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Whales sustain fisheries: Blue whales stimulate primary production in the Southern Ocean

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Abstract

It has previously been asserted that baleen whales compete with fisheries by consuming potentially harvestable marine resources. The regularly applied "surplus-yield model" suggests that whale prey becomes available to fisheries if whales are removed, and has been presented as a justification for whaling. However, recent findings indicate that whales enhance ecosystem productivity by defecating iron that stimulates primary productivity in iron-limited waters. While juvenile whales and whales that are pregnant or lactating retain iron for growth and milk production, nonbreeding adult whales defecate most of the iron they consume. Here, we modify the surplus-yield model to incorporate iron defecation. After modeling a simplistic trajectory of blue whale recovery to historical abundances, the traditional surplus-yield model predicts that 10^{11} kg of carbon yr^{-1} would become unavailable to fisheries. However, this ignores the nutrient recycling role of whales. Our model suggests the population of blue whales would defecate 3×10^{6} kg of iron yr^{-1}, which would stimulate primary production equivalent to that required to support prey consumption by the blue whale population. Thus, modifying the surplus-yield model to include iron defecation indicates that blue whales do not render marine resources unavailable to fisheries. By defecating iron-rich feces, blue whales promote Southern Ocean productivity, rather than reducing fishery yields.

Key words: ocean fertilization, blue whales, baleen whales, whaling, fisheries, iron, carbon, ecological history, marine populations, productivity, *Balaenoptera musculus*, allochthonous nutrients, autochthonous nutrients, nutrient cycling.

The idea that baleen whales compete with fisheries for marine resources has been widely debated in the scientific and political literature (*e.g.*, Komatsu *et al.* 2001; Lavigne 2003; Kaschner and Pauly 2004; Murase *et al.* 2007; Morissette *et al.* 2010). Scientific evidence of large-scale competition between baleen whales and fisheries for

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marine resources is lacking (Kaschner and Pauly 2004; Gerber *et al.* 2009; Morissette *et al.* 2010), however, policy makers have advocated commercial whaling as a method of ecosystem management to protect collapsing fish stocks from whales, in what has become known as the "whales eat fish" debate (Gerber *et al.* 2009, Morissette *et al.* 2010).

The "whales eat fish" hypothesis centers on the "surplus-yield" model which predicts that removal of a predator from an ecosystem will allow the prey that would have been consumed by that predator to become available for fisheries harvest (Yodzis 2001, Holt 2003). On the basis of this bottom-up model, the widespread removal of Southern Ocean whales during the industrial whaling era should have resulted in an increase in krill stocks proportional to the amount of krill consumed historically by the harvested whales. Studies in the 1970s predicted this "krill surplus" could be as large as 1.5×10^{11} kg krill annually (Laws 1977).

However, the predicted krill surplus never materialized; on the contrary, long term declines in Southern Ocean primary productivity (Boyce *et al.* 2010) and krill stocks (Atkinson *et al.* 2004) have been reported in the aftermath of large-scale removal of baleen whales. While previous explanations for this "krill paradox" have focused on effects of climate change (Atkinson *et al.* 2004), it has been proposed recently that whales can play an important role in recycling iron in the surface waters of the iron-limited Southern Ocean (Smetacek and Nicol 2005, Smetacek 2008, Lavery *et al.* 2010). These hypotheses are based on the premise that whales defecate high concentrations of limiting nutrients into ocean surface waters, which subsequently enhances primary production. The Southern Ocean has high concentrations of nitrogenous nutrients but a low biomass of phytoplankton due to iron limitation (Pollard *et al.* 2009). A series of large international iron fertilization experiments have demonstrated that adding iron in trace amounts into Southern Ocean surface waters stimulates production of phytoplankton (Blain *et al.* 2007, Pollard *et al.* 2009). Carbon which is removed from seawater and assimilated into phytoplankton cells during the process of photosynthesis then becomes bioavailable for incorporation into marine food webs (Blain *et al.* 2007, Pollard *et al.* 2009). Considering the potentially important, but previously overlooked, influence of iron defecation by whales on Southern Ocean primary production, we argue that the surplus-yield model must be appropriately modified to include this effect.

Recent investigations have provided data adding weight to the hypothesis that whales recycle iron, thereby underscoring the need to balance the surplus-yield model with this top-down component (Nicol *et al.* 2010). Iron is an obligate component of all life and concentrations of iron are at growth-limiting levels in the Southern Ocean. However, iron concentrations in whale feces are over seven orders of magnitude higher than background seawater concentrations (Nicol *et al.* 2010). Whale feces are defecated in a quasi-liquid state at the surface because whales slow down noncrucial biological functions (such as the glomular filtration rate and urine flow) when diving (Kooyman *et al.* 1981, Ortiz 2001). A substantial proportion of the liquid whale defecations disperses and persists in the photic zone (G. Johnson 2000–2005 and P. Gill 1999–2009, unpublished data[2]), where it is available for incorporation into marine food webs. The high nutrient cycling

[2]Personal communications from Dr. Peter Gill, Blue Whale Study Inc., % Post Office, Narrawong, Victoria 3285, Australia and Ms. Genevieve Johnson, Earth OCEAN, 95 Nelson Road, South Melbourne, Victoria 3205, Australia, March, 2010.

and uptake potential of bacteria defecated by marine mammals may further increase the residence time of defecated nutrients in surface waters, rendering the nutrients bioavailable for stimulating phytoplankton blooms (Lavery *et al.* 2012).

