Marine Chemistry 152 (2013) 20–31

Contents lists available at SciVerse ScienceDirect

Marine Chemistry

journal homepage: www.elsevier.com/locate/marchem

Availability of particulate Fe to phytoplankton in the Sea of Okhotsk

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ARTICLE INFO

Article history:
Received 10 April 2012
Received in revised form 28 March 2013
Accepted 29 March 2013
Available online 18 April 2013

Keywords:
Iron
Particulate iron
Bioavailability
Diatom
Sea of Okhotsk
Nepheloid layer

ABSTRACT

In a shipboard incubation study, we investigated the availability of particulate iron (Fe) to a Fe-starved phytoplankton community through the addition of suspended particulate matter (SPM; >1 μm) collected from the nepheloid layer in the coastal region of the Sea of Okhotsk. Surface seawater incubations were also conducted at three stations around the Bussol' Strait where the SPM that possibly originated from the coastal nepheloid layer could emerge to the surface mixed layer due to strong vertical mixing around the Kuril Islands. In the SPM-added experiment, the growth rate of phytoplankton was significantly enhanced by the addition of SPM compared to the unamended control. This result clearly indicates that Fe in the SPM collected from the nepheloid layer was available to marine phytoplankton. In addition, phytoplankton particularly coastal diatoms in the nepheloid layer were viable and showed healthy growth. In the surface seawater incubation experiments, phytoplankton growth and nutrient drawdown in unamended control conditions in two of the three stations may be supported by Fe from the particulate fraction (>0.22 μm), as estimated from stoichiometric calculation. We suggest that the bioavailable particulate Fe in SPM of the coastal region supports biological production and nutrient drawdown even after the depletion of dissolved Fe around the Kuril Islands, where strong vertical mixing occurs.
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1. Introduction

Iron (Fe) is the most important micronutrient for marine phytoplankton growth, because of its key role in processes such as photosynthesis and nitrate and nitrite assimilation (Raven et al., 1999). However, the thermodynamically stable oxidation state of Fe in oxic surface seawater is predominantly Fe(III), which has an extremely low solubility (Stumm and Morgan, 1996; Kuma et al., 1996). The Fe in the North Pacific Ocean is mainly derived from continental sources, such as eolian dust, riverine input, and sedimentary Fe from the continental shelf to coastal and oceanic waters (Johnson et al., 1999, 2005; Jickells et al., 2005; Lohan and Bruland, 2006; Nishioka et al., 2007). Moore and Braucher (2008) estimated the global-scale Fe cycle using the Biogeochemical Elemental Cycling ocean model and found that the sedimentary source of Fe contributes as much as 70% of dissolved Fe (D-Fe) in pools in the surface of the northwestern North Pacific. Previous studies indicated that the high Fe water mass possibly related to the sedimentary source would be transported from the western coast of the Sea of Okhotsk to the western North Pacific region via the Kurile Straits (Nishioka et al., 2007; Misumi et al., 2011).

In the Sea of Okhotsk, dense shelf water (DSW) is produced by brine rejection due to sea ice formation during winter, which originates in the region of the Siberian and Sakhalin continental shelves (Shcherbina et al., 2004; Matsuda et al., 2009). The DSW entrains continental sediments during the formation processes and is transported southward along the Sakhalin coast at an intermediate depth (~200–500-m), forming the Okhotsk Sea intermediate water (OSIW) (Fukamachi et al., 2004). Nakatsuka et al. (2004) reported that DSW has high particulate organic matter derived from coastal sediment, which should have high particulate Fe concentrations (e.g., Landing and Bruland, 1987; Elrod et al., 2008). The OSIW flows further southeastward and outflows into the western subarctic Pacific Ocean, through the Kurile Straits with strong vertical diapycnal mixing around the Kurile Islands (Nakamura and Awaji, 2004; Ito et al., 2010, 2011). The Bussol' Strait is a key channel with respect to the exchange of seawater between the Sea of Okhotsk and the Oyashio region (e.g., Yasuda et al., 2002) because the channel is deepest at the Kuril Straits. It can be assumed that the particles in the DSW advect into the surface of the Okhotsk and Oyashio waters via strong water mixing with the OSIW. Intrusion of such bio-active particles into the surface seawater would affect and play an important role in phytoplankton communities around the region. However, little attention has been paid to the importance of particulate matter on the dynamics of surface phytoplankton communities.

