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Iron defecation by sperm whales stimulates carbon export in the Southern Ocean

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The iron-limited Southern Ocean plays an important role in regulating atmospheric CO_2 levels. Marine mammal respiration has been proposed to decrease the efficiency of the Southern Ocean biological pump by returning photosynthetically fixed carbon to the atmosphere. Here, we show that by consuming prey at depth and defecating iron-rich liquid faeces into the photic zone, sperm whales (*Physeter macrocephalus*) instead stimulate new primary production and carbon export to the deep ocean. We estimate that Southern Ocean sperm whales defecate 50 tonnes of iron into the photic zone each year. Molar ratios of C_{export} : Fe_{added} determined during natural ocean fertilization events are used to estimate the amount of carbon exported to the deep ocean in response to the iron defecated by sperm whales. We find that Southern Ocean sperm whales stimulate the export of 4×10^5 tonnes of carbon per year to the deep ocean and respire only 2×10^5 tonnes of carbon per year. By enhancing new primary production, the populations of 12 000 sperm whales in the Southern Ocean act as a carbon sink, removing 2×10^5 tonnes more carbon from the atmosphere than they add during respiration. The ability of the Southern Ocean to act as a carbon sink may have been diminished by large-scale removal of sperm whales during industrial whaling.

Keywords: ocean fertilization; *Physeter macrocephalus*; allochthonous nutrients; carbon fixation;
carbon export; whaling

1. INTRODUCTION

The balance between photosynthesis and respiration in the photic zone determines whether the ocean acts as a sink or source of atmospheric carbon. Photosynthesis drives the 'biological pump' whereby roughly 20–40% of the carbon fixed by phytoplankton is ultimately exported to the deep ocean as sinking biogenic material (Eppley & Peterson 1979; Huntley *et al.* 1991) and lost from the atmosphere for centuries to millennia. Artificial ocean fertilization experiments have investigated the potential to use the biological pump to mitigate rising atmospheric CO_2 levels by fertilizing phytoplankton and subsequently enhancing carbon export. A favoured site for these experiments is the Southern Ocean because it is crucial for atmospheric carbon regulation (Buesseler & Boyd 2003) and has an abundance of nitrogenous nutrients, but a low phytoplankton biomass as a result of iron limitation (Pollard *et al.* 2009). Fertilization of the Southern Ocean with iron can stimulate phytoplankton

blooms and cause measurable increases in CO_2 drawdown from the atmosphere and carbon export to the deep ocean (Blain *et al.* 2007; Pollard *et al.* 2009).

Respiration by Southern Ocean endotherms (whales, seals and seabirds) has been presented as a significant inefficiency in the biological pump (Huntley *et al.* 1991), returning an estimated 0.3–23% of photosynthetically fixed carbon to the atmosphere as CO_2 (Huntley *et al.* 1991; Van Franeker *et al.* 1997). Implicit in this hypothesis is the assumption that marine endotherms cannot stimulate phytoplankton to fix carbon. However, the introduction of limiting nutrients to the water column in the defecations of other organisms, such as zooplankton, can indeed stimulate phytoplankton growth (Lehman & Scavia 1982). Marine mammals also defecate nutrient-rich waste, which may promote primary productivity in oligotrophic waters (Kanwisher & Ridgway 1983; Smetacek 2008; Nicol *et al.* 2010). However, unlike zooplankton, which defecate some portion of their waste at depth, all nutrients defecated by marine mammals are released into the photic zone (Kooyman *et al.* 1981). Whales defecate near the surface because they shut down non-crucial biological functions when diving (Kooyman *et al.* 1981). While a significant

proportion of zooplankton and fish defecations is in the form of faecal pellets, which sink below the thermocline where they are rendered unavailable to phytoplankton (Le Fevre *et al.* 1998), a substantial proportion of whale defecations is in a liquid form, which disperses and persists in the photic zone (G. Johnson 2000–2005 & P. Gill 1999–2009, unpublished data).

