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A preliminary model of iron fertilisation by baleen whales and Antarctic krill in the Southern Ocean: Sensitivity of primary productivity estimates to parameter uncertainty

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ABSTRACT

Large marine animals may play a crucial role in storing and recycling bioavailable iron in surface waters by consuming iron-rich prey and subsequent defecation of iron that is excess to their requirements. This biological recycling of iron could enhance primary productivity in iron-limited waters. However, quantifying the effects of marine animals on ocean primary productivity remains challenging because of a limited understanding of the key biogeochemical processes involved. In this paper, we develop a preliminary model that explores these uncertainties and examines the potential effects of historical populations of blue, fin and humpback whales, and the biomass of Antarctic krill required to support the whale populations, on primary productivity in the Southern Ocean.

Our results suggest that, despite conservative estimates for key processes in our model, pre-exploitation populations of blue whales and, to a lesser extent fin and humpback whales, could have contributed to iron recycling, resulting in enhanced phytoplankton production in iron-limited Southern Ocean waters. Iron-rich defecation by un-exploited whale populations in the Southern Ocean, and the biomass Antarctic krill required to support them, could have resulted in a contribution to primary productivity of between 1.5×10^{-4} to $23.4\,g\,C\,m^{-2}\,yr^{-1}$ (blue whales), 1.4×10^{-4} to $13.9\,g\,C\,m^{-2}\,yr^{-1}$ (fin whales), and 2.4×10^{-5} to $1.7\,g\,C\,m^{-2}\,yr^{-1}$ (humpback whales). However, only when all parameter estimates are at their upper limits does there appear to be this significant role for whales in enhancing primary productivity, and thus we need to assess the likelihood of these values arising.

The high degree of uncertainty around the magnitude of these increases in primary productivity is mainly due to our limited quantitative understanding of key biogeochemical processes. To reduce uncertainty regarding the effect of whales on Southern Ocean primary productivity, future research will need to refine our understanding of five influential model parameters: iron content in krill; krill consumption rates by whales; persistence of whale faecal iron in the photic zone; bioavailability of this retained iron; and the carbon-to-iron ratio of phytoplankton.

1. Introduction

Large regions of the Southern Ocean are characterised by low phytoplankton biomass despite high concentrations of major nutrients (e.g. nitrate, phosphate and silicate), and have been characterised as High Nutrient Low Chlorophyll (HNLC) waters (Boyd et al., 2007; Moore and Abbott, 2000). Multiple artificial iron fertilisation experiments have demonstrated that the major factor responsible for limiting the accumulation of phytoplankton in HNLC waters is the availability of the essential trace element iron (see de Baar et al., 2005; Boyd et al., 2007 for synthesis). Natural sources of iron into the upper ocean are from atmospheric dust depositions (Boyd et al., 2004; Cassar et al., 2007), shelf sediments

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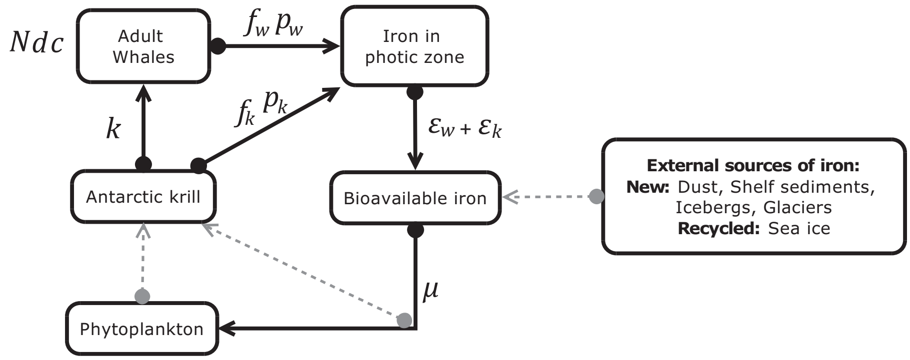

Fig. 1. Conceptual model of the biological recycling of iron in the Southern Ocean. Solid black lines represent interactions considered in this model. Dashed grey lines represent uncertain interactions not considered in this model. k is the concentration of iron in krill tissue (in mg kg^{-1}), N are the pre-exploitation population estimates for whales, c is the daily consumption rate (in kg day^{-1}), d is the feeding duration (in days), f is the proportion of iron defecated, p is the persistence of defecated iron, ε is the bioavailability of faecal iron and u is the carbon-to-iron ratio in phytoplankton (in mol mol^{-1}). w and k subscripts next to parameters f, p and ε stand for whales and krill respectively.