Phytoplankton blooms are the main source of food for krill. Ungrazed phytoplankton blooms sink from the surface taking the iron with them; however, grazing transfers the iron present in phytoplankton to zooplankton and further to krill biomass, thereby retaining iron in surface waters (Smetacek 2008). Whales feeding on krill convert much of the animal tissue into blubber (hydrocarbons) and hence recycle much of the iron they consume by defecating it into the surface layer where it can be taken up by phytoplankton again. Other nutrients (such as nitrogen and phosphate) may also be defecated simultaneously with iron (Roman and McCarthy 2010) and the cycle of whales consuming krill then defecating into surface waters may further enhance the retention of these nutrients in the Southern Ocean euphotic zone.

Recently we estimated that sperm whales that feed on deep-living prey and defecate at the surface transport new allochthonous iron into the euphotic zone and thereby raise the nutrient standing stock of surface waters (Lavery *et al.* 2010). This nutrient contribution significantly enhances new production, *i.e.*, net uptake of CO_2 from the atmosphere, and carbon export to the deep ocean (Lavery *et al.* 2010). In contrast, whales that feed in the surface euphotic zone do not contribute to new production or carbon export to depth because they do not add new iron to the euphotic zone. Whales that feed in the euphotic zone, however, do aid the retention of autochthonous (recycled) iron in surface waters and thereby promote regenerated or recycled production. Here we consider the extent to which baleen whales feeding in the euphotic zone fertilize the Southern Ocean with iron-rich defecations and provide initial estimations to predict what effect this will have on regenerated productivity of the Southern Ocean ecosystem.

We examine how iron defecation by baleen whales contributes to marine productivity and thus may modify the estimates of the surplus-yield model. Using the limited data available, we aim to provide an initial theoretical estimation that may indicate whether more costly and logistically challenging field work in this area is warranted. While the model presented here is relevant for all whales that consume prey in surface (euphotic zone) waters, we present estimations only for blue whales in the Southern Ocean because a crucial parameter of our model (measurements of iron in whale feces) has been measured adequately only in Southern Ocean blue whales (Nicol *et al.* 2010).

Blue whales amass to feed on patchy aggregations of euphausiids in upwelling and frontal regions worldwide (*e.g.*, Fiedler *et al.* 1998, Croll *et al.* 2005). While not currently a major whaling target due to their low population densities, Southern Ocean blue whale populations were dramatically targeted during the industrial whaling era and were estimated to be at 2% of their historical abundances in 2004 (Branch *et al.* 2004). Blue whales are obligate krill consumers in the Southern Ocean and some population models indicate that populations are recovering rapidly (Branch *et al.* 2004) in an area that is important for Antarctic krill fisheries (Nicol and Foster 2003). The Antarctic krill fishery is the largest fishery in the Southern Ocean (Nicol and Foster 2003) and is likely to become commercially more important if fisheries continue the current trend of “fishing down” marine food webs by targeting species in lower tropic levels (Pauly *et al.* 1998). The current surface-yield model could be used to suggest that the future recovery of blue whales in this area would reduce krill fishery stocks. It is not inconceivable that, if blue whales populations continue recovering concurrently with a rise in the importance of Antarctic krill fisheries, they may become a whaling target due to their increased population density, large body size, and their perceived threat to the sustainability of the krill fishery. We model the impact of recovery of blue whales to their former abundances on Southern Ocean primary productivity by augmenting the surplus-yield model to include the stimulatory effect of iron recycling by blue whales.

Methods

To modify the surplus-yield model we first consider published estimates of Southern Ocean blue whale abundance, the modeled rate of recovery, and the population structure. The population structure is important because whales have different iron requirements at different life stages. We use the traditional surplus-yield model to estimate the primary production that is required to support krill consumption of recovering blue whale populations. We assume that all blue whale consumption occurs in the euphotic zone because blue whales predominantly feed in waters less than 200 m depth (Croll *et al.* 1998, Fiedler *et al.* 1998, Croll *et al.* 2005). To incorporate the effect of iron recycling, we estimate the amount of iron defecated by the recovered whales and use C:Fe uptake ratios in phytoplankton to estimate the amount of primary production stimulated by the defecated iron. To determine the net effect of blue whales on Southern Ocean primary productivity, we modify the surplus-yield model to include the primary production required for consumption and the primary production stimulated by iron defecation.

Blue Whale Data

The Southern Ocean (south of 60ºS) encompasses 2×10^7 km^2. Baleen whales inhabit this area during the austral summer. Surveys conducted in the Southern Ocean estimated that the populations of blue whales numbered 1,700 in 1996 and Bayesian modeling was used to estimate that the historical abundance of Southern Ocean blue whales was 239,000 individuals before industrial whaling commenced in 1905 (Branch *et al.* 2004). The modeled rate of recovery of Southern Ocean blue whales was estimated to be between 1.4% and 11.6% annually, with a mean modeled recovery rate of 7.3% annually (Branch *et al.* 2004). We model blue whale population recovery by assuming that blue whale populations continue at their current mean rate of recovery (7.3% annually) until they reach their historical abundances. This deliberately simplistic model of recovery is inadequate to convey the myriad of factors influencing the recovery of blue whale stocks. However, the goal of this paper is not to speculate on factors influencing the rate of blue whale recovery but instead to examine the balance between consumption and productivity stimulated by iron defecation by a species that is increasing in abundance.