The role of whales as nutrient recyclers was initially discounted because the concentrations of defecated nitrogen were considered too low to support significant primary production (Katona & Whitehead 1988). However, recent interest has highlighted the role of baleen whales in recycling important limiting micronutrients such as iron and increasing the spatial extent of productive areas (Smetacek 2008; Nicol *et al.* 2010). To date, the role of whale defecation in influencing carbon export has been overlooked by disregarding the important distinction between the allochthonous (originating outside the photic zone) nutrient contributions of deep diving whales (e.g. sperm whales, *Physeter macrocephalus*), which consume prey beneath the photic zone, and the autochthonous (originating within the photic zone) nutrient contribution of baleen whales that consume prey in the photic zone. While autochthonous nutrients recycled by baleen whale defecation support total primary production, only allochthonous nutrient contributions (e.g. those provided by species that consume prey at depth and defecate waste at the surface) raise the nutrient standing stock of the photic zone and stimulate new primary production. New production is the fraction of primary production that is stimulated by nutrient inputs originating from outside the photic zone (Dugdale & Goering 1967) and is quantitatively equivalent to carbon export to the deep ocean (Eppley & Peterson 1979; Ducklow *et al.* 2001).

Here, we estimate the amount of iron defecated by Southern Ocean sperm whales, the persistence of this defecated iron within the photic zone, and the resultant carbon export to the deep ocean. Carbon export is compared with the amount of carbon respired to determine, when respiration and iron defecation are combined, whether sperm whales can be considered a net sink, or source, of carbon to the atmosphere. We restrict our investigation to the population of sperm whales in the Southern Ocean because the abundance of sperm whales in this area is well characterized. While recognizing that whales defecate other nutrients that may stimulate plankton growth in other areas, we restrict our focus to iron, as iron additions are crucial in these iron-limited, macronutrient-rich waters (Blain *et al.* 2007).

2. MATERIAL AND METHODS

(a) *Sperm whale data*

The current abundance of sperm whales inhabiting the Southern Ocean (south of 60° S) has been previously determined (Whitehead 2002). Historical Southern Ocean sperm whale populations are estimated to have been reduced by 85–95% (Baker & Clapham 2002), and here we assume that current populations in the Southern Ocean have been reduced by 90 per cent. To estimate the timeline of sperm whale declines, we simplified the trajectory of worldwide sperm whale declines determined in a previous population model (Whitehead 2002). In line with those findings (Whitehead 2002), we assume that 33 per cent of the

abundance reductions occurred during 1800–1880, with a 1 per cent recovery during 1880–1940, followed by 66 per cent of the total population declines during the industrial whaling period of 1940–1970.

Sperm whale diet consists of squid and fish (Barlow *et al.* 2008), the sizes and relative proportions of each varying with geographical location; off South Georgia and South Africa, the diet consists almost entirely of squid (Kawamura 1980). We assume here that the diet of Southern Ocean sperm whales consists entirely of cephalopods. The amount of cephalopod prey consumed by sperm whales was estimated by taking the average of seven published methods (electronic supplementary material) (Tamura & Ohsumi 2000; Barlow *et al.* 2008). Mean whole-body iron concentrations of cephalopods were taken from published sources and converted from dry weight to wet weight by assuming a moisture content of 80 per cent (Miramand & Bentley 1992; Bustamante *et al.* 2000). Annual prey consumption was multiplied by average cephalopod iron concentrations to estimate the amount of iron consumed annually by Southern Ocean sperm whales.