In general, one of the most bioavailable Fe species for photolithoautotrophic phytoplankton is dissolved inorganic Fe (Fe′)

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http://dx.doi.org/10.1016/j.marchem.2013.03.005

(Anderson and Morel, 1982; Morel et al., 2008). There are apparent exceptions to this model in that organic Fe-ligand complexes could be indirectly and/or directly utilized by the cells (Hutchins et al., 1999a; Maldonado and Price, 2001; Shaked et al., 2005; Kustka et al., 2007). In nature, almost all of the dissolved Fe(III) should be bound to organic ligands, which have high and low binding affinities for Fe (Rue and Bruland, 1995). A recent study demonstrated that saccharides are responsible for binding Fe with low affinity in the colloidal size fraction (Hassler et al., 2011). The bioavailability of Fe-saccharide complexes is higher than for Fe binding with high-affinity ligands for eukaryotic phytoplankton (Hassler and Schoemann, 2009; Hassler et al., 2011). There is increasing evidence that the bioavailability of D-Fe should be different depending on the binding affinity of the ligand or differences in the phytoplankton groups and their habitats (Hutchins et al., 1999b; Kuma et al., 2000; Hassler and Schoemann, 2009; Strzepek et al., 2011).

The bioavailability of D-Fe species including the colloidal fraction (between <200 kDa or 0.025 μm to 0.2 or 0.45 μm; e.g., Nishioka and Takeda, 2000; Nishioka et al., 2001) has been relatively well examined, although the availability of particulate Fe (P-Fe) is largely unknown. According to laboratory experiments (Kuma and Matsunaga, 1995; Yoshida et al., 2006), the surface reactivity or crystalline structure of solid inorganic Fe oxyhydroxide controls the supply of bioavailable D-Fe species for coastal diatoms. In natural conditions, Elrod et al. (2008) and Sugie et al. (2010a) reported that surface chlorophyll-*a* (Chl-*a*) concentrations have significant positive correlations with total dissolvable Fe concentrations (T-Fe), suggesting that particulate Fe supports a substantial portion of the ecosystem's Fe requirements. Using Chl-*a* and D- and P-Fe concentrations, Nakayama et al. (2010) calculated stoichiometrically that the phytoplankton biomass of intensive spring diatom blooms (>10 μg Chl-*a* L^{-1}) in the Oyashio region of the western subarctic Pacific region can be achieved by the utilization of D-Fe and also Fe from the particulate phase. Furthermore, Fitzwater et al. (2003) measured the T-Fe concentrations in the surface waters, which originated from the benthic boundary layer of the continental shelves during upwelling events that caused a substantial part of the Fe in the particulate fraction to be chemically labile (leachable by 25% acetic acid for 2 h). They also suggested that a small but substantial part of labile particulate Fe contributes to the bloom formation around the upwelling plumes (Fitzwater et al., 2003). Although those previous studies recognize the importance of particulate Fe as a source of bioavailable Fe, the availability of Fe in natural marine particles has not been examined before, except for Fe coming from aeolian dust (e.g., Paytan et al., 2009).

In this study, we conducted two types of bioassay experiments to examine the availability of P-Fe for the growth of phytoplankton. First, we examined the availability of Fe associated with marine suspended particulate matters for an Oyashio phytoplankton community through the addition of particulate matters collected in the DSW (SPM_{DSW}). Second, surface phytoplankton communities at three stations around the Bussol' Strait were incubated to investigate the importance of P-Fe for the growth of phytoplankton where SPM_{DSW} could appear in the surface mixed layer. The availability of the P-Fe in the surface waters was evaluated by stoichiometric calculations using Chl-*a* concentration increases and nutrient drawdown data with reported Fe:C and Fe:Chl-*a* values. Our results provide the first direct evidence of the availability of Fe in marine suspended particulate matters for natural phytoplankton communities.

