

The role of iron in the bacterial degradation of organic matter derived from *Phaeocystis antarctica*

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Abstract In high-nutrient low-chlorophyll areas, bacterial degradation of organic matter may be iron-limited. The response of heterotrophic bacteria to Fe addition may be directly controlled by Fe availability and/or indirectly controlled through the effect of enhanced phytoplankton productivity and the subsequent supply of organic matter suitable for bacteria. In the present study, the role of Fe on bacterial carbon degradation was investigated through regrowth experiments by monitoring bacterial response to organic substrates derived from *Phaeocystis antarctica* cultures set up in <1 nM Fe (LFe) and in Fe-amended (HFe) Antarctic seawater. Results showed an impact of Fe addition on the morphotype dominance (colonies vs. single cells) of *P. antarctica* and on the quality of *Phaeocystis*-derived organic matter. Fe addition led to a decrease of C/N ratio of *Phaeocystis* material. The bacterial community composition was modified as observed from denaturing gradient gel electrophoresis (DGGE) profiles in LFe as compared to HFe bioassays. The percentage of active bacteria as well as their specific metabolic activities (ecto-enzymatic hydrolysis, growth rates and bacterial growth efficiency) were enhanced in HFe bioassays. As a

consequence, the lability of *Phaeocystis*-derived organic matter was altered, i.e., after seven days more than 90% was degraded in HFe and only 9% (dissolved) and 55% (total) organic carbon were degraded in LFe bioassays. By inducing increased bacterial degradation and preventing the accumulation of dissolved organic carbon, the positive effect of Fe supply on the carbon biological pump may partly be counteracted.

Keywords Bacterioplankton · Iron · Organic matter · *Phaeocystis antarctica* · Remineralisation

Introduction

Phaeocystis antarctica recurrently produces large blooms in the Southern Ocean such as in Prydz Bay and the southern Ross Sea (e.g., El-Sayed et al. 1983; Davidson and Marchant 1992; Smith et al. 1996). In the Ross Sea, *P. antarctica* blooms early in the season, in waters characterized by relatively high Fe levels (Sedwick et al. 2000). Among the phytoplankton community, *P. antarctica* showed indeed the strongest response to Fe addition, increasing its relative abundance from <5 up to 20% in 2.5 nM Fe-enriched seawater (Coale et al. 2003).

The question of the fate of the carbon produced by *P. antarctica* in the Southern Ocean is still unresolved. Bacterial degradation has been proposed to be a major pathway in polar waters. However, several

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cases of dissolved organic carbon (DOC) accumulation have been observed in Prydz Bay (e.g., Bölter and Dawson 1982; Davidson and Marchant 1992). This DOC accumulation can either results from the refractory nature of the organic matter and/or from the limitation of its consumption by bacteria (Thingstad et al. 1997).

The biodegradability of organic carbon depends on the physico-chemical properties of the organic matter itself such as molecular size, chemical structure and elemental composition. In high-nutrient low-chlorophyll (HNLC) regions, Fe addition can have a positive effect on primary production and consequently increases the production of organic substrates. In addition, it can have an impact on the quality of the organic matter for example the quality of phytoplankton-derived organic matter is related to nutrient growth conditions with more proteins synthesized under nonlimiting conditions (Lancelot et al. 1986). In the case of *P. antarctica*, it can also control the dominant morphotype, colonies versus flagellated cells (Smith et al. 2003), generally characterized by contrasted elemental ratio (Schoemann et al. 2005).

Bacterial degradation of organic carbon may be limited by temperature (Pomeroy et al. 1991), predation (Thingstad et al. 1997), but also by ambient inorganic nutrients. For example, results reported for northern European *Phaeocystis* blooms suggested that the degradation of *Phaeocystis*-derived organic carbon could be nutrient-limited by phosphorus and nitrogen (Thingstad and Billen 1994). In HNLC waters, inorganic major nutrient limitation of bacterial degradation is unlikely, whereas Fe can be limiting. Dissolved Fe concentration are extremely low in January (<0.2 nM), at the senescent stage of *P. antarctica* bloom in the Ross Sea (Sedwick et al. 2000). Heterotrophic bacteria, with their high surface-to-volume ratio and ability to produce siderophores (e.g., Granger and Price 1999), are probably very efficient competitors for Fe acquisition even in environments experiencing picomolar concentrations of Fe commonly encountered in HNLC areas. However, the large Fe requirement of the respiratory system requiring 60% more Fe per mol of cytochrome-*c* than the photosynthetic respiratory system (Raven 1988), suggest that these organisms can still be Fe-limited *in situ*.

Bacterial processes such as the ectoenzymatic hydrolysis of polymeric organic matter, the uptake of monomeric substrates and respiration can be directly controlled by Fe availability and/or indirectly controlled through the effect of enhanced phytoplankton productivity and the subsequent supply of organic matter suitable for bacteria. Moreover, Fe availability can affect the bacterial community structure and also the proportion of metabolically active cells playing a role in the degradation of organic matter. During Fe enrichment bottle experiments conducted in the coastal Southern Ocean (Gerlache Strait), Pakulski et al. (1996) found that Fe induces increases of both heterotrophic bacterial abundance and cell-specific growth rates. These experiments, conducted in the dark and in the absence of phytoplankton and bacterivores, suggest a direct stimulation of heterotrophic bacterial growth by Fe enrichment. In other controlled experiments, carbon seemed to be the first growth-limiting factor of the bacteria although Fe quickly became limiting when carbon limitation was alleviated (Church et al. 2000; Kirchman et al. 2000). Fe may also produce an increase in bacterial carbon metabolism efficiency. Indeed, enhanced bacterial growth efficiency (BGE) in Fe-enriched conditions has been previously observed (Tortell et al. 1996; Kirchman et al. 2003). Although increasing Fe availability alone seems to have little effect on bacterial diversity, changes in the organic matter source derived from Fe-enhanced algal production may affect bacterial community structure in favour of species having appropriate enzymes (Hutchins et al. 2001; Arrieta et al. 2004).

In this work we conducted laboratory-controlled experiments to investigate the role of Fe in the bacterial degradation of *P. antarctica*-derived organic matter. Our specific objectives were to determine how Fe affects the production and quality of *Phaeocystis* organic matter and to assess the role of Fe in bacterial processes involved in the degradation of this organic matter. The experimental strategy was to mimic post-phytoplankton bloom events by running bacterial regrowth experiments enriched with *Phaeocystis*-derived organic matter obtained under limiting and nonlimiting Fe conditions. Finally, the effects of Fe availability on the organic matter degradability are discussed in terms of significance for the carbon biological pump.