Fully grown adult mammals expel most of the iron they consume as faeces, and the actual proportion of iron defecated may exceed 90 per cent (Candela *et al.* 1984). Here, we assume iron retention rates are 15 per cent, which is in line with an experimental study of seal nutrient (nitrogen) retention (Ronald *et al.* 1984). It is necessary to estimate the proportion of defecated iron that persists in the photic zone. Extensive observations of sperm whale defecations (by G. Johnson) reveal that squid beaks quickly sink from the surface (as documented by others, e.g. Smith 1992) while the remaining faecal material floats or slowly disperses outwards. No quantitative analysis exists regarding the retention of faecal material in the photic zone; however, it can be noted that dietary iron is largely present in the gut as ferrous salts (Naikare *et al.* 2006), and absorption of these salts is inefficient. When ferrous salts are defecated, they easily bind to ligands which will enhance their persistence in the photic zone, allowing the iron to quickly dissolve from the faeces (Hunter & Boyd 2007). We can assume then that all iron except that contained in cephalopod beaks will persist in the photic zone. We estimate here that 75 per cent of the total iron defecated by sperm whales persists in the photic zone.

(b) *Carbon export and respiration*

It is well documented that allochthonous iron inputs in the Southern Ocean stimulate large phytoplankton blooms and ultimately lead to carbon export (Blain *et al.* 2007; Pollard *et al.* 2009). Molar ratios quantifying the amount of carbon exported to the deep ocean (C_{export}) in response to iron additions (Fe_{added}) have been measured directly during natural and artificial iron fertilization events (Boyd *et al.* 2004; Buesseler *et al.* 2004; Blain *et al.* 2007; Pollard *et al.* 2009). Molar ratios determined during natural iron fertilization events are typically larger than those determined during artificial iron fertilization experiments, presumably because in natural events iron is introduced in a more bioavailable form simultaneously with other co-limiting nutrients (Pollard *et al.* 2009). As whales defecate iron in a liquid form simultaneously with co-limiting nutrients, we use molar ratios determined from natural iron fertilization events to estimate the carbon export resulting from iron inputs by whales. The mean molar ratio from two widely cited natural

fertilization events (Blain *et al.* 2007; Pollard *et al.* 2009) is $C_{export} : Fe_{added} = 5 \times 10^4$. Carbon release during respiration was calculated following the methods of Van Franeker *et al.* (1997) whereby prey was assumed to comprise 10 per cent carbon and 75 per cent of the carbon consumed is respired.

3. RESULTS

(a) *Sperm whale data*

Published estimates suggest 12 000 sperm whales currently inhabit the Southern Ocean (Whitehead 2002). By taking the mean of seven published methods for determining consumption rates of sperm whales (Tamura & Ohsumi 2000; Barlow *et al.* 2008), we estimate that each sperm whale consumes 2×10^2 tonnes of prey per year. Published concentrations of mean iron in the whole body of cephalopods ranged from 0.8×10^{-5} to 5.2×10^{-5} tonnes of iron per tonne prey wet weight (Miramand & Bentley 1992; Bustamante *et al.* 2000; Miramand *et al.* 2006) and resulted in an average of 2.6×10^{-5} tonne of iron per tonne prey wet weight. The Southern Ocean population of 12 000 sperm whales thus consumes 2×10^6 tonnes of prey per year, and this prey contains 60 tonnes of iron. Assuming a nutrient retention rate of 15 per cent (Ronald *et al.* 1984), we estimate these whales defecate 50 tonnes of iron annually. If 75 per cent of defecated iron persists in the photic zone, Southern Ocean sperm whales contribute 36 tonnes of iron to the photic zone per year.

(b) *Carbon export and respiration*

Using a molar ratio of $C_{export} : Fe_{added} = 5 \times 10^4$, we estimate that the 36 tonnes (10^6 mol) of iron that persists in the photic zone annually stimulates the export of 4×10^5 tonnes (3×10^{10} mol) of carbon to the deep ocean. Assuming that prey contain an average of 10 per cent carbon per wet weight (Van Franeker *et al.* 1997), the population of sperm whales consumes 2×10^5 tonnes of carbon per year. Approximately 75 per cent of the carbon consumed by sperm whales is respired (Huntley *et al.* 1991); thus the sperm whale populations of the Southern Oceans respire 1.6×10^5 tonnes of carbon per year.