The population structure of historical Southern Ocean blue whale populations was estimated using data collected during the Discovery cruises in the 1920s (Mackintosh and Wheeler 1929), which recorded the relative proportions of adult males, immature males, nonreproductive "resting" females, pregnant and lactating females, and immature females. The traditional surplus-yield model and the modified surplus-yield model are estimated for each subset of the blue whale populations before being summed to give an indication of the overall effect of recovering blue whale populations on primary production (carbon) availability in the Southern Ocean.

Surplus-yield Model

The surplus-yield model assumes that all marine production consumed by whales will become unavailable for fisheries and is thus equivalent to the primary production requirement of blue whales. The surplus-yield model (*S-Y*) can be calculated based on accepted methodologies (Barlow *et al.* 2008):

$$S - Y = Q \sum d_g c_g (1/T_e)^{(Lg-1)} \tag{1}$$

where d_g is the proportion of prey$_g$ in the whales' diet. As blue whales are obligate consumers of krill in the Southern Ocean $d_g = 1$ (Nicol *et al.* 2010). The proportion of carbon per kg wet weight of prey$_g$ (c_g) = 0.1 for krill (Farber-Lorda *et al.* 2009). The trophic transfer efficiency, (the efficiency of energy transfer between trophic levels) $T_e = 0.1$ (Barlow *et al.* 2008) and L_g is the trophic level of krill = 2.2 (Pauly *et al.* 1998). Q is the total annual prey consumption of Southern Ocean blue whale population subsets (kg wet weight), and can be calculated by estimating the daily ration (R in kg) of each population subset (Eq. 2) where A and B are constants ($A = 0.42$ and $B = 0.67$) derived from surveys of marine mammals and M (mass in kg) (Barlow *et al.* 2008):

$$R = (AM^B) \tag{2}$$

Mass data for blue whales are rare due to their immense size. Females are larger than males (Mackintosh and Wheeler 1929) and a common estimation of mass is 1×10^5 kg to 1.5×10^5 kg (Mizroch *et al.* 1984). Here we assume that adult females weigh 1.2×10^5 kg and males weigh 1×10^5 kg. Juvenile whales obviously vary greatly in weight depending on their age so we assume juveniles of each sex weigh on average 50% of adult weight, which is likely to be an adequate estimation over the time a juvenile whale matures. Multiplying by the days in the year and population abundance (N) gives Equation 3:

$$Q = 365RN \tag{3}$$

Carbon Fixation Stimulated by Iron Defecation

The dry weight iron concentration (Fe) of blue whale feces has been measured directly and averages 172 mg Fe kg^{-1} (Nicol *et al.* 2010). The large variation in fecal iron concentrations recorded among blue whales (range = 65 mg Fe kg^{-1} dry weight to 439 mg Fe kg^{-1} dry weight, $n = 15$) may be due to the different iron requirements of whales during different life stages. Mammals can only lose assimilated iron through blood loss and the production of milk. While ingested iron is assimilated during periods of growth (including pregnancy and lactation), the vast majority of iron ingested by nonpregnant or lactating adult whales is not assimilated and is defecated.

To estimate the amount of iron defecated by blue whales in different stages of growth we assume that the range of fecal iron concentrations measured by Nicol *et al.* (2010) is representative of the variability across the blue whale population as a whole. We average the three highest fecal iron concentrations (439 mg Fe kg^{-1}, 387 mg Fe kg^{-1}, 258 mg Fe kg^{-1} dry weight) and use this as an estimate of high iron defecation that likely results from adult blue whales that are not pregnant or lactating (362 mg Fe kg^{-1} dry weight). The mean of the lowest three fecal iron concentrations (91 mg Fe kg^{-1}, 65 mg Fe kg^{-1}, 65 mg Fe kg^{-1} dry weight) are used as an estimate of low iron defecation levels typical of immature blue whales or whales that are pregnant or lactating (74 mg Fe kg^{-1} dry weight).

The amount of iron defecated (Fe_d) by blue whales in the Southern Ocean (kg yr^{-1}) can be estimated:

$$\mathrm{Fe}_d = 0.25\mathrm{Fe}(T_Q) \tag{4}$$

where Fe is the mean dry weight concentration of Fe in the feces of blue whales (mg Fe kg^{-1}), 0.25 is a conversion factor used to convert dry weight to wet weight concentrations (Masterton and Lewis 1957) and T_Q is the total amount of feces defecated by blue whales. The amount of feces defecated (T_Q) can be estimated from food intake (Eq. 3) which consists of 20% dry matter and 80% water by weight (Ikeda and Dixon 1982, Nordoy *et al.* 1993). Marine mammals assimilate 90% of the dry matter consumed and defecate the remaining 10% dry matter and 91% of the water consumed (Ronald *et al.* 1984). Thus, 75% of the weight of prey biomass consumed is ultimately defecated:

$$TQ = 0.75Q \tag{5}$$

To estimate the effect of iron-rich defecation on phytoplankton growth in the iron-limited Southern Ocean, we consider the C:Fe uptake ratios measured in Southern Ocean phytoplankton stocks. The amount of carbon assimilated into phytoplankton cells (C_{fixed}) in response to the iron defecated by blue whales can be estimated:

