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Krill as a central node for iron cycling in the Southern Ocean

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[1] In order to establish the potential role of Antarctic krill (*Euphausia superba*) in the recycling of bioactive elements, we have quantified the release of iron, phosphate, and ammonia by these organisms along the Antarctic Peninsula sector of the Southern Ocean. The experimental results suggested that the presence of krill has a significant impact on ambient iron concentrations, as large amounts of this trace element were released by the krill (22–689 nmol Fe g Dry Weight^{-1} h^{-1}, equivalent to 0.2 to 4.3 nmol Fe L^{-1} d^{-1}). Half of this iron release occurred within the first hour of the experiment, and differences in iron and phosphate release rates (3.1 to 14.0 μmol PO_4^{3-} g DW^{-1} h^{-1}) seemed to reflect differences in food availability. These results identify krill as a major node in iron cycling in the Southern Ocean, potentially influencing iron residence time in the upper water column of this region. **Citation:** Tovar-Sanchez, A., C. M. Duarte, S. Hernández-León, and S. A. Sañudo-Wilhelmy (2007), Krill as a central node for iron cycling in the Southern Ocean, *Geophys. Res. Lett.*, *34*, L11601, doi:10.1029/2006GL029096.

1. Introduction

[2] The Southern Ocean plays an important role in regulating climate variability on time scales ranging from centuries to millennia [*Watson et al.*, 2000; *Boyd*, 2002]. This ocean is considered a "high-nutrient, low-chlorophyll" (HNLC) region, where phytoplankton stocks are unable to fully assimilate the high N and P concentrations available in surface waters [*Boyd*, 2002; *Smetacek et al.*, 2004; *Maher and Dennis*, 2001]. Several hypotheses have been proposed to explain this inefficient nutrient utilization, including low phytoplankton growth rates due to light limitation, high grazing pressure [*de Baar et al.*, 2005], and low iron availability [*Martin et al.*, 1990]. The importance of iron in controlling primary production in the Southern Ocean has been confirmed by several mesoscale enrichment experiments [*de Baar et al.*, 2005]. However, as external inputs of this bioactive trace element to HNLC regions are typically low [*de Baar et al.*, 1995; *Bowie et al.*, 2001], recycling must be an important mechanism providing bioavailable iron to phytoplankton.

[3] We hypothesize that Antarctic Krill (*Euphausia superba*) can potentially recycle considerable amounts of iron in the Southern Ocean. This hypothesis is supported by the high abundance ($\sim$170 $\times$ 10^6 tons [*Siegel*, 2005]) estimated for the Antarctic and high metal content of this organism [*Stoeppler and Brandt*, 1979]. Although it is well established that zooplankton grazing is a very important process affecting the recycling of trace metals in other marine systems [*Hutchins and Bruland*, 1994], the role of krill in the recycling of iron has not yet been addressed. Therefore, we have evaluated the release rate of this trace element (and other major nutrients) by Antarctic krill at three different stations within the Antarctic Peninsula region of the Southern Ocean. Our results strongly suggest that, in addition to the well-known function of krill in Antarctic food web dynamics and fisheries [*Atkinson et al.*, 2001], these organisms also play an important role in the biogeochemical cycling of the Southern Ocean.