2. Methods

2.1. SPM_{DSW} addition experiment

Phytoplankton incubations were performed aboard the R/V Professor Khromov during August to September 2007 (Kh-07 cruise). Natural phytoplankton communities used in incubation experiments for the bioavailability of Fe in the SPM_{DSW} were collected in the Oyashio region (Stn Oy: 46°00′N 152°30′E; Fig. 1) using an acid-cleaned Teflon-coated 10 L Niskin X sampling bottle (General Oceanics) attached to a CTD-carousel multi-sampling system (Nishioka et al., 2007, 2011). Hydrographic data (salinity, temperature, and depth) and transmittance were obtained using a CTD (Sea-Bird, Model 9-puls) and transmissometers (Wet Labs, C-Star). Seawater for a natural phytoplankton stock was sieved with 100 μm acid-cleaned Teflon-mesh to eliminate mesozooplankton and nutrients were added [27 μmol L^{-1} NO_3, 2 μmol L^{-1} PO_4 and 47 μmol L^{-1} $Si(OH)_4$] to induce probable Fe-starved conditions for the phytoplankton community before use. Nutrient stock solutions were passed through Chelex-100 ion-exchange resin (Bio-rad) to remove trace metals (Morel et al., 1979). The natural phytoplankton stock was incubated for 6 days in an on-deck incubator. The temperature of the incubator was maintained at near-ambient sea surface temperature (~10 °C) by a surface seawater flow-through system. The incubator was covered with a single layer of neutral density screening to achieve approximately 30% of surface irradiance.

The SPM_{DSW} was collected at 320 m depth east of Sakhalin (Stn DSW: 52°15′N, 144°35′E; Fig. 1) using an *in situ* filtration system (McLane Research Laboratories Inc.). The DSW mass was detected by the anomalous values in low temperature (<~0 °C) with low transmittance around the sigma-t = 26.8 kg m^{-3} layer as reported previously (Fukamachi et al., 2004; Shcherbina et al., 2004). Approximately 454.5 L of DSW was filtered through a 1.0 μm acid-washed polycarbonate filter (Nuclepore). The water on the filter was flushed by vacuum, and the filter was frozen at −20 °C for ~3 h. Prior to the experiment, the SPM_{DSW} on the filter was suspended in 500 mL of 0.2 μm filtered seawater (FSW) which was collected from a depth of 200 m in the Oyashio region during the HK07-1 cruise aboard the R/V Hokko-Maru (January 2007). The FSW contained 40 μmol L^{-1} $NO_3 + NO_2$, 3.0 μmol L^{-1} PO_4, 63 μmol L^{-1} $Si(OH)_4$ and 0.88 nmol L^{-1} D-Fe. Six treatments were prepared as follows (Table 1): (1) control: 270 mL of FSW plus 45 mL of Fe-starved natural phytoplankton stock culture prepared above; (2) Fe-added: added inorganic Fe to the control condition to make a final concentration of 5 nmol L^{-1}; (3) DFB (desferrioxamine B): amended with 1 μmol L^{-1} DFB (Sigma Chem. Co. Ltd.) to the control condition to prevent Fe uptake from the ambient seawater as achieved previously (Wells, 1999; Iwade et al., 2006; Sugie et al., 2010b, 2011); (4) SPM_{DSW}: 250 mL of FSW plus 45 mL of Fe-starved phytoplankton stock plus 20 mL of resuspended SPM_{DSW} solution as prepared above, i.e., SPM_{DSW} was concentrated 63.5-fold vs. *in situ* condition; (5) SPM_{DSW} − Phy: 295 mL of FSW plus 20 mL of resuspended SPM_{DSW} solution without the addition of the Fe-starved phytoplankton stock; and (6) DSW_{raw}: 315 mL of prescreened DSW using 100 μm acid-washed Teflon-mesh collected from 247 m at Stn DSW (Table 1). The SPM_{DSW} − Phy treatment was intended to examine the viability of the phytoplankton in the SPM_{DSW}, which was once frozen. The DSW_{raw} was set to elucidate the viability of phytoplankton in the DSW mass, which mimics their appearance to the sunlit surface waters by tidally induced and strong vertical mixing, such as that observed during winter (Nakamura and Awaji, 2004).

The treatments were incubated in an on-deck incubator as described above. The treatments were prepared in 9-replicate 320 mL polycarbonate bottles in addition to the DSW_{raw} treatment, which was prepared in 4-replicate. Three bottles were sacrificed and measured after 1, 3 and 5 days for analysis of macronutrients and Chl-*a* concentrations except for the samples of the DSW_{raw} treatment, which were obtained after 3 and 5 days sacrificing two bottles for each day. The concentrations of total dissolvable Fe (unfiltered; T-Fe) and background Fe in the FSW were measured at the beginning of the experiment. The samples for diatom cell densities and species compositions were collected at 0 and 5 days of incubation. Although the abundance of the small flagellates can be expected to be high in the incubation bottles, the large number of particles in the SPM_{DSW} and SPM_{DSW} − Phy treatments obscured the counts of the flagellates. Therefore, we measured only the

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