$$\mathrm{C}_{\mathrm{fixed}} = (\mathrm{mol}_{\mathrm{Fe}} r)12 \times 10^3 \tag{6}$$

where $\mathrm{mol}_{\mathrm{Fe}}$ is the number of moles of Fe defecated by blue whales and r is the mol/mol C:Fe uptake ratio in phytoplankton cells. The C:Fe ratio (r) in phytoplankton cells is typically higher in iron-depleted Southern Ocean waters compared to iron replete oceans (Falkowski and Woodhead 1992, Sunda and Huntsman 1995, Sunda 1997). C:Fe uptake ratios of 2×10^5 are used here in line with the C:Fe uptake ratios and C:Fe cellular ratios of 2×10^5 measured during a natural iron fertilization even in the Southern Ocean (Blain *et al.* 2007).

Modified Surplus-yield Model

To encompass the effect of primary production stimulated by iron defecations, we modified the surplus-yield (*MS–Y*) model to incorporate terms for the primary production consumed by whales (the traditional surplus-yield model) and the primary production stimulated by iron defecation (C_{fixed}):

$$MS - Y = C_{fixed} - S - Y. \quad (7)$$

Sensitivity Analysis

A number of uncertainties may affect our estimations of the amount of carbon fixed by blue whale iron defecations (C_{fixed}). We explored the effect of these uncertainties by using plausible ranges of three areas of uncertainty; the population structure of Southern Ocean blue whales, the fecal iron concentration of different blue whale population subsets, and the C:Fe ratio of Southern Ocean phytoplankton. The population structure of Southern Ocean blue whales was estimated using data collected during the Discovery cruises of the 1920s (Mackintosh and Wheeler 1929), and thus likely represents the population structure before large scale commercial whaling. It is reasonable to suggest that whaling may have altered the population structures, however, the current population structure of Southern Ocean blue whales is not known. To examine the sensitivity of our model to changes in population structure, we explored the model findings based on the known population structure of a highly depleted baleen whale, the North Atlantic right whale (*Eubalaena glacialis*) (Hamilton *et al.* 1998). To explore uncertainty associated with the concentration of fecal iron in different population subsets we firstly exploited the full range of blue whale fecal iron concentrations measured by Nicol *et al.* (2010) by using the largest recorded fecal iron concentration (439 mg Fe kg^{-1} dry weight) to represent the higher iron defecation of mature males and nonreproductively active mature females and the lowest recorded iron concentration (65 mg Fe kg^{-1} dry weight) to describe the lower fecal iron defecation by pregnant and lactating females and juveniles of both sexes. Secondly, we used the mean fecal iron concentration (172 mg Fe kg^{-1} dry weight) measured by Nicol *et al.* (2010) to describe the fecal iron concentration of all population subsets. Our base model uses C:Fe ratios based on the mean uptake ratio of phytoplankton cells during a natural iron fertilization event in the Southern Ocean (Blain *et al.* 2007). We explored sensitivity to the C:Fe ratio by using the mean uptake ratio + 1 SD (3.2×10^5 mol/mol) as an upper limit and the mean uptake ratio – 1 SD (8.2×10^4 mol/mol) as a lower limit, as measured in the Southern Ocean natural fertilization event (Blain *et al.* 2007).

Results

Blue Whale Population Recovery

Southern Ocean blue whale population models suggest these populations are recovering towards their former abundances of 239,000 individuals at a rate of 7.3% per year (Branch *et al.* 2004). Assuming this rate of recovery continues, Southern Ocean blue whale populations would be expected to number approximately 5,000 individuals in 2012 and would reach their former abundance of 239,000 individuals in the year 2066 (Fig. 1).

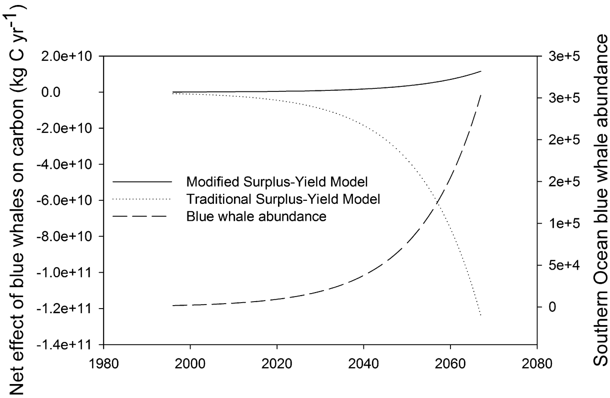

Figure 1. The influence of the projected recovery of blue whales to their historical abundances on net carbon availability in the Southern Ocean. The traditional surplus-yield model assumes that all the primary production required to support krill consumption by whales is rendered unavailable to fisheries. The modified surplus-yield model introduced here takes into account both the primary production required to support krill consumption and the primary production stimulated by iron defection into the surface waters. The deliberately simplistic modeled rate of blue whale population recovery assumes a constant recovery rate of 7.3% annually and, by ignoring the myriad of factors that influence population growth, is not intended to convey an accurate representation of blue whale recovery.