2. Methods

[4] The release of iron, NH_4^+, and PO_4^{3-} by krill (*Euphausia superba*) was examined during the ICEPOS 2005 cruise on board the R/V Hespérides along the Antarctic Peninsula sector of the Southern Ocean. Krill were collected within the upper 100 m at three stations with different oceanographic characteristics [*Klinkhammer et al.*, 2001; *Sañudo-Wilhelmy et al.*, 2002]: Station I was located south of the Polar Circle in the Bellinghausen Sea (Feb-03-2005); station II in the Antarctic Sound (Feb-09-2005); and station III north of Deception Island (Feb-17-2005) (Figure 1). Krill biomass was estimated using a 1 m^2 BIONESS net [*Sameoto et al.*, 1980] equipped with 200 μm mesh size nets. Biomass estimates (0.26, 0.33 and 0.50 g dry weight m^{-3}, for stations I, II and III, respectively) were relatively low compared with previous values reported for the region (10–150 g dry weight m^{-3} [*Lascara et al.*, 1999]). Krill swarms were located using a SimradTM EK60 multifrequency echosounder, and the net was deployed and trawled in order to sample the 10–40, 40–70, 70–100, 100–200, 200–300 and 300–400 m depth layers. Krill was mostly present within the upper 100 m, with abundance typically highest at 40–70 m. Each krill sample was photographed and digitized using image analysis software (Global Lab Image). After correcting for grey-level threshold, the area obtained by the computer-generated perimeter of the organisms was recorded and stored. Biomass was estimated from the relationship between the area of the individuals and their dry weight [*Hernández-León and Montero*, 2006].

[5] Krill specimens used in the release experiments were captured using an IKMT net (1 cm mesh size), trawled for a few minutes at the depth where krill was most abundant (<40 m depth). Immediately upon retrieval, the organisms, which had their guts full as evidenced by their intense green color, were transferred to a 50-L plastic container filled with

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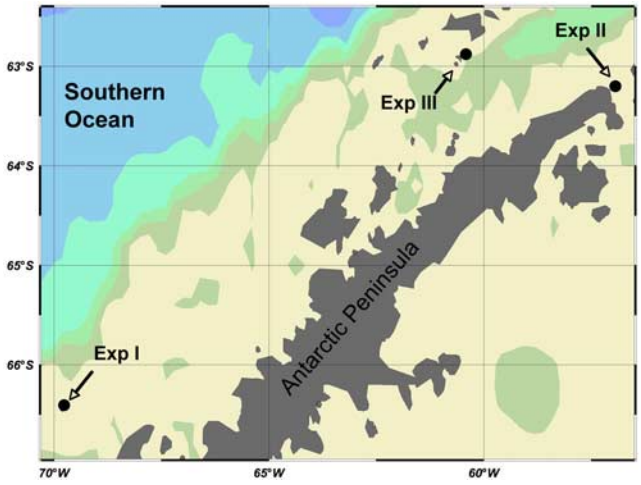

Figure 1. Location of the areas where krill iron release experiments were conducted in the Southern Ocean.

seawater, and held briefly there (<5 min) prior to experimentation.

[6] Three (from stations I and II) and four (station III) randomly selected similar-sized krill individuals (mean ± s.d.; 44.5 ± 10.1 mm, range 30.5 to 62.7 mm) were transferred, using a plastic spoon, into each of 4 to 6 cleaned (acid-washed) 2-L opaque polycarbonate bottles. A total of 12–18 animals were used per experiment, with a total of 46 animals tested altogether. At each station, surface seawater was collected from a zodiac deployed from the research vessel. Surface seawater (1 m depth) was pumped through acid-cleaned Teflon tubing coupled to C-flex tubing (for the Cole-Parmer peristaltic pump head), filtered through an acid-cleaned polypropylene cartridge filter (0.22 μm, MSI, Calyx®), and collected in 1 L LDPE bottle for iron analysis and in 2 L bottles for release experiments.

[7] Experimental bottles, including control bottles without krill, were incubated in the dark in an incubation chamber set at surface water ambient temperature ±1°C. In a class-100 HEPA hood, water samples from the experimental bottles were collected at 2 h intervals, from 1 h up to 11 h from the onset of each experiment. Samples were then analyzed for total iron, Chl *a* and nutrients (NH_4^+, PO_4^{3-}). Individual krill specimens were dried to constant weight in a drying oven set at 60°C and weighed to the nearest mg. All experiments were carried out following trace-metal clean techniques [*Sañudo-Wilhelmy et al.*, 2002].

