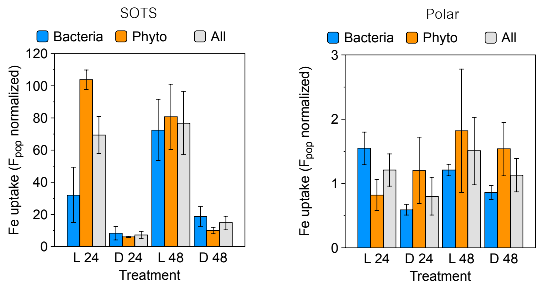
We then incubated both fractions in temperature-controlled on deck incubators under *in situ* irradiance (**L**) (12.4 % incident irradiance (Io) = 18.8 m at SOTS; 1.1 %Io = 83.2 m at the polar site) and in the dark (**D**) to examine the dependency of Fe uptake on irradiance. We then again used size fractionation (post-incubation filtration) to separate the heterotrophic **bacteria** (0.2 – 0.8 µm) and **phytoplankton** communities (>0.8 µm). Each treatment was sampled for FRRF, Fe and C uptake, and flow cytometry after 24 and 48 h (2).

RESULTS

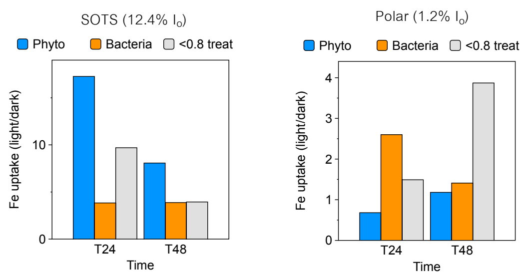
1 **A blunt tool made a sharp cut.** Whilst unsophisticated, filtering through a 0.8 µm porosity filter did an exceptionally good job of separating phytoplankton from heterotrophic bacteria.



2 **Phytoplankton hold their own.** Bacteria take up more iron than phytoplankton due to their abundance. However, when Fe uptake is normalized to biomass (F_{pop}) **the rates of phytoplankton often meet or exceed those of bacteria**, despite their larger size and disadvantageous surface area:volume ratios.



3 **Light accelerates iron uptake.** SOTS: 8- to 17-fold higher rates of Fe uptake for phytoplankton in the light vs the dark; 3.8- to 10-fold higher rates of Fe uptake for heterotrophic bacteria. This effect was greatly attenuated at the lower irradiance of the Polar site.



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References: 1. Seymour et al. (2017) DOI: 10.1038/nmicrobiol.2017.65 2. Ellwood et al. (2020) https://doi.org/10.1038/s41467-020-14464-0 3. Bach et al. (2018) https://doi.org/10.1038/s41559-018-0474-x

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