Surplus-yield Model

Current (2012) populations of blue whales in the Southern Ocean consume a total of 1.6×10^9 kg krill yr^{-1} and this consumption would increase to 7.3×10^{10} kg krill yr^{-1} if blue whales recovered to their former abundance of 239,000 individuals (Table 1). Using the surplus-yield model, the primary production required to support this krill consumption is 2.6×10^9 kg C yr^{-1} for current blue whale populations and 1.2×10^{11} kg C yr^{-1} for recovered blue whale populations. Thus the traditional surplus-yield model predicts that 1.2×10^{11} kg C yr^{-1} would be removed from supporting fishery stocks if Southern Ocean blue whales recovered to their former abundances.

Carbon Fixation Stimulated by Iron Defecation

Currently, blue whales defecate approximately 6.5×10^4 kg Fe yr^{-1} (1.2×10^6 mol Fe yr^{-1}) which likely stimulates primary production to a level of 2.8×10^9 kg C yr^{-1} (2.4×10^{11} mol C yr^{-1}) (Table 1). If blue whales were to recover to their former abundances and population structure, they would defecate approximately 2.9×10^6 kg Fe yr^{-1} (5.3×10^7 mol Fe yr^{-1}) which would stimulate primary production to a level of 1.3×10^{11} kg C yr^{-1} (1.1×10^{13} mol C yr^{-1}).

Modified Surplus-yield Model

By modifying the surplus-yield model to incorporate the effect of primary production stimulated by iron defecation, we find that each nonreproductively active, mature Southern Ocean blue whale stimulates approximately 5×10^5 kg more

Table 1. Parameters used to calculate the modified surplus-yield model. Current blue whale abundance is estimated from compounding the 1996 abundance of blue whales by 7.3% annually. The modified surplus-yield model incorporates the effect of the primary production that would be stimulated as a result of iron defecated by blue whales (C_{fixed}) and the primary production that is required to support their krill consumption (S-Y).

		Male		Female			
		Adult	Immature	Resting adult[a]	Pregnant/ lactating	Immature	Total
P_n	Proportion of population (%)	29	21	13	16	21	100
M	Mass per whale (kg)	1×10^5	5×10^4	1.2×10^5	1.2×10^5	6×10^4	
Current blue whales							
N	Whale abundance	1.5×10^3	1.1×10^3	7×10^3	8.2×10^2	1.1×10^3	5.2×10^3
Q	Prey consumption (kg krill yr^{-1})	5.2×10^8	2.4×10^8	2.7×10^8	3.2×10^8	2.7×10^8	1.6×10^9
Fe_d	Fe defecation (kg yr^{-1})	3.5×10^4	3.3×10^3	1.8×10^4	4.4×10^3	3.7×10^3	6.5×10^4
C_{fixed}	Fe stimulated production (kg C yr^{-1})	1.5×10^9	1.4×10^8	7.9×10^8	1.9×10^8	1.6×10^8	2.8×10^9
S-Y	Surplus-yield model (kg C yr^{-1})	8.3×10^8	3.8×10^8	4.3×10^8	5×10^8	4.3×10^8	2.6×10^9
MS-Y	Modified surplus-yield (kg C yr^{-1})	7×10^8	-2.4×10^8	3.6×10^8	-3.2×10^8	-2.7×10^8	2.4×10^8
Recovered blue whales							
N	Whale abundance	6.8×10^4	5×10^4	3.1×10^4	3.7×10^4	5×10^4	2.4×10^5
Q	Prey consumption (kg krill yr^{-1})	2.4×10^{10}	1.1×10^{10}	1.2×10^{10}	1.4×10^{10}	1.2×10^{10}	7.3×10^{10}
Fe_d	Fe defecation (kg yr^{-1})	1.6×10^6	1.5×10^5	8.3×10^5	2×10^5	1.7×10^5	2.9×10^6
C_{fixed}	Fe stimulated production (kg C yr^{-1})	6.8×10^{10}	6.4×10^9	3.6×10^{10}	8.5×10^9	7.2×10^9	1.3×10^{11}
S-Y	Surplus-yield model (kg C yr^{-1})	3.7×10^{10}	1.7×10^{10}	1.9×10^{10}	2.3×10^{10}	1.9×10^{10}	1.2×10^{11}
MS-Y	Modified surplus-yield (kg C yr^{-1})	3.1×10^{10}	-1.1×10^{10}	1.6×10^{10}	-1.4×10^{10}	-1.2×10^{10}	1.1×10^{10}
ms-y	Modified surplus-yield per whale (kg C yr^{-1})	4.6×10^5	-2.1×10^5	5.2×10^5	-3.8×10^5	-2.4×10^5	1.4×10^5

Note: All numbers were rounded to the nearest decimal place.

[a]Resting refers to adult females who are not currently pregnant or lactating

carbon per year per whale than is required to support their own consumption (Fig. 2). Pregnant or lactating females consume vast quantities of prey but retain much of the iron they consume, thus each pregnant or lactating female requires 4×10^5 kg more carbon per year than they stimulate *via* their iron defecations. Immature blue whales consume less prey and hence require only approximately 2×10^5 kg more carbon per whale per year than they stimulate *via* their iron defecations. Since mature males and females make up a large proportion of the population (42%), the overall net impact of the Southern Ocean blue whale population on carbon availability is an extra 1.4×10^5 kg carbon per whale per year.