[8] For total iron analysis, samples were acidified with sub-boiling quartz distilled HCl (Q-HCl) to pH less than 1.5 and stored for at least 1 month prior to analysis. Iron concentrations were determined by ICP-MS (ThermoFinigan, Element 2) after pre-concentration with APDC/DDDC organic extraction [*Bruland et al.*, 1985]. The accuracy of the analysis was established using Seawater Reference Material for Trace Elements (CASS3, NRC-CNRC) with recoveries ranging from 91.4 to 107.4%. Ammonium was analyzed spectrofluorimetrically within 2 h of sample collection [*Kerouel and Aminot*, 1997]. Samples for PO_4^{3-} analysis were frozen and analyzed in the lab onshore following standard procedures [*Hansen and Koroleff*, 1999]. Total chlorophyll *a* was determined at 5 to 6 depths within the mixed layer from the locations where krill samples were collected, using Niskin bottles attached to a Rosette sampler system. About 200 mls of seawater was filtered through Whatman GF/F filters to estimate Chl *a* concentrations fluorometrically (Turner Designs fluorometer) in 90% acetone extracts [*Parsons et al.*, 1984].

3. Results and Discussion

[9] Our experimental results showed that the presence of krill has a significant effect on ambient iron concentrations. The concentrations of iron in krill-free controls remained low throughout the three experiments (average ± s.d. = 0.55 ± 0.49 at station I; 0.13 ± 0.03 at station II; 0.62 at station III; all in nmol L^{-1}; see Figure S1 of the auxiliary material[1]; control 2 from station III was not used because the high iron (4.18 nmol L^{-1}) concentration suggests contamination during handling). In contrast, total iron concentrations increased rapidly in the presence of krill, with values as high as 140 nmol L^{-1} at station III and 120 nmol L^{-1} at station II (Figure S1). Although the highest concentration of iron at station I (14 nmol L^{-1}) was about an order of magnitude lower than those measured at stations II and III, it was about 25 times higher than the iron levels in the control (Figure S1). Initial (one hour) iron and phosphorous release rates from freshly-captured animals were also very high, but variable among the three locations (ranging from 22 to 689 nmol Fe gDW^{-1} h^{-1} and 3.1 to 14.0 μmol PO_4^{3-} g DW^{-1} h^{-1}, at stations I and III, respectively). Those rates declined rapidly (82% for iron and 96% for phosphorous) after the organisms were confined in the absence of a food source for seven hours (Figure 2). We observed similar initial ammonium release rates in samples from all three stations (24.1, 20.0 and 20.1 μmol $NH4^+$g DW^{-1} $h^{-1}$for I, II, and III, respectively), which also declined significantly by the end of the experiments (71% decline, Figure 2). Our results showed that half of the total release products were released by the krill within the first hour of the experiment (Figure 2). The rapid decline in release rates measured in our study is consistent with the gut clearance rate of <1 hour reported for krill [*Morris et al.*, 1983; *Clarke et al.*, 1988] and other zooplankters [*Hutchins and Bruland*, 1994].

[10] The differences in iron and phosphate release rates observed in the different experiments appear to reflect differences in food availability, as suggested by the positive relationship between iron and phosphate release rates and in situ phytoplankton biomass (reported as chlorophyll *a* concentrations, Figure 3). Our hypothesis that the different release rates observed in the different locations reflect variable food abundance seems to be supported by the similar Fe:P ratios measured in our krill experiments and those reported for plankton. For example, the slope of the linear regression between initial (one-hour) iron and phosphorous release rates in our experiments (0.014 ± 0.006; data not shown) was similar to the Fe:P composition reported for Antarctic plankton (0.007–0.012 [*Collier and Edmond*, 1984]) N:P:Fe release ratios (1.4:1:0.05 to 7.7:1:0.007) were consistent with N:P release ratios previously reported for krill [*Ikeda and Mitchell*, 1982]. In

[1]Auxiliary materials are available in the HTML. doi:10.1029/2006GL029096.