(Bowie et al., 2009; Sedwick et al., 2008), melting icebergs (Lin et al., 2011; Smith et al., 2007) and sea ice (Lannuzel et al., 2007; Sedwick and Di Tullio, 1997), and mediated through upwelling and vertical mixing. These external sources of iron to HNLC waters are typically very low (Bowie et al., 2001; Boyd et al., 2000; de Baar et al., 2005); consequently, biological recycling could increase the availability of iron to phytoplankton (Fig. 1).

Marine animals may play a crucial role in storing and recycling iron in surface waters through their iron-rich diet, and subsequent defecation (Lavery et al., 2010, 2014; Nicol et al., 2010; Ratnarajah et al., 2014; Roman et al., 2014; Roman and McCarthy, 2010; Smetacek, 2008; Wing et al., 2014). Increased persistence and availability of iron in surface waters could enhance overall marine primary productivity in HNLC waters. However, the contribution of Antarctic krill (*Euphausia superba*) and whales to iron recycling is difficult to study, let alone quantify, in situ. Consequently, our current understanding of iron recycling by Antarctic krill and whales is limited. Here, we have collated published information about key processes and measurements to estimate the effects of Antarctic krill and baleen whales on primary productivity in the Southern Ocean, and identify major sources of uncertainty in our understanding of iron recycling by marine animals in the Southern Ocean.

Lower trophic level crustaceans are capable of taking up iron from their diet, and from the surrounding water through their gills or other permeable cuticles (Marsden and Rainbow, 2004). The iron is then either stored in their body tissue, cuticle and ventral caeca (gut) for physiological requirements or excreted through their antennal glands, gills, guts and moulting (Marsden and Rainbow, 2004). Specifically, passive diffusion contributes to fluoride uptake in Antarctic krill (Nicol and Stolp, 1991), but there is no knowledge of similar uptake through diffusion of other elements such as iron. Moreover, there is no information on iron requirements of crustaceans. Recent studies, however, have demonstrated that Antarctic krill could play a key role in storing and recycling iron in the Southern Ocean (Nicol et al., 2010; Ratnarajah et al., 2014; Tovar-Sanchez et al., 2007).

During their feeding season in the Southern Ocean, balaenopterid whales feed on iron-rich Antarctic krill as their main dietary source (Lockyer, 1981; Nicol et al., 2010). Mammals require iron for the production of red blood cells (haemoglobin), the oxygen storage protein in muscles (myoglobin), and the iron containing centres in many enzymes (Ganz and Nemeth, 2006; Ordway and Garry, 2004). However mammals are only able to excrete assimilated iron by shedding of intestinal and skin cells, and through minor blood loss in the intestine (Ganz and Nemeth, 2006). The limited ability of mammals to excrete iron means that the iron absorbed during the growth phase of the whale is retained until adulthood and recycled for future use (e.g. the recycling of iron from senescent red blood cells for the production of new red blood cells, Ganz and Nemeth, 2006), and excess iron not used in these processes is defecated. Consequently, their buoyant, fluid-like faeces of baleen whales is iron-rich and could act a fertiliser for phytoplankton growth; with iron concentrations over 10 million times higher than Antarctic surface waters (Nicol et al., 2010; Ratnarajah et al., 2014).

Here, we develop a preliminary model for iron recycling by historical Southern Ocean population levels of blue (*Baleoptera musculus*), fin (*Baleoptera physalus*), and humpback (*Megaptera novaeangliae*) whales and the biomass of Antarctic krill required to support each whale population. In this model we only consider the component of the ecosystem that comprises historical populations of whales, the krill consumed by these whales (we do not consider the entire, unknown, historical population of krill in the Southern Ocean), and the phytoplankton biomass that might be stimulated through iron recycling of these two components. The objective of our study was to analyse the influence of parameter uncertainty on the estimated contribution of iron recycling by whales and Antarctic krill to primary productivity, and to identify the most influential and uncertain parameters that could usefully be targeted as priorities for future data collection. We use a local sensitivity analysis (*sensu* Cariboni et al., 2007) in which parameters are varied individually from their baseline (hereafter referred to as mean) values, to assess changes in estimates of primary productivity. To our knowledge, this study is the first to consider uncertain quantification of key biogeochemical processes involved in biological recycling of iron.

2. Methods

2.1. Model description

We modelled iron recycling in the Southern Ocean, which we defined as the area south of 60° S latitude that encompasses 2×10^7 km^2 around Antarctica. We used published estimates of historical blue, fin and humpback whale populations (N) in the Southern Ocean, feeding duration in polar waters (d, in days per year), species-specific daily consumption rates (c, in kg day^{-1}), and a conversion factor from wet weight to dry weight (α), to determine the biomass of Antarctic krill (B, in kg dry weight yr^{-1}) required to support pre-exploitation levels of whales (Eq. (1)).

$$B = Nd(\alpha c) \quad (1)$$