Overall, the traditional surplus-yield model estimates that the current blue whale population renders 2.6×10^9 kg C yr^{-1} unavailable to fisheries; however, we find that whales would stimulate 2.8×10^9 kg C yr^{-1}. Thus, whales currently increase the primary production available to support fisheries by 2.4×10^8 kg C yr^{-1}. If Southern Ocean blue whales recovered to former abundances they would render 1.2×10^{11} kg C yr^{-1} unavailable to fisheries, but stimulate 1.3×10^{11} kg C yr^{-1} by defecating iron in surface waters. Incorporating these terms, our modified surplus-yield model estimates that if Southern Ocean blue whales recovered to former abundances they would increase the primary productivity of the Southern Ocean by 1.1×10^{10} kg C yr^{-1}, or 0.23% of current Southern Ocean primary production levels (Arrigo *et al.* 1998).

Sensitivity Analysis

The plausible ranges of uncertainty in model parameters (Table 2) reveal that the modified surplus-yield model is sensitive to changes in the population age structure, the fecal iron concentrations and the C:Fe ratio. Changes in population age structure in line with that experienced by depleted North Atlantic right whales (Hamilton *et al.* 1998) increase the positive impact of blue whales on Southern Ocean productivity to 3.8×10^{10} kg C yr^{-1} for recovered blue whale populations. Changes in the fecal

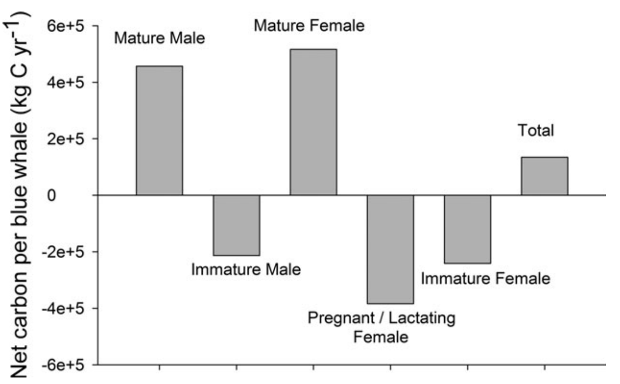

Figure 2. The modified surplus-yield model showing the net effect of blue whale population subsets on carbon availability in the Southern Ocean. Different life stages have different iron requirements so adult males and nonreproductively active adult females defecate more iron (and therefore stimulate fixation of more carbon) than immature individuals and reproductively active females. Averaged over all population subsets, the net effect is moderately positive, indicating that blue whales populations in the Southern Ocean stimulate more primary production than is required to support their own krill consumption.

iron concentration influence the modified surplus-yield model, resulting in changes from -1.4×10^{10} kg C yr^{-1} to 3×10^{10} kg C yr^{-1} for recovered blue whale populations. Changes in the C:Fe ratio in line with the mean $\pm$ 1 SD uptake ratio measured by Blain *et al*. (2007) result in changes in the modified surplus-yield, ranging from -6.4×10^{10} kg C yr^{-1} to 8.6×10^{10} kg C yr^{-1} for recovered blue whale populations.

Discussion

Baleen whales are recovering from previous exploitation at the same time that fisheries are collapsing globally (Worm *et al.* 2006). The surplus-yield model has been used to estimate the vast quantities of marine production that will be lost to fisheries if whale populations are allowed to recover (Holt 2003). However, this model ignores the important role of whales in nutrient cycling (Smetacek 2008, Lavery *et al.* 2010, Nicol *et al.* 2010), which may enhance primary production in such a way that the productivity of fisheries can be markedly enhanced. Here we present a model that investigates the consequence of modifying the traditional surplus-yield model to include an estimate of iron recycling by blue whales.

The traditional surplus-yield model estimates that if Southern Ocean blue whales recovered to historical abundances of 2.4×10^5 animals they would consume 7.3×10^{10} kg krill yr^{-1} and remove 1.2×10^{11} kg C yr^{-1} from the ecosystem. Our

Table 2. Estimates of the modified surplus–yield model based on a variety of plausible input values for population age structure, C:Fe ratio and fecal iron concentrations. The base model uses the population age structure measured by the Discovery Cruises of the 1920s (Mackintosh and Wheeler 1929), mean C:Fe ratios indicative of uptake by phytoplankton during natural iron fertilization in the Southern Ocean (Blain *et al.* 2007) and the mean values of the three highest and three lowest measured fecal iron concentrations (Nicole *et al.* 2010) to represent the fecal iron concentration of nonreproductively active adults, and juveniles, and pregnant or lactating females respectively.

Model	Fe stimulated production (C_{fixed} kg C yr^{-1})	Surplus–yield model (S-Y kg C yr^{-1})	Modified surplus–yield (MS-Y kg C yr^{-1})
Current population			
Base model	2.8×10^9	2.6×10^9	2.4×10^8
Depleted population structure	3.6×10^9	2.7×10^9	8.4×10^8
C:Fe ratio = 8.2×10^4	1.2×10^9	2.6×10^9	-1.4×10^9
C:Fe ratio = 3.2×10^5	4.5×10^9	2.6×10^9	1.9×10^9
Full range of fecal iron	3.2×10^9	2.6×10^9	6.8×10^8
Fecal iron = mean	2.3×10^9	2.6×10^9	-3.2×10^8
Recovered population			
Base model	1.3×10^{11}	1.2×10^{11}	1.1×10^{10}
Depleted population structure	1.6×10^{11}	1.2×10^{11}	3.8×10^{10}
C:Fe ratio = 8.2×10^4	5.2×10^{10}	1.2×10^{11}	-6.4×10^{10}
C:Fe ratio = 3.2×10^5	2×10^{11}	1.2×10^{11}	8.6×10^{10}
Full range of fecal iron	1.5×10^{11}	1.2×10^{11}	3×10^{10}
Fecal iron = mean	1×10^{11}	1.2×10^{11}	-1.4×10^{10}