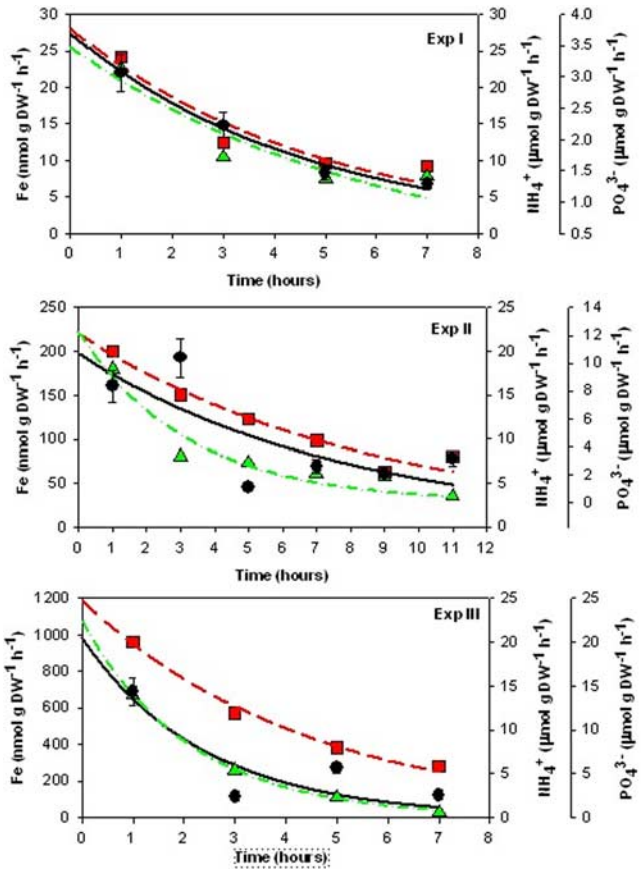

Figure 2. The relationship between incubation time and weight-specific krill total iron (circles), ammonium (squares), and phosphates (triangles) release rates at each of the experimental stations. Lines represent the fitted exponential regression equations ($R^2 = 0.99$, 0.56, and 0.74, respectively for iron; 0.89, 0.95, and 0.99, respectively for ammonium; and 0.85, 0.91, and 0.99 respectively for phosphate; $p < 0.05$ for all regressions). Error bars represent the analytical error (as s.d.).

contrast to the results obtained for iron and phosphorus experiments, we did not observe any significant differences in ammonium release rates at the three locations (Figure 2). These results suggest that iron and phosphorus release by krill follow different paths than that of N, which, is largely associated with fecal pellets [*Ikeda and Mitchell*, 1982; *Atkinson and Whitehouse*, 2000]. Further studies are required to explain the different release pathways observed for these bioactive elements.

[11] A simple calculation validates the plausibility of our release results. Using the reported Antarctic particulate iron (PFe) concentrations from the Ross Sea (0.64–3.87 nmol Fe L^{-1} in the upper 100 m of the water column [*Coale et al.*, 2005]) and the reported krill filtration rates (FR) (0.5–3.5 L $krill^{-1}$ h^{-1} [*Quetin et al.*, 1994]), the calculated (i.e., PFe × FR) krill iron ingestion rate (0.33–13.5 nmol Fe $krill^{-1}$ h^{-1}) is of the same order of magnitude as the release rates derived experimentally in this study (4.4–30.8 nmol Fe $krill^{-1}$ h^{-1}). Combining the initial weight-specific iron release rates obtained in our experiment (22–689 nmol Fe g dry $weight^{-1}$ h^{-1}) with the average krill biomass measured at each experimental location, we estimated that krill could potentially release from 0.18 to 4.30 nmol Fe L^{-1} d^{-1}. These release rates suggest that krill is a major player in iron recycling, potentially enhancing recycled production in the Southern Ocean.