4. DISCUSSION

Comparing carbon export (4×10^5 tonnes yr^{-1}) with carbon respired (1.6×10^5 tonnes yr^{-1}), we find Southern Ocean sperm whales act as a carbon sink, removing 2.4×10^5 tonnes more carbon from the atmosphere annually than they add via respiration. The 4×10^5 tonnes of carbon currently exported annually by the activity of Southern Ocean sperm whales is equivalent to only 0.05 per cent of the 8×10^9 tonnes of carbon added to the atmosphere in 2005 by fossil fuel burning (Marland *et al.* 2008), and represents just 0.04 per cent of the total annual carbon export south of 50° S (Schlitzer 2002). However, before industrial whaling, sperm whale populations were an order of magnitude higher (Baker & Clapham 2002) and the reduction in sperm whale numbers owing to whaling has resulted in an extra 2×10^6 tonnes of carbon remaining in the atmosphere annually (figure 1). This is a previously overlooked impact of industrial whaling.
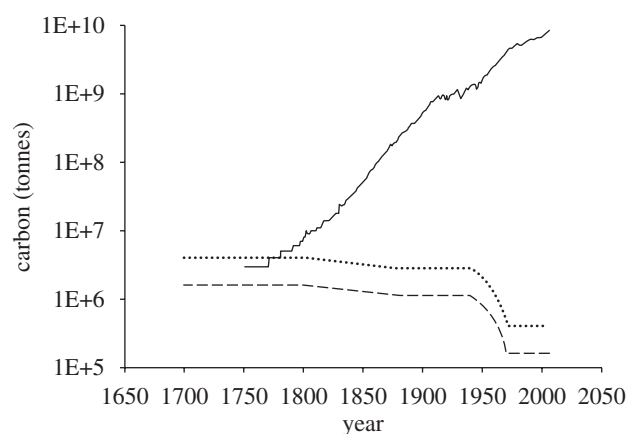
Figure 1. Carbon export from, and input to, the atmosphere from 1700 to 2005 including carbon emissions from fossil fuel burning, carbon export stimulated by iron defecated by Southern Ocean sperm whales and carbon respired by Southern Ocean sperm whales. Solid line, carbon from fossil fuels; dotted line, carbon exported; dashed line, carbon respired.

The estimates presented here highlight a previously overlooked process whereby iron defecation by sperm whales increases carbon export to the deep ocean. In line with previous findings we assume a linear relationship between iron additions and carbon export (Blain *et al.* 2007; Pollard *et al.* 2009), which necessarily overlooks the complex series of events and the food-web interactions that determine carbon export. Seasonal and spatial heterogeneity of sperm whale diet may change the nutrient composition and buoyancy of defecated waste. To investigate the influence of prey iron concentration on carbon export, we plot the amount of carbon respired against carbon exported by an individual sperm whale consuming prey with whole-body iron concentrations ranging from 0.8×10^{-5} to 5.2×10^{-5} tonnes of iron per tonne prey wet weight (the range of average concentrations reported in the literature; Miramand & Bentley 1992; Bustamante *et al.* 2000; Miramand *et al.* 2006). Sperm whales act as a net carbon sink (i.e. carbon export is greater than carbon respired) when consuming prey with iron concentrations greater than 1.2×10^{-5} tonnes of iron per tonne prey wet weight (figure 2). This is towards the lower limit of iron concentrations measured in wild cephalopods (Miramand & Bentley 1992; Bustamante *et al.* 2000; Miramand *et al.* 2006), suggesting that, even under conservative scenarios, sperm whales will act as a carbon sink.