modified surplus-yield model indicates that an equivalent amount of carbon (1.3×10^{11} kg C yr^{-1}) would be stimulated *via* the action of blue whales defecating of iron into surface waters, suggesting that the recovery of blue whale stocks would increase the marine productivity of the Southern Ocean by 10^{10} kg C yr^{-1}.The difference in values between the primary productivity required to support krill consumption by recovered blue whales (1.2×10^{11} kg C yr^{-1}) and the primary productivity stimulated by iron defecation (1.3×10^{11} kg C yr^{-1}) is negligible considering the error margins of values used to estimate these parameters. Blue whales likely have a net neutral influence on primary production available to fisheries in the Southern Ocean. Our findings do, however, highlight a significant conceptual flaw in the current surplus-yield model by indicating that the recovery of blue whale stocks is unlikely to significantly influence fishery yields in the Southern Ocean.

Nonbreeding adult whales are shown here to have a moderate net positive influence on primary production (shown in Fig. 2). The mechanism by which this occurs deserves further exploration. Whales can increase net primary production by transporting allochthonous iron into the photic zone from the deep ocean (Lavery *et al.* 2010). Baleen whales have been recorded diving to depths of 500 m in search of prey (Panigada *et al.* 1999, Baumgartner and Mate 2003, Goldbogen *et al.* 2006) and thus may defecate allochthonous nutrients originating from deep water prey into surface waters. However, blue whales feed predominantly in subsurface waters less than 200 m deep (Croll *et al.* 1998, Fiedler *et al.* 1998, Croll *et al.* 2005) and so are unlikely to be defecating the significant quantities of allochthonous nutrients required to explain the net positive rates of primary productivity calculated here.

Assuming the Southern Ocean operates as a spatial and temporal steady state, the recycled nutrient defecations of surface feeding blue whales may increase primary production *via* changes in nutrient stoichiometry (*e.g.*, the nutrient ratio) or by increasing the persistence of nutrients in surface waters (Smetacek 2008). A mechanism by which blue whales may enhance the persistence of iron in Southern Ocean surface waters has been explored by Smetacek (2008) who hypothesized that krill consumption of protistan grazers alters phytoplankton species composition by favoring flagellate blooms over small pennate diatoms which ultimately enhances the residence time of individual iron atoms in the surface layer, thereby allowing for enhanced levels of primary production. Additionally, the nutrients in marine mammal feces may be retained in the euphotic zone due to the high nutrient uptake and cycling potential of the bacteria defecated by marine mammals (Lavery *et al.* 2012). Through a process known as "uncoupled solubilization" (Azam *et al.* 1994), the uptake and metabolism of nutrients by defecated bacteria may increase the residence time of nutrients in surface waters, allowing for greater opportunities for assimilation of the nutrients into marine food webs.

The model presented here supports a growing body of evidence showing that marine mammals play a significant role in the nutrient dynamics of marine ecosystems. Nutrient transport by whales may influence the biogeochemistry (Lavery *et al.* 2010, Lavery *et al.* 2012) and productivity (Smetacek and Nicol 2005, Smetacek 2008, Nicol *et al.* 2010) of ocean ecosystems and increase regional carrying capacity for higher trophic levels (Roman and McCarthy 2010). Our findings help explain the paradox of exceptionally large animal biomass (krill and whales) concentrated in the former whaling grounds in the Southwest Atlantic Sector—the Antarctic Peninsula Plume (APP)—that today can only be classified as moderately productive based on satellite-derived data (Gregg and Conkright 2002). Yet, during the 1920s and 1930s the region was considered one of the most productive in the ocean (Hart 1934). The region receives more iron (from land runoff, contact with shelf sediments, and Patagonian dust) than other regions of the Southern Ocean, and it has been hypothesized that this iron was retained in the surface in the form of krill biomass and recycled by whales (Smetacek 2008). In this scenario, the "short food chain of the giants" was maintained by environmental conditioning by whales and then declined with decimation of the whale stocks and subsequent shrinking of the krill population: the iron reservoir "tapped" by the whales and taken up by diatoms.

If whales stimulate primary productivity with their iron-rich feces, and if no other krill predator has expanded to fill the trophic void left by depleted whale stocks, one can expect that primary production will have decreased in proportion to whale populations. Indeed, declines in satellite-measured surface chlorophyll concentrations since the 1970s indicate declining levels of marine production in the APP (Gregg and Conkright 2002) and there have been reports of an 80% decline in APP krill stocks since the Discovery surveys of the 1920s (Atkinson *et al.* 2004). The spread of salps (Salpidae spp.) into areas of the APP have been interpreted as indicating a decline in primary production because salps are characteristic of open-ocean, iron-limited waters (Pakhomov *et al.* 2002). As recently highlighted by Roman and McCarthy (2010), the decline in whale abundances and marine production is not limited to the APP. Global marine production may have decreased (Boyce *et al.* 2010, although see Mackas 2011 for discussion of the validity of Boyce's methodology) concomitant with industrial whaling and the destruction of whale stocks. Whether the decline in whale abundances has contributed to the decreased levels of primary production is unknown but it is interesting to note that the most significant declines in primary productivity have occurred in areas such as the Southern and Arctic Oceans that are also whale feeding grounds.