[12] The iron released by krill does not represent a new input, but rather a recycled flux. However, the potential large magnitude of this flux unambiguously identifies krill as the major node in iron cycling in the Southern Ocean, thereby influencing the recycling of limiting elements. The high release rates measured in our experiments is consistent with the omnivorous feeding habits of krill, which consume micro- and mesoplankton along with sestonic detritus [*Price et al.*, 1988; *Kawaguchi and Toda*, 1997] as well as their high and continuous feeding rates [*Morris et al.*, 1983]. Iron recycling by krill may be essential for maintaining primary production and food web dynamics in the Southern Ocean, where new iron inputs are characteristically low [*de Baar et al.*, 1995; *Bowie et al.*, 2001]. We hypothesize that iron recycling by krill precludes losses that, in the absence of krill grazing, would result from the sinking flux of the large diatoms that dominate Southern Ocean phytoplankton, and thereby helps to retain iron within the upper ocean waters. The efficiency of krill grazing in preventing the sinking loss of iron depends, however, on the partitioning of the release products between a dissolved flux and a flux associated with fecal pellets, which have fast sinking rates [*Bruland and Silver*, 1981].

[13] Because a large percentage of krill feces are recycled in the upper ocean [*González*, 1992] and iron inputs stimulate primary production with a time lag of a few days [*Boyd et al.*, 2000], the iron released by krill may seed future phytoplankton blooms, potentially providing food to be subsequently harvested by krill. This mechanism may condition the environment for the population as a whole, maintaining a high biomass of krill and leading to complex food web interactions that may generate a patchy landscape dynamic in regions of high krill abundance. The high iron release rate of krill is supported by its superfluous feeding compared to other zooplankters [*Clarke et al.*, 1988], which may have unexplored ecological and evolutionary conse-

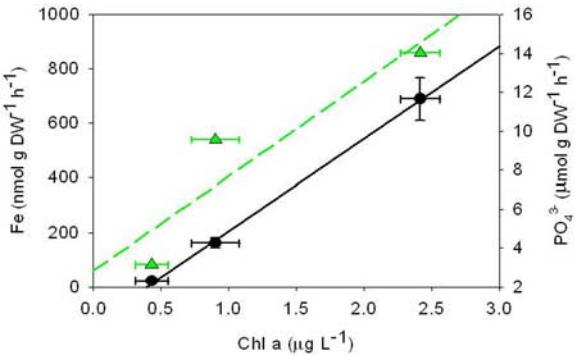

Figure 3. The relationship between the initial (1 h) release rates of iron (circles; error bars represent the analytical error, as s.d.) and phosphorous (triangles) and the average (±1 s.d.) chlorophyll *a* concentration in the upper 100 m where the specimens were collected. Solid and dashed lines represent the fitted regression equation for iron ($R^2 = 0.999$, Slope = 339.3, $p = 0.019$) and phosphorous ($R^2 = 0.85$, Slope = 4.86, $p = 0.27$), respectively.

quences. Our results strongly support the key role that krill plays in the Southern Ocean ecosystem [*Smetacek and Nicol*, 2005]. Indeed the role of krill in controlling primary production and recycling processes in the Southern Ocean has been compared to that of elephants in the African savannah [*Smetacek*, 2006].

[14] Clearly, our conclusions obtained in a small region of the Southern Ocean need to be expanded to other regions to fully understand the efficiency of krill activity as a recycling mechanism for increasing iron residence time in the upper Ocean. However, our results do suggest that the recently reported changes in krill biomass associated with reduced ice cover [*Loeb et al.*, 1997; *Atkinson et al.*, 2004] may have cascading effects on the food web, particularly affecting iron recycling and associated microbial food webs in the Southern Ocean. The impact of recycled iron by krill on the vertical flux of organic carbon needs to be further investigated because of its important implications for sequestration of atmospheric carbon dioxide to the deep ocean.

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