Sperm whales are not uniformly distributed across the Southern Ocean, but rather are concentrated in areas of high productivity (Tynan 1998). Defecation in these areas may create a positive feedback loop that promotes productivity and ensures continued prey availability. The same is suggested for baleen whales and the 'krill paradox', which states that after removal of their baleen whale predators during commercial whaling, krill numbers decreased. Removal of baleen whales may have led to a deficit of bioavailable nutrients at the base of the food chain, causing krill populations to decline (Smetacek 2008; Nicol *et al.* 2010). While the overall nutrient contribution of whales may be moderate on a global scale, these nutrients are not added arbitrarily across the ocean but
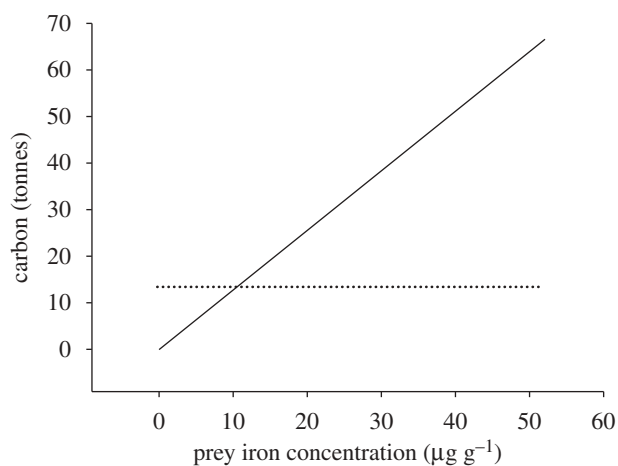
Figure 2. The amount of carbon respired annually by an individual sperm whale in the Southern Ocean, compared with the varying amounts of carbon export stimulated by sperm whale defecations after consuming prey containing differing iron concentrations. Solid line, carbon exported; dotted line, carbon respired.

rather are concentrated in the most productive areas, where high background levels of phytoplankton exist that can quickly use such nutrient pulses (Raimbault & Gentilhomme 1990).

Southern Ocean sperm whales represent just 3 per cent of the global sperm whale population (Whitehead 2002). Over 20 per cent of the world's oceans may be iron-limited (Pitchford & Brindley 1999) and sperm whales may be significantly contributing to iron fertilization and carbon drawdown in these areas. We have restricted our analysis to sperm whales; however, any organism that consumes prey outside the photic zone and defecates nutrient-rich waste that persists in the photic zone would stimulate new production and carbon export (Dugdale & Goering 1967). Pygmy and dwarf sperm whales (*Kogia* spp.) and beaked whales (Family Ziphiidae) fulfill these criteria. The proportion of time baleen whales consume prey at depth is currently unknown, but fin whales (*Balaenoptera physalus*) dive to at least 470 m while feeding (Panigada *et al*. 1999). Seals and sealions often consume prey at depth, but whether the waste is liquid (and buoyant) requires further investigation. The combined effects of the defecations of several species of marine mammals may therefore ultimately represent a significant source of nutrients that sustain phytoplankton growth. This may have important local effects on production and carbon export, particularly in the absence of other seasonal nutrient inputs.

Previous studies suggesting whales are a source of CO_2 have overlooked the important role of sperm whales in promoting nutrient cycling and carbon export (Huntley *et al*. 1991; Van Franeker *et al*. 1997). Our results strongly suggest that Southern Ocean sperm whales are not a net source of CO_2, but rather promote the removal of carbon from the atmosphere into the deep ocean. The extent of this effect may be heightened in future if higher concentrations of carbon in the atmosphere increase the flux of carbon into the ocean. Industrial harvesting of whales represents one of the most dramatic known alterations of mammalian species abundance by humans (Butman *et al*. 1995), and here we highlight an

overlooked consequence of this large-scale biomass loss. Harvesting of sperm whales in the Southern Ocean has decreased allochthonous iron inputs to the photic zone by 450 tonnes annually. This nutrient loss has undoubtedly altered the dynamics and food-web structure of these environments and this has decreased carbon export to the deep ocean.

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