It is worth noting that humans tend to remove nutrients from the surface layer of the ocean through harvesting of invertebrates, fish and whales, whereas whales appear to assist in the retention of nutrients in surface ecosystems. Most of the world's large fisheries are concentrated in surface waters and blue whales enrich surface ecosystems at the cost of deep-ocean and deep-benthic ecosystems which are dominated by microbes and dispersed invertebrates of no fisheries value (FAO 2010). Maintaining or increasing whale numbers may be a significant long term strategy for restoration of surface fisheries if whales aid in the retention of surface nutrients.

Resolving Uncertainties

The modified surplus-yield model we introduce here is a hypothesis based on published data and estimates (see Table 1) that are often subject to extensive debate. Model outputs are sensitive to changes in the population age structure of blue whales. Whaling efforts typically focus on the removal of large mature adults from the population and thus bias population age structures towards greater proportions of juvenile animals (Roman and Palumbi 2003). The results presented in our base model show that mature, nonbreeding adult whales have a net positive influence on Southern Ocean primary productivity because they stimulate the production of more carbon than they require for their own consumption. In contrast, juvenile and breeding whales have proportionally higher iron requirements and consume more productivity than they stimulate and consequently have a net negative effect on Southern Ocean primary productivity. The estimations presented in the base model made use of historical population structures based on surveys from the 1920s (Mackintosh and Wheeler 1929). Using the population structure of depleted North Atlantic right whales, which contain a higher proportion of mature, nonreproductively active whales (58% compared to 42% in the base model) altered the modified surplus-yield significantly and suggested that recovered blue whale populations would increase the primary production in the Southern Ocean by 3.8×10^{10} kg C yr^{-1}. Whether the North Atlantic right whale population age structures adequately represent that of current blue whale populations is unknown and accurate information on the population age structure of current stocks of blue whales is needed to resolve this uncertainty.

Model outputs were sensitive to variations in the fecal iron concentrations of different population subsets. Using the highest and lowest measured value to represent the fecal iron concentrations of mature, nonreproductively active animals, and juveniles and pregnant or lactating females respectively (Nicol *et al.* 2010) changed the modified surplus-yield slightly and indicated that recovered blue whale populations would stimulate 3×10^{10} kg C yr^{-1}. Using the mean measured fecal iron concentration for all population subsets changed the surplus-yield significantly by indicating that recovered blue whale populations would remove 1.4×10^{10} kg C yr^{-1} from the Southern Ocean. While this figure indicates that whales exert a net negative impact on Southern Ocean productivity, it is almost an order of magnitude less than that predicted by the traditional surplus-yield model. Using the mean value for all population subsets ignores the different iron requirements in different life stages and thus may not adequately convey the expected range of fecal iron concentrations. Data regarding the fecal iron concentrations in different population subsets are needed to resolve this issue and refinement of this model based on those data is necessary.

Changes in the C:Fe ratio also exerted impacts on model outputs. Blain *et al.* (2007) measured carbon uptake ratios in phytoplankton during a natural iron fertilization event in the Southern Ocean. Our base model employs the mean uptake ratio. We also examined using the mean + 1 SD as an upper rate, which increased the modified surplus yield to 8.6×10^{10} kg C yr^{-1}. Using the input value of mean-1SD changed the modeled modified surplus yield model to -6.4×10^{10} kg C yr^{-1}, indicating that recovered blue whale populations would remove more carbon from the ecosystem that they would stimulate *via* iron fertilization. This value is significantly less than the -1.2×10^{11} kg C yr^{-1} that is predicted by the surplus yield model. The ranges in C:Fe ratio used here are clearly within the range measured during natural iron fertilization events, however, it might be considered an extreme case if all C:Fe ratios were a full SD removed from the mean value.

The figures above show the model sensitivity to input parameters. Given the uncertainty surrounding model input parameters, it is premature to make quantitative conclusions regarding the influence of blue whales on carbon fixation in the Southern Ocean. However, even the most conservative estimates employed here indicate that the current form of the surplus-yield model significantly misrepresents the impact of blue whales on krill fishery stocks. Blue whales are highly unlikely to negatively influence the sustainability of the Southern Ocean krill fisheries as can be suggested using the current surplus-yield model. For this reason, we suggest further research in this area is warranted in order to improve the accuracy of this model and provide clarity as to the impact of blue whales on Southern Ocean productivity.

Conclusion

In the face of a worldwide fisheries collapse, the argument that whale populations should be culled to protect commercial fish stocks and alleviate world hunger may gain further prominence. We have shown that this argument is based on an incomplete assessment of the role of whales in marine ecosystems. By modifying the surplus-yield model to encompass the effect of iron defecated by blue whales we find that krill consumed by whales is not equivalent to krill that is lost to the fishery. By defecating in surface waters, blue whales essentially fertilize their own feeding grounds with the nutrients needed to sustain the growth of their krill prey. The recovery of Southern Ocean blue whales to their historical abundances and population structures dominated by large adult animals is thus unlikely to reduce fishery yields and may in fact enhance ecosystem productivity in the Southern Ocean.

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